

NITROGEN IN WEST AFRICA: THE REGIONAL CYCLE¹

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Abstract. We have calculated a nitrogen cycle budget for West Africa south of the northern Sahara that quantifies biologically important pools of nitrogen in the region and major fluxes associated with these pools. Major compartments of our model include noncultivated systems broken down by vegetation zone, successional status, and plant components; annual and perennial crops each broken down by crop species and plant and harvest components; wetlands; anthropic systems; and soils and sediments. Base reference year is 1978.

Biological nitrogen fixation and precipitation fluxes dominated nitrogen inputs to West Africa in 1978. Approximately 12×10^9 kg were fixed in noncultivated systems; about half of this was fixed in early successional (0–6 yr) rain forests, and much of the rest in grazed or fallow savanna grasslands and woodlands. Less than 0.7×10^9 kg were fixed in cultivated systems; legumes accounted for $\approx 25\%$ of this. Total anthropic sources (fossil fuel combustion, fertilizer production, and agricultural commodity imports) were minor ($< 0.3 \times 10^9$ kg). Precipitation inputs to the region were $\approx 0.4 \times 10^9$ kg.

Most nitrogen leaving West Africa did so volatilized by fire ($\approx 8.3 \times 10^9$ kg), principally in non-cropped systems. Major losses also occurred via hydrologic export to the Atlantic Ocean (1.5×10^9 kg) and via denitrification (1.1×10^9 kg). Total N losses from West Africa exceeded 11.0×10^9 kg. The nitrogen immobilized in growing woody vegetation appeared to have amounted to $\approx 5.6 \times 10^9$ kg. Most was immobilized in forested regions by vegetation regrowth during the fallow phase of the bush fallow crop rotation cycle, the dominant cropping system in West Africa. A very small amount was immobilized by perennial crops such as cacao and rubber. Net immobilization in soil was not estimated; total soil N was assumed to be in steady state for the region as a whole.

Our overall budget balances within 1%, despite independent calculations of all major fluxes. The balance portrays a nitrogen cycle dominated by pools and fluxes in noncropped systems. In contrast to N balances in developed regions, direct anthropic fluxes are a minor part of the West Africa cycle. Indirect human influences, however, mainly through effects on vegetation cover, appear to be a major determinant of both the rates at which nitrogen is cycled in West Africa and the relative importance of most pools and fluxes.

Key words: global biogeochemistry; nitrogen; nitrogen models; tropical nutrient cycling; West Africa.

INTRODUCTION

Increased recognition of the importance of the major biogeochemical cycles to global climate and primary productivity has drawn attention recently to the value of large-scale element models for assessing the effects of human activity on these cycles. Global models of the carbon, nitrogen, sulfur, and phosphorus cycles (e.g., Söderlund and Svensson 1976, Bolin et al. 1979, Rosswall 1981, Bolin et al. 1983) have led to useful insights into global-level problems such as increasing concentrations of atmospheric CO₂, N₂O-mediated ozone degradation in the stratosphere, and acid precipitation.

Most research on complete biogeochemical cycles has thus far focused on particular sites in specific biome

types (e.g., Likens et al. 1977, Rosswall and Granhall 1980, Sollins et al. 1980, Batey 1982), and data from these studies form the basis for extrapolations to global levels. The conceptual jump between individual watershed studies and global syntheses is a large one, however, and the development of budgets at intermediate, regional levels could improve substantially the resolution of future global models (NAS 1978). Regional level cycles also are valuable for assessing what is known about element cycle processes in particular ecosystems of a region (Robertson 1982), and for addressing region-specific environmental policy questions (NAS 1978, Keeney 1979, Hauck and Tanji 1982).

Regional budgets for nitrogen have been compiled for parts of the United States (Lipman and Corybear 1936, Ayers and Branson 1973, Miller and Smith 1976, NAS 1978, Keeney 1979, Messer and Brezonik 1983), for the undisturbed forests of Amazonia (Salati et al. 1982), and for the open ocean (Fogg 1982) and Baltic Sea (Rönner 1985), but at present there are no such syntheses for developing regions of the tropics or subtropics. We believe that this lack is unfortunate because these regions constitute an important part of the terrestrial biosphere and should not be underrepresented

¹ Manuscript received 15 August 1983; revised 25 January 1985; accepted 16 April 1985.

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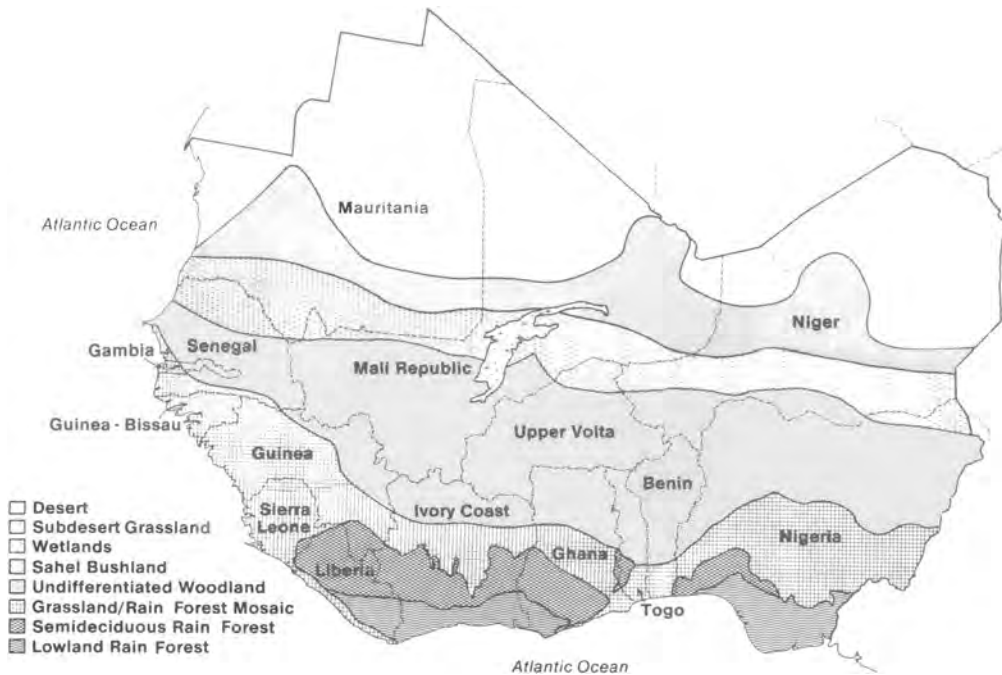


FIG. 1. Geographic boundaries and major vegetation zones in West Africa (from White 1983). Precipitation isohets follow roughly the vegetation zones.

in future global syntheses. Moreover, well-managed nitrogen resources are central to stemming the trend of stagnating per capita agricultural productivity present in many developing regions of the tropics (CEQ 1980, Greenwood 1982). Since nitrogen fertilizers are not generally available in these areas, conserving existing nitrogen resources and enhancing natural sources of nitrogen are closely related to improving crop and livestock production. Rapidly changing patterns of land use in these regions also dictate an urgent need for tropical budgets: land-use transformations imply concomitant changes in nitrogen and other nutrient fluxes, and some of these changes may have global consequences through effects on climate and atmospheric chemistry.

In this paper we present a detailed model of the nitrogen cycle for West Africa south of the northern Sahara (Fig. 1). For a number of reasons this region is a logical choice for a first tropical synthesis. First, as a region, West Africa suffers markedly from declining agricultural productivity relative to population growth (Fig. 2). The decline has been especially severe in those parts of the region affected by the 1970–1980 Sahelian drought (Franke and Chasin 1980), and recent evidence showing that Sahelian grassland productivity may be as restricted by nitrogen and phosphorus as by precipitation (Penning de Vries et al. 1980a, Breman and de Wit 1983) illustrates the importance of nitrogen resources even in arid portions of the region.

Second, West Africa is geographically discrete, with abrupt biogeochemical boundaries on all sides but the

east. To the north is the Sahara Desert and to the west and south, the Atlantic Ocean. Arbitrary political boundaries that include the eastern shore of Lake Chad and that approximate watershed boundaries define the easternmost edge of the region (Fig. 1).

Third, precipitation patterns result in a number of well-defined vegetation zones similar to regions in many other tropical areas. Vegetation types range from desert vegetation in the north to lowland rain forest in the south, and thus the larger area can be straightforwardly divided into biogeochemical subunits that may be directly compared with such zones in other regions.

Fourth and finally, there is a relatively strong research base on which to construct a regional nitrogen budget (see, for example, Rosswall 1980). That this base is actively growing suggests that a regional synthesis may be useful for summarizing existing system-level work and for focusing attention on neglected but potentially important processes.

CLIMATIC, VEGETATION, AND LAND USE PATTERNS IN WEST AFRICA

West Africa as defined in this model comprises 15 adjoining states covering 606×10^6 ha (Fig. 1). It is bounded by the Sahara Desert and by the Atlantic Ocean, and on the east by the eastern borders of Niger and Nigeria. With minor exceptions, topographic relief throughout the region is gentle or flat, ranging from sea level to 500 m elevation, with occasional highland projections to >900 m. Major watersheds include 206×10^6 ha drained by the 4200-km Niger River, and wa-

tersheds of the 1430-km Senegal River and the 1600-km Volta River in Ghana.

Jones and Wild (1975) and Okigbo (1980) provide detailed overviews of the region's geology and climate. Crystalline igneous and metamorphic rocks of the Precambrian Basement Complex underlay the southern landscape, with the northern underlain by unconsolidated or poorly consolidated sands and undifferentiated Basement Complex. Extensive sedimentary areas occur in the northwest Terminal Continental region, and scattered pockets of volcanic origin occur in the highlands and near Dakar, Senegal. Active dune fields extended as far south as the present 1000-mm isohyet at various times during the Pleistocene.

West African precipitation isopleths describe latitudinal bands increasing southward from <25 to >3000 mm/yr. Climates correspondingly range from arid in the north to perhumid and humid along the southern coast. The annual north-south migration of the Inter-tropical Zone of Convergence, in which north-flowing oceanic air meets the dry Harmattan wind from the Sahara, results in rainy seasons of <2.5 mo near the Sahara to 10–12 mo in coastal regions. Major vegetation zones correspond broadly to these precipitation patterns; White (1983) recently identified >24 major phytogeographic associations within the region, synthesized in Fig. 1.

Intense and increasing population pressures in the south and drought-exacerbated overgrazing in the north have left little of the natural vegetation undisturbed in recent years. Less than 2% of the lowland rain forest is currently estimated to be >40 yr old (Vitousek et al. 1980), and increasingly shorter fallow periods in the traditional and widespread rotational bush fallow cultivation cycle are reducing the proportion of forest in mid successional (7–40 yr) growth stages (Fig. 3). Rapid rates of mature forest disappearance (Myers 1980) show little sign of abating, so that older (mature and mid-successional) forests will likely represent far less than the present 13% of total forested area in West Africa by the end of the century.

Deforestation in the savanna and Sahel regions is also rapidly altering previous equilibria; rising population pressures brought about by increased life expectancies and mechanically dug wells have stimulated overgrazing, increased the proportion of land under cultivation, and significantly elevated the demand for firewood, the predominant cooking fuel in both rural and urban areas (Fishwick 1970). In addition, recent dry years with little herbaceous ground cover have resulted in repeated defoliation of woodland trees by pastoralists' herds for fodder. This defoliation may have permanent consequences (Wickens and White 1979).

West African cultivation systems range from traditional forms of shifting cultivation to intensive monocultures (Fig. 4), although variants of the former still predominate (Okigbo 1980). Large farms are rare; >80% of the farms in both southern and northwestern

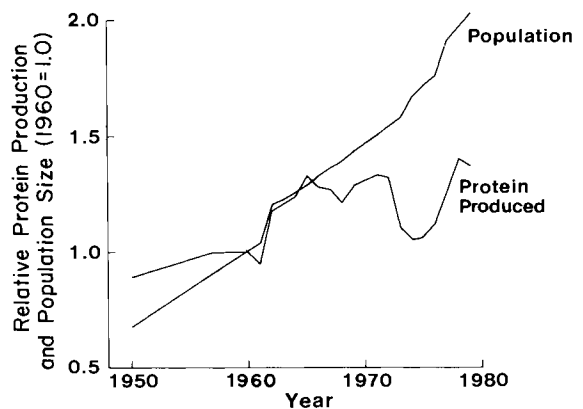


FIG. 2. Human population size and estimated crop protein production in West Africa, 1950–1979, relative to 1960 levels. Population size in 1960 was 67.2×10^6 individuals; estimated protein production was 3.53×10^9 kg, based on 1960 crop production estimates of 11.4×10^9 kg cereals (3.2% N fresh mass), 2.87×10^9 kg grain legumes (4.0% N fresh mass), and 25.0×10^9 kg roots and tubers (0.33% N fresh mass). Livestock production is not included. Annual production estimates calculated from FAO (1971, 1975, 1980a).

Nigeria, e.g., are <2 ha in area (Okigbo 1980), and cacao (*Theobroma cacao*), oil palm (*Elaeis guineensis*), and other perennial crops amenable to large plantation systems are grown principally on small holdings (Wills 1962, Hance 1975). Farm size is at least partly a function of the absence of draft animals; endemic trypanosomiasis in the south and the lack of year-round fodder in the north restrict most permanent farms to small livestock such as goats, sheep, and poultry.

In the subdesert, Sahel, and much of the savanna regions nomadic pastoralism and transhumance is common. Herds of cattle, sheep, and goats are driven south annually with the rainfall, and although the 1970–1980 drought has forced many of the pastoralists onto farms or into cities (Franke and Chasin 1980), extensive grazing remains the predominant land use for the Sahel and savanna zones of West Africa (Penning de Vries et al. 1980b).

THE WEST AFRICAN NITROGEN CYCLE

We have attempted below to compile a regional nitrogen budget for West Africa. The values reported refer to West Africa of the late 1970's, and where possible and appropriate, particularly for agricultural fluxes, to 1978. We recognize that the region is not in steady state. Land use patterns and agricultural management practices change year by year, and climatic fluctuations result in annual variations that will be reflected in biological activity and thus in nitrogen fluxes in both managed and noncropped portions of the region. Comparisons of nitrogen pools and fluxes reported here with those for other regions should therefore be made with care; our goal is to provide a context for such comparisons mainly within the region.

Central to all large-scale biogeochemical models is

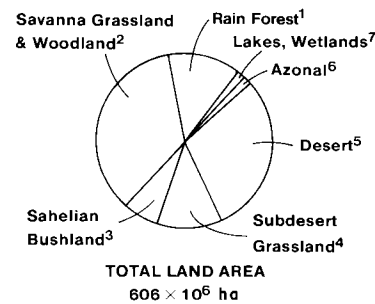
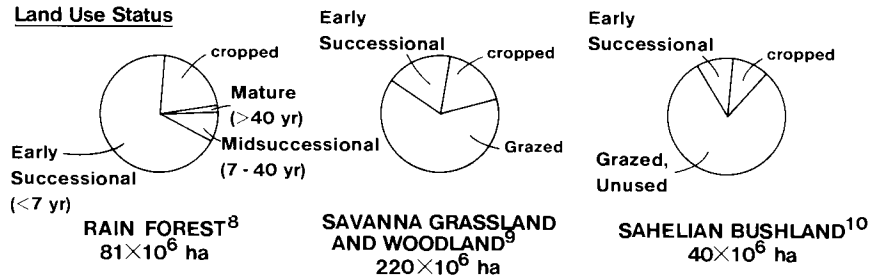
Vegetation Zones**Land Use Status**

FIG. 3. Vegetation zones and land use within zones in 1978 West Africa. Superscript numbers refer to the following notes: 1. Value includes 39.5×10^6 ha of lowland rainforest and 41.6×10^6 ha of moist semideciduous forest; lowland rainforest (LRF) includes White's (1983) wet type LRF plus 50% of his wet-dry mosaic, 25% of his LRF-successional grassland mosaic, and 17% of his LRF-*Isobertinia* woodland-successional grassland mosaic. Moist semideciduous forest (MSDF) includes White's (1983) drier type LRF and the same percentages of the LRF mosaics. 2. Value includes 36×10^6 ha of derived savanna grassland and 184×10^6 ha of Guinea savanna woodland. Derived savanna includes 50% of White's (1983) lowland rainforest (LRF)-successional grassland mosaic, 33% of the LRF-*Isobertinia* woodland-successional grassland mosaic, and all of the $<1 \times 10^6$ ha coastal mosaic. Guinea savanna includes White's (1983) Sudanian woodland with *Isobertinia* and undifferentiated, and 33% of the LRF-*Isobertinia* woodland-successional grassland mosaic. 3. 40×10^6 ha, includes White's (1983) Sahel acacia wooded grassland and deciduous bushland. 4. 72.6×10^6 ha. 5. 180×10^6 ha includes White's (1983) absolute desert, coastal desert, desert dunes with and without perennial vegetation, and regs, hamadas, and wadis. 6. 5.5×10^6 ha, includes White's (1983) halophytic and mangrove swamp vegetation. 7. 8.2×10^6 ha; from UNESCO (1978), FAO (1980a), and White (1983). 8. 90% of the zone is assumed to be part of a cultivation cycle, with 23% in a crop phase and 77% in an early successional bush-fallow phase (Nye and Greenland 1960, Braun 1973, Greenland 1980); of the 20% in forest, 18% is assumed to be in mid successional vegetation (7-40 yr) and 2% in mature (>40 yr) forest (Vitousek et al. 1980). 9. Assumes 35% of the area is cultivated (Penning de Vries et al. 1980b, Singh and Balasubramanian 1980a) with 50% of this in an early successional fallow phase (Nye and Greenland 1960, Braun 1973, Singh and Balasubramanian 1980a). 10. Assumes 10% of the area is cultivated (Penning de Vries et al. 1980b) with 50% of this in fallow (see note 8).

an early decision regarding the scale at which to aggregate model compartments. We have chosen a level of aggregation for the present model that we believe provides insight into interactions among most major nitrogen pools and processes in the region. For many compartments this level was predetermined by the limited availability of data; further resolution will thus in many cases depend on future research.

Regional nitrogen inputs

Nitrogen enters West Africa primarily via atmospheric deposition, biological nitrogen fixation, and imported agricultural commodities. From <1 to 28 kg/ha has been estimated to enter various West African systems in bulk precipitation each year (Table 1). Rates of deposition vary monotonically with rates of annual precipitation, suggesting that most of the nitrogen arrives dissolved in rainwater rather than in dry partic-

ulate forms. No direct measures of nitrogen in dry fallout are available, although in at least one case (Jones 1972), nitrogen in sample containers open only during rainfall events did not differ much from previous open-container measurements. Although Harmattan winds that sweep south from the Sahara during the dry season transport substantial amounts of Saharan dust to sub-Saharan and coastal areas, this dust appears to contain little nitrogen. McTainsh (1980), for example, measured dust deposition rates in northern Nigeria in excess of $1700 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for 1978-1979; of this, 990 kg appeared to be from nonlocal sources. However, because aeolian Saharan soils typically contain $<0.01\%$ N and $<0.05\%$ P (FAO-UNESCO 1977), nitrogen inputs from Harmattan dust are likely to be $<0.1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.

Most nitrogen enters West Africa by way of biological nitrogen fixation in noncropped ecosystems (Table

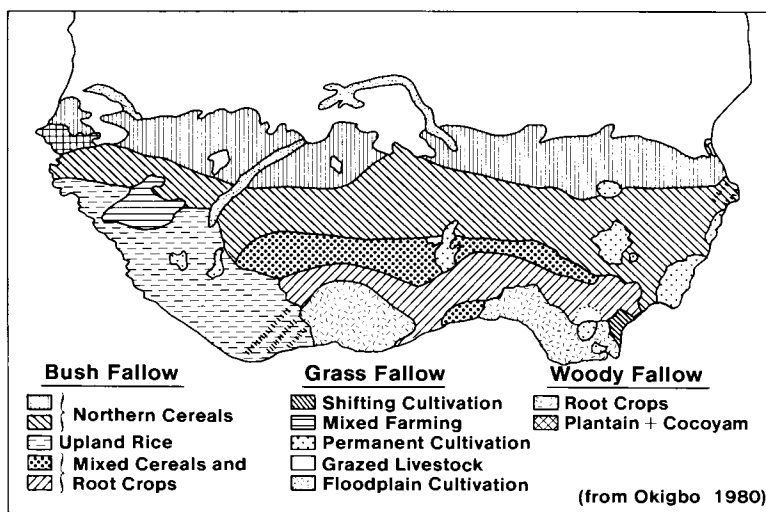


FIG. 4. Major crop zones in West Africa.

2). Fixation rates within these systems vary substantially both by vegetation zone and, within zones, by land use and the successional status of the vegetation. Nitrogen fixed in early rain forest successions amounted to $\approx 100 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Table 2), but this probably tapers to $\approx 15 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in mature rain forests. In noncultivated savannas, nitrogen fixation rates appear to be on the order of $30 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, with rates for Sahelian noncultivated areas near half of this.

The source of the nitrogen fixed in rain forests is not known with certainty, although the importance of non-symbiotic sources is implied by the relative absence of nodulated legumes in many rain forest successions (Beirnaert 1941, Keay 1953, Bonnier 1957, Nye and Greenland 1960, Norris 1969). In savanna regions, symbiotic, algal, and other nonsymbiotic sources appear to be equally responsible for the nitrogen fixed in noncultivated sites, and lower Sahelian rates appear to be largely due to the relative absence of both nodulated legumes (Bernhard-Reversat and Poupon 1980, Penning de Vries et al. 1980b) and nonsymbiotic nitrogen fixers (Penning de Vries et al. 1980b). Blue-green algal crusts appear to represent an important source of fixed nitrogen in savanna and particularly in Sahel regions; Reynaud and Roger (1981) reported nitrogen fixation rates by rain-stimulated algal mats that approached 60 kg/ha over the course of a recent rainy season in a low-lying area typical of 10% of the Senegalese Sahel.

We are not aware of estimates for nitrogen fixation in West African lakes. Horne and Viner (1971) estimated nitrogen inputs of $\approx 44 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for Lake George, Uganda, and West African rates are probably similar. Nitrogen fixation in temperate lakes ranges to $\approx 60 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Lean et al. 1978).

Approximately 17% of the total biologically fixed nitrogen in West Africa was fixed in cultivated systems. Legumes account for $\approx 30\%$ of the $788 \times 10^6 \text{ kg}$ fixed

in cultivated systems in 1978 (Table 3). In unfertilized, low-nutrient soils typical of much of West Africa, grain legumes such as cowpeas (*Vigna unguiculata*) and groundnuts (*Arachis hypogaea*) acquire most of their nitrogen from the atmosphere. Substantial rates of nitrogen fixation may also occur under sugarcane and rice crops (Table 2), although on a regional basis fixation under nonleguminous upland crops in cultivated forest and savanna systems is substantially more important.

TABLE 1. Annual deposition inputs of nitrogen (dry + wet) to West Africa. na = not available.

Annual precipitation (mm)	Deposition-N $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$		Regional total N ⁹ 10^6 kg/yr
	Mineral N	Total N	
> 1800	6 ¹	25 ²	985
1200–1800	8 ³	12 ⁴	499
800–1200	5 ⁵	7 ⁶	1540
300–800	na	3 ⁷	116
0–300	na	3 ⁸	759
Total			3899

¹ Roose (1974).² Nye and Greenland (1960): $15 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Bernhard-Reversat (1975b): 23–25; Roose (1974): 21; Roose (1978): 28.³ Meyer and Pamper (1959): $5.4 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Nye (1961): 14.⁴ Vitousek et al. (1980): $10\text{--}15 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.⁵ Jones and Bromfield (1970): $4.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Jones (1971, 1972): 4.6 for wet only.⁶ Thornton (1965): $40\text{--}42 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Penning de Vries et al. (1980b): 5; Roose (1978): 5.4.⁷ Thornton (1965): $13 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Bernhard-Reversat (1982): 0.4; Penning de Vries et al. (1980b): 3; Bernhard-Reversat and Poupon (1980): 4; Bille (1977): 2.3.⁸ P. Reynaud (personal communication).⁹ Based on areal extents in Fig. 1; >1800 mm rainfall = lowland rain forest, 1200–1800 mm = semideciduous rain forest, 800–1200 mm = savanna grassland and woodland, 300–800 mm = Sahel bushland, 0–300 mm = subdesert grassland and desert.

TABLE 2. Nitrogen fixed in West African vegetation zones, except N fixed by leguminous crops (see Table 3) and from anthropic sources (see Table 5). na = not available.

System*	Local N fixation (kg·ha ⁻¹ ·yr ⁻¹)			Total	Regional total (10 ⁶ kg/yr)
	Symbiotic	Algal	Other†		
Forests					
Cultivated	na	na	6 ²	6	102
Early successional	na	na	na	100 ³	5590
Mid-successional	na	na	na	60 ⁴	390
Mature	na	na	na	15 ⁵	24
Savanna					
Cultivated	na	1 ⁶	6 ²	7 ¹	276
Grazed, fallow	10 ⁸	10 ¹⁰	10 ⁹	30	5400
Sahel					
Cultivated	na	1 ⁶	6 ²	7 ¹	27
Grazed, fallow	2 ⁷	10 ¹¹	0 ⁷	12	415
Subdesert					
Grazed, unused	0	<1 ¹²	0	<1	36
Wetlands					
Lakes	0	44 ¹³	0	44	361
Lowland rice ²³	0	18 ¹⁴	53 ¹⁶	71 ¹⁵	56
Dryland crops					
Sugarcane ²⁴	3 ¹⁷	6 ¹⁹	40 ¹⁸	49	3
Upland rice ²³	0	5 ²²	6 ¹⁹	11	17
Coffee and cacao ²⁵	0 ²⁰	0	<1 ²¹	<1	<1
Total					12 698

* Areal extents of systems are from Fig. 3 unless noted otherwise.

† Other = nonsymbiotic, nonalgal sources included in Total.

¹ Does not include N₂ fixation by leguminous crops.

² Moore (1966) in Greenland (1977): 30 kg·ha⁻¹·yr⁻¹; Tjepkema and van Berkum (1977): 1; Singh and Balasubramanian (1980a): 10; Steyn and Delwiche (1970) in Burns and Hardy (1975): 4; Barber et al. (1976) in Knowles (1978): 0.9; Balandreau (1975) in Knowles (1978): 8; Odu and Vine (1968): 4.

³ Bartholomew et al. (1953): 114 kg·ha⁻¹·yr⁻¹; Nye and Greenland (1960): 106; Jaiyebo (1961) in Moore (1966): 181; Dommergues (1963): >100.

⁴ Bartholomew et al. (1953): 39 kg·ha⁻¹·yr⁻¹; Vitousek et al. (1980): 50–150 (lowland rain forest) and 20–80 (moist semideciduous forest).

⁵ Greenland and Nye (1959): 56–169 kg/ha over lifetime; Vitousek et al. (1980): 10–20 kg·ha⁻¹·yr⁻¹; F. Bernhard-Reversat (*personal communication*): 15 kg·ha⁻¹·yr⁻¹.

⁶ Penning de Vries et al. (1980b): 0–1 kg·ha⁻¹·yr⁻¹; P. Reynaud (*personal communication*): 1 (dry land) to 60 (irrigated) kg·ha⁻¹·yr⁻¹.

⁷ Penning de Vries et al. (1980b): 2 kg·ha⁻¹·yr⁻¹ by rhizobia, 0 by Other.

⁸ Kass and Drosdoff (1970) in Sanchez (1976): 0 kg·ha⁻¹·yr⁻¹ (tall-grass) and 0–10 (short-grass); Penning de Vries et al. (1980b): 10; Singh and Balasubramanian (1980a): 20.

⁹ Odu and Vine (1968): 40 kg·ha⁻¹·yr⁻¹; Odu (1977): 20–50; Kass and Drosdoff (1970) in Sanchez (1976): 0–23 (tall-grass) and 0–12 (short-grass); Penning de Vries et al. (1980b): 5.

¹⁰ Kass and Drosdoff (1970) in Sanchez (1976): 0–10 kg·ha⁻¹·yr⁻¹ (short-grass and tall-grass); Penning de Vries et al. (1980b): 5; Isichei (1980): 8 (3–9); Stewart et al. (1978): 30. Nonsymbiotic + algal: Balandreau and Villemain (1973): 7.5 kg·ha⁻¹·yr⁻¹; Greenland (1980): <20; Singh and Balasubramanian (1980a): <5; Singh and Balasubramanian (1980b): <15; Balandreau et al. (1974, 1976): 4–9.

¹¹ Penning de Vries et al. (1980a): 1 kg·ha⁻¹·yr⁻¹; Stewart et al. (1978): 3.0; Reynaud and Roger (1981): 57; P. Reynaud (*personal communication*): 0–60.

¹² P. Reynaud (*personal communication*): 0–1 kg·ha⁻¹·yr⁻¹.

¹³ Horne and Viner (1971): 44 kg·ha⁻¹·yr⁻¹ for Lake George, Uganda.

¹⁴ Range 3–40 kg·ha⁻¹·yr⁻¹, *n* = 12; Yoshida et al. (1973): 3 kg·ha⁻¹·yr⁻¹; Reynaud and Roger (1978): 3–8; Yoshida and Ancajas (1973): 3–14; Alimagno and Yoshida (1977) in Buresh et al. (1980): 18–33; Watanabe et al. (1978) in Buresh et al. (1980): 19; Traore et al. (1978): 25–40; Watanabe and Lee (1977): 18–33. Data for crops not fertilized as far as known. The estimate is based on 1 crop/yr and includes fixation by *Azolla*.

¹⁵ Koyama and App (1979): 35–50 and 8–38 kg·ha⁻¹·yr⁻¹; Yoshida and Ancajas (1973): 60–77; Yoshida (1971) in Balandreau et al. (1975): 80. Data for crops not fertilized as far as known. The estimate is based on 1 crop/yr.

¹⁶ Balandreau et al. (1974) in Balandreau et al. (1976): 36 kg·ha⁻¹·yr⁻¹; Balandreau et al. (1974, 1975): 45; Rinaudo et al. (1971) and Rinaudo and Dommergues (1971): 60–80.

¹⁷ 2–6 kg·ha⁻¹·yr⁻¹, *n* = 3; Döbereiner et al. (1972): 2; Ruschel et al. (1978b) in Ruschel and Vose (1982): 2–6. Data for fixation within plant.

¹⁸ Döbereiner et al. (1972): 67 kg·ha⁻¹·yr⁻¹; Ruschel et al. (1978b) in Ruschel and Vose (1982): 50; also Döbereiner et al. (1973) estimates total (including symbiotic) = 50 kg·ha⁻¹·yr⁻¹.

¹⁹ 5–7 kg·ha⁻¹·yr⁻¹, *n* = 2; Yoshida and Ancajas (1973).

²⁰ Leguminous shade trees not present.

²¹ 0.4–0.6 kg·ha⁻¹·yr⁻¹, *n* = 2; Roskoski (1982).

TABLE 3. Nitrogen fixed by leguminous crops. N uptake values are from Table 7.

Crop	Total N uptake (10 ⁶ kg/yr)	Percent N fixed symbiotically	Total N fixed (10 ⁶ kg/yr)
Soybeans	7.6	90*	6.8
Cowpeas	85.5	89†	76.1
Groundnuts	80.8	85	68.7
Others	25.9	85	22.0
Total			174

* Range 40–90%, $n = 8$; based on ¹⁵N (Ruschel et al. 1979), nodulated vs. non-nodulated isolines (Weber 1966, Lynch 1968, Hashimoto 1971, Vest 1971 in Vest et al. 1973, Pal and Saxena 1975) and solution culture (Allos and Bartholomew 1959); estimate assumes unfertilized crops grown on soils of low fertility (E. Kuinen, *personal communication*).

† Eaglesham et al. (1977).

In 1978, the nitrogen content of commercial fertilizer produced in the region was 14.3×10^6 kg (FAO 1979f), which was apparently <0.5% of the total nitrogen fixed biologically in West Africa that year. An additional 73.5×10^6 kg of fertilizer nitrogen was imported (Table 4), but fertilizers still accounted for only a small amount of the nitrogen added to systems of the region. This contrasts with recent estimates that $\approx 20\%$ of the total nitrogen fixed in terrestrial systems globally is fixed via commercial fertilizer production (Söderlund and Svensson 1976). Almost three times the amount of fertilizer nitrogen fixed in West Africa was indirectly fixed via fossil-fuel combustion in the region (Table 5). A portion of this NO_x-N may subsequently enter terrestrial and aquatic systems via precipitation, although in West Africa prevailing winds in the principal industrial zone along the coast may take much of this nitrogen out to sea. Nonetheless, elevated rates of nitrogen deposition may occur near urban areas.

Another 227×10^6 kg of nitrogen entered West Africa by way of agricultural trade in 1978 (Table 4). About 32% of this arrived as N-fertilizer, with most of the remainder arriving in marine fish, wheat, and rice.

Agricultural pools and fluxes

Major crop zones in West Africa include those for root crops, plantains (*Musa* spp.), and maize (*Zea mays*) along the eastern coast, a rice (*Oryza sativa*) zone along the western coast, and a mixed-cereal zone in the north (Harris 1976 in Okigbo 1980; Fig. 4). Cereals, in particular millet (*Pennisetum typhoideum* and *Panicum*

TABLE 4. Nitrogen inputs to West Africa in 1978 via agricultural trade (net agriculture imports). Fertilizer and crop import data are from FAO (1979f and 1979a, respectively), and crop N contents are from Table 8, except as noted. na = not available.

Commodity	Mass (10 ⁹ kg/yr)	N content (%)	N input (10 ⁶ kg/yr)
Fertilizer	na	na	73.5
Agricultural products			
Wheat and other cereals	2.2*	2.2	47.7
Rice	1.5	1.8	26.8
Maize	0.3	2.6	6.5
Fibre	<0.1	2.0	0.4
Potatoes	<0.1	0.38	0.1
Other vegetables	<0.1	0.15	0.1
Tobacco	<0.1	2.0	0.2
Fish	1.3†	3.0	69.3
Meat	<0.1‡	3.0	2.6
Total			227

* Includes 0.14×10^6 kg malt, and 0.17×10^6 kg other cereals.

† FAO (1979c, d); imports plus marine catches; all national exports (10.15×10^6 kg) are assumed to be consumed within region.

‡ Includes 81.5×10^6 kg fresh and frozen meat, 6.6×10^6 kg live ruminants.

milliaceum), sorghum (*Sorghum vulgare*), maize, and rice provide the major source (65–75%) of indigenous protein in the region (FAO 1979a). Grain legumes such as cowpeas, groundnuts (peanuts), and soybeans (*Glycine max*), and roots and tubers such as yams (*Dioscorea* spp.), cassavas (*Manihot esculenta*), and cocoyams (*Colocasia esculenta* and *Xanthosoma*

TABLE 5. Annual nitrogen oxide (mainly NO₂ and NO) emissions from the combustion of fossil fuels.

Source	(Units)	Amount consumed* (10 ⁹ units)	NO _x -N emission factor (g/unit)	N emitted (10 ⁶ kg/yr)
Natural gas	(m ³)	0.08	2.9†	0.2
Gasoline	(kg)	2.31	5.1†	12.0
Kerosene	(kg)	1.12	5.1	5.7
Fuel oil	(kg)	4.54	5.1	23
Total				41

* UN (1977) figures for 1975, increased by 15% to correct for 15% population increase between 1975 and 1978 (FAO 1980a).

† EPA (1973) in NAS (1978: 658); assumes most natural gas used for power production and a mean gasoline use efficiency of 3.8 km/L.

²² P. Reynaud (*personal communication*): 0–10.

²³ Total rice extent = 2.4×10^6 ha (FAO 1980a); estimates assume that 33% of rice area is lowland rice, 67% upland rice (NAS 1974).

²⁴ Areal extent = 0.06×10^6 ha (FAO 1980a).

²⁵ Areal extent = 3.9×10^6 ha (FAO 1980a).

TABLE 6. Annual-crop biomass in 1978. Primary (1°) harvest biomass is yield mass reported by FAO (1979a); secondary (2°) harvest is the biomass removed at the same time as at primary harvest but not included in FAO figure (e.g., shells and pods). Total crop biomass = primary harvest + secondary harvest + litter + root residue. na = not available.

Crop	1° harvest biomass ¹ (10 ⁹ kg)	Aerial residue (AR) ²			Root residue (RR) ²		
		1° harvest : AR ratio	2° harvest : AR ratio	2° harvest (10 ⁹ kg)	Litter (10 ⁹ kg)	1° harvest : RR ratio	Biomass (10 ⁹ kg)
Cereals							
Millet	6.8	0.26 ³	0.7 ⁴	18	7.8	0.73 ⁵	9.3
Sorghum	5.1	0.24 ⁶	0.7 ⁴	17 ⁷	4.5	1.0 ⁸	5.3
Maize	3.2	0.67 ⁹	0.16 ¹⁰	1.7 ¹¹	3.1	2.0 ¹²	1.6
Lowland rice	2.4 ¹³	0.85 ¹⁴	<0.1	<0.1 ¹⁵	2.8	0.33 ¹⁶	7.2
Upland rice	0.9 ¹³	1.1 ¹⁷	<0.1	<0.1 ¹⁵	0.8	0.33 ¹⁸	2.6
Others ¹⁹	0.3	1.0 ²⁰	0.7 ²¹	0.2	0.1	0.90 ²¹	0.3
Legumes							
Cowpeas	1.3 ²²	0.67 ²³	0.3 ²⁴	0.8 ²⁵	1.2	14 ²⁶	0.1
Groundnuts	0.8 ²⁷	0.34 ²⁸	0.3 ²⁹	1.1 ³⁰	1.1	1.3 ³¹	0.6
Soybeans	0.1	0.73 ³²	0.3 ³³	0.1 ³⁴	0.1	14 ³³	<0.1
Others ⁶¹	0.4	0.70 ³⁵	0.3 ³⁵	0.4 ³⁶	0.3	8.0 ³⁵	0.1
Roots and tubers							
Yams	20 ³⁷	20 ³⁸	0.1 ³⁹	0.1	0.9	60 ³⁸	0.3
Cassavas	16	0.76 ⁴⁰	<0.1 ³⁹	<0.1	21	60 ⁴¹	0.3
Cocoyams	3.4 ³⁷	6.7 ⁴²	0.1 ³⁹	0.1	0.5	60 ⁴¹	0.1
Others ⁴³	0.7	20 ⁴¹	0.1 ³⁹	<0.1	<0.1	60 ⁴¹	<0.1
Other crops							
Vegetables ⁴⁴	5.1	1.0	0.5	2.6	2.5	10	0.5
Cotton	0.5	0.34 ⁴⁵	0.8 ⁴⁶	1.1	0.3	1.3 ⁴⁷	0.4
Other fibres ⁴⁸	<0.1	0.33 ⁴⁹	0.9 ⁴⁹	<0.1	<0.1	1.0	<0.1
Sesame	0.1	0.48 ⁵⁰	0.8 ⁵¹	0.2	<0.1	3.8 ⁵²	<0.1
Tobacco	<0.1	0.76 ⁵³	<0.1	<0.1	<0.1	1.0 ⁵⁴	<0.1
Sugar cane	2.8	4.0 ⁵⁵	0.3 ⁵⁹	0.2	0.5	14.5 ⁵⁶	0.2
Bananas	4.7	3.1 ⁵⁷	<0.1	<0.1	1.5	21 ⁵⁸	0.2
Pineapples	0.4	0.7 ⁵⁹	<0.1	<0.1	0.6	na ⁶⁰	na ⁶⁰
Total	74¹			43	49		29

¹ Fresh biomass as reported by FAO (1979a). All other biomass estimates are on a dry-mass basis.

² Except as noted, total aerial residue (AR) biomass = (1° harvest biomass)/(1° harvest : AR ratio); 2° harvest biomass = (total AR biomass) × (2° harvest : AR ratio); litter biomass = (total AR biomass) - (2° harvest biomass); root residue (RR) biomass = (1° harvest biomass)/(1° harvest : RR ratio).

³ 0.13-0.33; Poulain (1980), Balasubramanian and Nnadi (1980), Blondel (1971), Kassam and Stockinger (1973), IRAT (1975).

⁴ Poulain (1980), Balasubramanian and Nnadi (1980), Ofori (1980), FAO (1979b); 80% of aerial residue removed over 88% of West Africa.

⁵ Poulain (1980).

⁶ 0.08-0.36, $n = 11$; Poulain (1980), Balasubramanian and Nnadi (1980), Blondel (1971), Kassam and Stockinger (1973), Goldsworthy (1970), IRAT (1975), Ofori (1972), de Geus (1973).

⁷ Includes 11.8 × 10⁹ kg chaff taken with 1° harvest (Kowal and Kassam 1978).

⁸ 0.42-1.1, $n = 3$; Goldsworthy (1970), Poulain (1980).

⁹ Poulain (1980), Balasubramanian and Nnadi (1980), Blondel (1971b), IRAT (1975), Jones (1974).

¹⁰ 80% of aerial residue removed for fodder over 80% of region (Poulain 1980); does not include cob.

¹¹ Includes 10.9 × 10⁹ kg cob taken with 1° harvest (Kowal and Kassam 1978, Drysdale 1965) that was not included in 2° harvest : AR ratio.

¹² Poulain (1980).

¹³ Assumes 67% of rice area planted to upland rice (NAS 1974), with upland productivity ≈ 40% of lowland (Kowal and Kassam 1978, da Silva 1978).

¹⁴ 0.49-1.1, $n = 6$; Grist (1975), Wu (1966) in IRRI (1975), Balasubramanian and Nnadi (1980), FAO (1979b).

¹⁵ 22% of husks removed (FAO 1979b) but included in 1° harvest.

¹⁶ Penders (1941).

¹⁷ 0.31-2.9, $n = 7$; Balasubramanian and Nnadi (1980), Wu (1966) in IRRI (1975), Poulain (1980), IRAT (1975).

¹⁸ Penders (1941), Chang et al. (1973).

¹⁹ Mainly wheat.

²⁰ FAO (1979b) for wheat, barley, and oats; Balasubramanian and Nnadi (1980) for wheat.

²¹ As for millet and sorghum.

²² Cowpeas not reported separately for 1978 (FAO 1979a, 1980a); estimate based on 1974 cowpea proportion (75%) of "cowpeas + other pulses" (FAO 1975).

²³ Balasubramanian and Nnadi (1980), Dart et al. (1977), Eaglesham et al. (1977).

²⁴ As for groundnuts (Balasubramanian and Nnadi 1980).

²⁵ Includes 0.20 × 10⁹ kg shells; grain = ≈ 87% of pod (Dart et al. 1977, Eaglesham et al. 1977, Akinola and Davies 1978).

²⁶ 1.2-1.5; Dart et al. (1977), Eaglesham et al. (1977).

²⁷ Kernels only; kernels = 65% of pod (de Geus 1973, FAO 1979a).

sagittifolium) account for 20–30% of the region's protein production, and various other protein sources provide another 5% (FAO 1979a). Plantains, bananas, and sugarcane (*Saccharum* sp.) are also important West African crops. Perennial crops include cacao, coffee (*Coffea* spp.), oil palm, coconut (*Cocos nucifera*), rubber (*Hevea brasiliensis*), and citrus (*Citrus* spp.); cacao and coffee together with groundnuts make up the bulk of West Africa's agricultural exports (FAO 1979b).

Rates of nitrogen flux through these crops, and in particular the fates of the nitrogen contained in yields and in harvest residues, have important consequences for crop productivity. A hectare of cassava that yields 10^4 kg fresh roots, for example, commonly removes ≈ 30 kg of nitrogen with the harvested crop. In the absence of significant fertilizer inputs, this loss can represent a substantial drain on the system's nitrogen store that is not likely to be fully replaced by nitrogen deposition and nitrogen fixation inputs during a following nonlegume crop cycle. Additionally, another 30 kg/ha remain in the aboveground crop residues, and further nitrogen losses occur when this residue is not left to decompose in situ. Such is the case in most of West Africa: most crop residues are removed for fuel or building material, or used for fodder for farmyard animals or tethered livestock. The residue not removed

is commonly burned before planting the next crop in order to clear the field and inhibit insect pests (Kowal and Kassam 1978, Nnadi and Balasubramanian 1978a, FAO 1979g, Balasubramanian and Nnadi 1980, Mokuwunye 1980, Ofori 1980, Poulain 1980). Plowing crop residues into the soil, as is commonly practiced in temperate agriculture, is generally precluded in West Africa by hard-packed soil in the north and by the absence of draft animals in the south.

Crop nitrogen budgets for temperate regions are usually estimated by extrapolating nitrogen pools and fluxes per unit area of monoculture to the regional level using estimates of the area under the particular crop. In West Africa and most tropical regions, however, such a procedure is impractical because of intercropping and differential planting densities. In multiple crop systems, the density of a given crop species may vary by an order of magnitude or more from one field to another even within the same watershed. Consequently, we have used published estimates of regional crop production to estimate the nitrogen removed in annual crop yields, and then used harvest indices (fresh yield: dry residue ratios) to estimate harvest residue biomass and nitrogen pools. Perennial crops tend to be planted at more constant densities than annual crops and in only 1–2 vegetation zones, so we have extrapolated

←

²⁸ $n = 2$; Nnadi et al. (1976), Balasubramanian and Nnadi (1980).

²⁹ 75% of residue removed for fodder $\approx 40\%$ of time (Poulain 1980, Balasubramanian and Nnadi 1980, Kowal and Kassam 1978, Nnadi et al. 1976, Ofori 1980, FAO 1979b).

³⁰ Includes 0.40×10^9 kg shells.

³¹ Poulain (1980).

³² 0.38–0.91, $n = 3$; Boakyee-Boateng and Hume (1975), Johnson et al. (1975), Kang (1975).

³³ As for cowpeas (Balasubramanian and Nnadi 1980), but ratio does not include shells.

³⁴ Includes 0.04×10^9 kg shells at groundnut shelling efficiency; see footnote 33.

³⁵ Ohlrogge and Kamprath (1968); ratio does not include shells.

³⁶ Includes 0.21×10^9 kg shells; bambara groundnut grain = 75% of pod (Kay 1979); see footnote 35.

³⁷ Not reported separately for 1978 (FAO 1979a, 1980a); based on 1974 proportion of yam (84.7%) + cocoyam (14.9%) + other (0.4%) (FAO 1975).

³⁸ Sobulo (1972).

³⁹ Estimated from Balasubramanian and Nnadi (1980).

⁴⁰ $n = 2$; Kay (1973), Kowal and Kassam (1978).

⁴¹ As for yams.

⁴² De la Pena and Plucknett (1972) if tuber = 72% moisture (Kay 1973).

⁴³ Includes sweet potatoes, potatoes, and others.

⁴⁴ Does not include legumes or tubers.

⁴⁵ 0.18–0.67, $n = 22$; Deat and Sement (1974), Poulain (1980), Balasubramanian and Nnadi (1980).

⁴⁶ Balasubramanian and Nnadi (1980), FAO (1979b).

⁴⁷ Poulain (1980).

⁴⁸ Kenaf and roselle mainly.

⁴⁹ Kowal and Kassam (1978).

⁵⁰ 0.31–0.58, $n = 5$; van Rheenan (1973), Sen and Lahiri (1960), Weiss (1971), Bascones and Lopez Ritas (1961).

⁵¹ As for cotton, once threshed in field.

⁵² 2.5–4.9, $n = 4$; Sen and Lahiri (1960), Weiss (1971), Bascones and Lopez Ritas (1961).

⁵³ Akehurst (1968), Kowal and Kassam (1978), Bascones and Lopez Ritas (1961).

⁵⁴ Based on 2:1 shoot:root ratio; shoot biomass = (1° harvest biomass less 23% moisture) plus total aerial residue.

⁵⁵ FAO (1979b).

⁵⁶ Based on 15:1 shoot:root ratio (Humber 1963 in Ruschel et al. 1978); shoot biomass = (1° harvest biomass less 23% moisture) plus total aerial residue.

⁵⁷ 1.4–3.9, $n = 3$; Burenrich (1913 in Jacob and Uexküll 1963), Baillon et al. (1933), Marten-Prevel et al. (1968).

⁵⁸ Baillon et al. (1933) assuming roots turn over once every 4 yr (Wills 1962, Williams 1975).

⁵⁹ Penders (1941); includes roots and assumes 2-yr crop.

⁶⁰ Included in aerial residue.

⁶¹ Mainly bambara groundnut.

TABLE 7. Nitrogen in annual crop biomass and its fate. Primary harvest values for % N are on a yield mass basis (8–15% moisture for grains, 70–90% for roots and tubers); other values are on dry mass basis. na = not available.

Crop	Primary harvest N ¹					Secondary harvest N ¹		
	Bio- mass (%)	N (10 ⁶ kg)	Fate			Bio- mass (%)	N (10 ⁶ kg)	Fodder ⁴ (10 ⁶ kg)
			Consumed (10 ⁶ kg)	Seed ² (10 ⁶ kg)	Exported ³ (10 ⁶ kg)			
Cereals								
Millet	4.4 ⁶	292	289	2.9	<0.1	0.7 ⁷	126	63
Sorghum	3.0 ⁹	152	151	1.5	<0.1	0.7 ¹⁰	107	54
Maize	2.6 ¹¹	84	83	0.8	<0.1	0.7 ¹²	12	5.8
Rice (lowland)	1.8 ¹³	43	42	0.4	<0.1	na	<0.1	<0.1
Rice (upland)	1.8 ¹³	16	16	0.2	<0.1	na	<0.1	<0.1
Others	2.2 ¹⁶	5.5	5.4	0.1	<0.1	0.7 ¹⁷	1.2	0.6
Legumes								
Cowpeas	3.6 ¹⁸	48	47	0.5	<0.1	1.8 ¹⁹	14	7.1
Groundnuts	4.3 ²²	32	17	0.3	15 ²³	1.5 ²⁴	17	8.3
Soybeans	6.3 ²⁷	4.4	4.4	<0.1	<0.1	0.9 ²⁸	0.6	0.2
Others	4.3 ³¹	17	16	0.2	0.3 ³²	1.3 ³³	4.9	1.7
Roots and tubers								
Yams	0.4 ³⁵	75	74	0.8	<0.1	2.6 ³⁶	2.6	1.3
Cassavas	0.3 ³⁸	43	43	<0.1	<0.1	na	<0.1	<0.1
Cocoyams	0.3 ⁴¹	11	11	0.1	<0.1	2.6 ⁴²	1.3	0.7
Others	0.3 ⁴⁴	2.1	2.1	<0.1	<0.1	1.8 ⁴⁴	<0.1	<0.1
Other crops								
Vegetables	0.2 ⁴⁵	7.6	7.5	0.1	<0.1	2.0 ⁴⁶	52	26
Cotton	2.9 ⁴⁸	14	13	0.1	0.7	1.3 ⁴⁹	14	7.8
Other fibers	0.5	<0.1	<0.1	<0.1	<0.1	1.0	0.2	0.1
Sesame	3.7 ⁵¹	3.3	3.3	<0.1	<0.1	0.9 ⁵²	1.3	0.7
Tobacco	2.0 ⁵⁴	0.4	0.4	<0.1	<0.1	na	<0.1	<0.1
Sugar cane	0.1 ⁵⁵	3.0	3.0	<0.1	<0.1	0.2 ⁵⁶	0.4	<0.1
Bananas	0.4 ⁵⁷	19	19	<0.1	<0.1	na	<0.1	<0.1
Pineapples	0.1 ⁵⁹	0.3	0.3	<0.1	<0.1	na	<0.1	<0.1
Total		870	846	8.0	16		354	177

¹ See Table 6 for biomass.² Assumes 1% of crops return as seed.³ FAO (1979b).⁴ Assumes 50% used as fodder for farmyard animals, 40% burned for fuel at 100% burn efficiency, and 10% returned to field with household wastes (Poulain 1980, FAO 1979g, 1980b, Balasubramanian and Nnadi 1980, Nnadi and Balasubramanian 1978a), except where used as processing fuel (100% burned).⁵ Assumes 50% used as fodder, 40% burned in field at 90% burn efficiency, and remainder either left in field or used as building material eventually returned to field (Poulain 1980, FAO 1979g, 1980b, Nnadi and Balasubramanian 1978a, Balasubramanian and Nnadi 1980, Kowal and Kassam 1978).⁶ Blondel (1971), IRAT (1975); 4.1–4.5% N, *n* = 4.⁷ French (1943), Poulain (1980), Balasubramanian and Nnadi (1980), Singh and Balasubramanian (1980b); 0.65–0.83% N, *n* = 5.⁸ Poulain (1980), Ganry et al. (1978a, b); 0.41–0.90% N, *n* = 2.⁹ Poulain (1980), Gigou (1980), Blondel (1971), IRAT (1975); 1.3–3.8% N, *n* = 4.¹⁰ Poulain (1980), Balasubramanian and Nnadi (1980), Singh and Balasubramanian (1980b); 0.29–1.5% N, *n* = 4.¹¹ Blondel (1971), IRAT (1975); 2.4–2.7% N, *n* = 3.¹² French (1943), Poulain (1980), Balasubramanian and Nnadi (1980), Singh and Balasubramanian (1980b); 0.51–0.80% N, *n* = 4.¹³ Blondel (1971), IRAT (1975), Grist (1975); 0.96–2.5% N, *n* = 4.¹⁴ Grist (1975), Balasubramanian and Nnadi (1980), Singh and Balasubramanian (1980b); 0.45–0.58% N, *n* = 4.¹⁵ Grist (1975).¹⁶ Wheat; French (1943); 2.0–2.4% N, *n* = 3.¹⁷ As for sorghum.¹⁸ IBAN (1936), Purseglove (1968), Nnadi et al. (1976), Rachie and Roberts (1974), Eaglesham et al. (1977), Kay (1979); 3.0–4.0% N, *n* = 9, assumed 10% moisture if dry mass basis.¹⁹ Assumed 13% of secondary harvest = shells at % N for groundnut shells, remainder at litter % N.²⁰ French (1943), Dart et al. (1977), Eaglesham et al. (1977), Kay (1979); 1.0–2.9% N, *n* = 5.²¹ Nnadi et al. (1976), Nnadi and Balasubramanian (1978b), Dart et al. (1977), Eaglesham et al. (1977).²² Purseglove (1968), Nnadi et al. (1976), IBAN (1936); 3.7–4.9% N, *n* = 10, grain only.²³ 2.5 × 10⁶ kg N as groundnuts, 12.4 × 10⁶ kg N as cake and meal (at 7.4% N; IBAN 1936); from FAO (1979b).²⁴ Assumed 35% of secondary harvest = shells at 0.85% N (IBAN 1936, Gillier 1966, Balasubramanian and Nnadi 1980, Singh and Balasubramanian 1980b; 0.73–1.0% N, *n* = 7), remaining 65% at litter % N.²⁵ Poulain (1980), Balasubramanian and Nnadi (1980), French (1943); 1.3–2.3% N, *n* = 3.²⁶ Poulain (1980), Balasubramanian and Nnadi (1980), Nnadi and Balasubramanian (1978b); 1.2–3.5% N, *n* = 3.²⁷ IBAN (1936), Purseglove (1968), Kang (1975); 5.8–8.2% N, *n* = 6.

TABLE 7. Continued.

Secondary harvest N ¹			Litter N				Belowground residue	
Fate ⁴		Bio-mass (%)	N (10 ⁶ kg)	Forage (10 ⁶ kg)	Fate ⁵		Bio-mass (%)	N (10 ⁶ kg)
Burned (10 ⁶ kg)	Returned (10 ⁶ kg)				Burned (10 ⁶ kg)	Returned (10 ⁶ kg)		
50	13	0.77	54	27	19	7.5	0.6 ⁸	56
43	11	0.7 ¹⁰	30	15	11	4.1	0.6 ⁸	32
4.6	1.2	0.7 ¹²	21	11	7.6	3.0	0.6	9.6
<0.1	<0.1	0.5 ¹⁴	14	7.2	5.1	2.0	0.24 ¹⁵	17.3
<0.1	<0.1	0.5 ¹⁴	4.0	2.0	1.4	0.6	0.24 ¹⁵	6.2
0.5	0.1	0.7 ¹⁷	0.5	0.3	0.2	0.1	0.6	1.7
5.7	1.4	1.9 ²⁰	23	11	8.2	3.2	1.1 ²¹	1.0
6.6	1.7	1.8 ²⁵	20	9.9	7.1	2.8	2.1 ²⁶	12
0.1	<0.1	0.9 ²⁹	0.5	0.3	0.2	0.1	1.2 ³⁰	0.5
1.3	0.3	1.5 ³⁴	5.9	2.9	2.4	0.6	1.6 ³⁴	0.8
1.0	0.3	0.9 ³⁷	7.7	3.9	2.8	1.1	0.77 ³⁷	2.5
<0.1	<0.1	0.3 ³⁹	52	26	19	7.3	0.45 ⁴⁰	1.2
0.5	0.1	1.8 ⁴³	8.3	4.2	3.0	1.2	0.32 ⁴⁴	0.2
<0.1	<0.1	1.0 ⁴⁴	0.3	0.2	0.1	0.0	0.36 ⁴⁴	<0.1
21	5.2	2.0 ⁴⁶	50	25	18	7.0	1.3 ⁴⁷	6.6
6.2	1.6	1.3 ⁵⁰	3.6	1.8	1.3	0.5	1.0 ⁵⁰	3.6
0.1	<0.1	na	<0.1	<0.1	<0.1	<0.1	0.6	0.1
0.5	0.1	0.9 ⁵²	0.3	0.2	0.1	<0.1	0.37 ⁵³	0.1
<0.1	<0.1	1.9 ⁵⁴	0.6	0.3	0.2	0.1	1.0	0.2
0.4	<0.1	0.2 ⁵⁶	1.0	0.5	0.4	0.1	1.0	0.9
<0.1	<0.1	0.6 ⁵⁷	9.2	4.6	3.3	1.3	0.6	1.4
<0.1	<0.1	0.2 ⁶⁰	1.1	0.6	0.4	0.1	na ⁶¹	na ⁶¹
142	35		306	154	111	43		154

²⁸ As for groundnuts calculation.
²⁹ Morrison (1954), Ohlrogge (1960), de Mooy et al. (1973); 0.44–2.0% N, *n* = 5.
³⁰ Nnadi and Balasubramanian (1978*b*), Hanway and Weber (1971); 0.9–1.4% N, *n* = 2.
³¹ Mean of other legumes + bambara groundnut (2.8% N; Kay 1979).
³² May include cowpeas and soybeans (FAO 1979*b*).
³³ Assumed 25% = shells at % N for groundnut shells, remainder at litter % N.
³⁴ Mean of other legumes.
³⁵ Kay (1973), Sobulo (1972), Doku (1967); 0.32–0.50% N, *n* = 3; assumed 65% moisture where necessary.
³⁶ French (1943); tops.
³⁷ Sobulo (1972).
³⁸ IBAN (1936), du Fournet et al. (1957) in de Geus (1973), Doku (1967), Johnson and Raymond (1965), de Geus (1973); 0.11–0.68% N, *n* = 11.
³⁹ du Fournet et al. (1957) in de Geus (1973).
⁴⁰ Howeler (1981); 0.17–0.93% N.
⁴¹ Doku (1967), Kay (1973); 0.28–0.35% N, *n* = 2.
⁴² As for yams.
⁴³ de la Pena and Plucknett (1972); 1.6–2.1% N, *n* = 2.
⁴⁴ Mean of other roots and tubers.
⁴⁵ IBAN (1936), USDA (1971); 0.04–0.32% N, *n* = 6 crops.
⁴⁶ Greenwood et al. (1980); 0.7–3.5% N, *n* = 12.
⁴⁷ Greenwood et al. (1980), *n* = 7.
⁴⁸ IBAN (1936), Purseglove (1968), Prentice (1972), Deat and Sement (1974), Deat et al. (1976); 1.3–4.0% N, *n* = 16.
⁴⁹ Poulain (1980), Balasubramanian and Nnadi (1980), Singh and Balasubramanian (1980*b*); 0.66–1.9% N, *n* = 20.
⁵⁰ Poulain (1980).
⁵¹ IBAN (1936), Bascones and Lopez Ritas (1961), van Rheenan (1973); 2.9–5.4% N, *n* = 6.
⁵² Bascones and Lopez Ritas (1961), Sen and Lahiri (1960), 0.78–0.94% N, *n* = 2.
⁵³ Bascones and Lopez Ritas (1961).
⁵⁴ Akehurst (1968).
⁵⁵ Jacob and von Uexküll (1963), FAO (1965, 1979*b*); 0.06–0.12% N, *n* = 4.
⁵⁶ Based on cane N: top N ratio of 0.14:0.24 (Morrison 1954); cane % N = 0.11 (footnote 55).
⁵⁷ IBAN (1936), Marten-Prevel et al. (1968); 0.05–1.3% N, *n* = 7.
⁵⁸ Jacob and von Uexküll (1963).
⁵⁹ IBAN (1936), Penders (1941), Jacob and von Uexküll (1963); 0.072–0.083% N, *n* = 4.
⁶⁰ Penders (1941).
⁶¹ Included in aerial residue.

TABLE 8. Area covered by, and maximum standing biomass and nitrogen contents of, the major perennial crops. All values are expressed on a dry-matter basis.

Crop	Area planted (10 ⁶ ha)	Leaf		Wood		Roots		Inflorescence and fruit		Total N	
		Biomass (10 ³ kg/ha)	N (%)	Biomass (10 ³ kg/ha)	N (%)	Bio-mass (10 ³ kg/ha)	N (%)	Bio-mass (10 ³ kg/ha)	N (%)	Local (kg/ha)	Re-gional (10 ⁶ kg)
		Coffee	1.0 ¹	0.2 ²	2.0 ²	0.4 ²	0.50 ²	0.5 ²	1.8 ²	0.67 ⁴	20 ⁵
Cacao	2.9 ¹	0.6 ⁶	1.8 ⁶	6.8 ⁶	0.80 ⁷	3.6 ⁶	1.2 ⁶	1.1 ⁸	103	294	
Citrus	0.02 ⁹	1.6 ¹⁰	2.1 ¹¹	5.8 ¹⁰	0.44 ¹¹	2.1 ¹⁰	0.70 ¹¹	0.4	2.6 ¹²	81	2
Rubber	0.13 ¹³	6.3 ¹⁴	2.8 ¹⁴	290 ¹⁴	0.45 ¹⁴	59 ¹⁵	0.44 ¹⁴	0.2 ¹⁴	1.06 ¹⁴	1738	226
Oil palm and coconut	1.2 ¹⁶	16.1 ¹⁷	1.2 ¹⁷	38 ¹⁷	0.48 ¹⁷	17 ¹⁷	0.48 ¹⁸	3.6 ¹⁸	0.83 ¹⁹	488	591
Total	5.3										1134

¹ FAO (1979a).² Roskoski et al. (1982) assuming 1200 trees/ha.³ Calculated from inflorescence and fruit % N and N yield (kg/ha).⁴ From Table 5 assuming 8.2% moisture in primary harvest and a 1° harvest residue ratio of 0.35.⁵ Inflorescence and fruit N yield (kg/ha) based on primary harvest biomass (Table 5) and area covered (FAO 1980a).⁶ Roskoski et al. (1982), assuming 1500 trees/ha (Urquhart 1961).⁷ Boyer (1973), Roskoski et al. (1982); 0.29–1.3% N, *n* = 2.⁸ Boyer (1973).⁹ Based on regional production (FAO 1979a) and average yield of $\approx 16 \times 10^3$ kg/ha (Ayers and Branson 1973; unfertilized California trees).¹⁰ Cameron and Compton (1945), assuming 100 trees/ha.¹¹ Cameron and Compton (1945).¹² Cameron and Compton (1945), FAO (1970), Hume (1957), Wallace et al. (1951); 0.85–3.6% N, *n* = 8.¹³ Based on regional production (FAO 1979a) and average latex yields of ≈ 1400 kg/ha (Shorrocks 1965b: 1700 kg/ha; Rosenquist 1966 in de Geus 1973: 1430 kg/ha; de Geus 1973: 560–1700 kg/ha).¹⁴ Shorrocks (1965a), assuming that 25% of all trees are <10 yr old, and 75% are 10–33 yr.¹⁵ Shorrocks (1965a); roots = 16.5% total tree (15.8–17.8%, *n* = 4).¹⁶ Based on regional production (FAO 1979a); for oil palm, average fresh kernel yields of $\approx 0.46 \times 10^3$ kg/ha (Godin and Spensley 1971: 0.54×10^3 kg/ha; Johnson and Raymond 1954: 0.18×10^3 kg/ha; Georgi 1931: 0.41×10^3 kg/ha); for coconut, average harvest yield (whole nut less husk) of ≈ 2500 kg/ha (copra 400 kg/ha \times 6 husked nuts/kg copra [Purseglove 1975] \times fresh matter 1 kg/nut [Child 1974]).¹⁷ Tinker and Smilde (1963) for oil palm.¹⁸ Rees and Tinker (1963) for oil palm.¹⁹ Georgi (1931); 0.55–1.1% N, *n* = 2.

typical local pools and fluxes for perennial crops to the regional level based on published estimates of cultivated areas.

West African annual crops yielded $\approx 77 \times 10^9$ kg of primary harvest fresh biomass in 1978 (Table 6). Another 122×10^9 kg of dry biomass were produced as nonyield biomass or aerial and root residue, with $\approx 35\%$ of this removed from the fields in the form of secondary harvest products such as pod walls, shells, and chaff. West African crops vary substantially in their capacities to produce residue; ratios of primary harvest biomass to aerial residue range from <1.0 for most cereals and grain legumes to >19 for some roots and tubers. Over 70% of the aerial residue produced in the region is derived from millet, sorghum, and cassava crops.

Associated with the annual crop yield removed from the region's fields in 1978 were $\approx 870 \times 10^6$ kg N (Table 7). Most of the nitrogen in these yields was consumed within the region, although some ($\approx 16 \times 10^6$ kg) was exported and a small portion ($\approx 1\%$) was presumably set aside for return to the soil the following year as seed. Another 660×10^6 kg were immobilized

in aerial residue, $\approx 50\%$ of which was harvested with the primary yield as secondary harvest products. Almost half of all aerial residue nitrogen ($\approx 331 \times 10^6$ kg) was probably consumed by domestic livestock either fed secondary harvest products directly or grazed in the harvested fields. Most of the remaining aerial residue N was likely burned ($\approx 253 \times 10^6$ kg), either for fuel or in the field, but some ($\approx 78 \times 10^6$ kg) was left on the soil surface to eventually mineralize. Aerial residue used for building materials (e.g., thatched roofs) and fencing is presumed to eventually burn or decompose in the field. Belowground crown and root residue contained $\approx 120 \times 10^6$ kg N, all of which remained in the soil.

Perennial crops covered an effective area of $\approx 5.3 \times 10^6$ ha of West Africa in 1978, principally in the coastal regions. As much as 1.13×10^9 kg of nitrogen were immobilized in the standing biomass of these crops at one time during the year (Table 8); on a regional basis over half of this N was immobilized in aboveground wood, though this proportion varied substantially by crop. Rubber trees, for example, immobilize in wood around 1.3×10^3 kg/ha, whereas oil palm and coconut

trees immobilize $\approx 0.2 \times 10^3$ kg/ha. Collectively, N removed in perennial crops in 1978 was $\approx 44 \times 10^6$ kg in their primary yield, $\approx 33 \times 10^6$ kg in harvest residue, and $\approx 104 \times 10^6$ kg in litterfall and throughfall leachates (Table 9). Of that N removed by harvest residue and litterfall, $\approx 35\%$ (75×10^6 kg) was subsequently volatilized when burned, and the remainder returned to the soil (Table 10).

The nitrogen content of secondary producers (principally humans, terrestrial vertebrates, and fish) in West Africa, including those in noncultivated systems, was $\approx 23 \times 10^6$ kg in 1978 (Table 11). Cattle and other livestock accounted for $\approx 47\%$ of this pool, humans 31%, and inland fish most of the remainder. Of N in the secondary producer pool, $\approx 2.8 \times 10^6$ kg was consumed by humans. Population growth (FAO 1980a) between 1977 and 1978 indicates that $\approx 0.2 \times 10^6$ kg were immobilized into humans in 1978 (see Table 11). Likewise, about 0.1×10^6 kg appears to have been immobilized in the growing livestock population (FAO 1980a).

Nitrogen in noncultivated systems

Approximately 63×10^9 kg of nitrogen were immobilized in the vegetation and litter biomass of noncultivated ecosystems in West Africa in 1978 (Table 12). Almost half of this was in early secondary forest growth, with $\approx 50\%$ of the remainder in late successional savanna systems and 30% in older forests. Nitrogen flux estimates for noncultivated systems are particularly limited by a restricted data base, but rough extrapolations (Table 13) show that $\approx 22 \times 10^9$ kg were taken up by the West African native vegetation in 1978. Early secondary forest vegetation accounted for $\approx 50\%$ of this uptake; of the remainder, $\approx 60\%$ was removed by late successional savanna vegetation and $< 10\%$ by older forests. On a regional level, both total biomass nitrogen and net nitrogen uptake in mature Guinea Savanna Woodland vegetation exceeded that for all other systems except early secondary Lowland Rain Forest, although this rank was largely the result of geographic size. At the local level rankings by uptake generally followed woody biomass content, with forests $>$ derived savanna grassland $>$ Guinea savanna woodland $>$ Sahel bushland $>$ subdesert grassland.

Lakes cover $\approx 8.0 \times 10^6$ ha of West Africa. There is little information available regarding nitrogen within these lakes or within tropical lakes in general. However, using Table 14 nitrogen concentration estimates of 0.10% in lake water and 90 kg/ha in the upper 30 cm of lake sediments, we calculate that there were $\approx 318 \times 10^9$ kg in West African lakes in 1978, of which $> 99\%$ was in the sediments. Our estimates of N_2 fixation in West African lakes (Table 2) are based on Horne and Viner's (1971) estimate of ≈ 44 kg \cdot ha $^{-1}$ \cdot yr $^{-1}$ for Lake George, Uganda. Nitrogen fixation in temperate lakes ranges to ≈ 60 kg \cdot ha $^{-1}$ \cdot yr $^{-1}$ (Lean et al. 1978).

Nitrogen losses from West Africa

Nitrogen is lost from West Africa by gaseous, hydrologic, and anthropic pathways. Principal gaseous vectors include NO_x production via biomass burning and abiotic soil processes, N_2 and N_2O production by microbes in soils, and NH_3 volatilization from unamended soil, manure, and commercial fertilizer applications.

Fire appears to account for the bulk of all nitrogen lost from the region. Approximately 8300×10^6 kg were lost by this pathway in 1978 (Table 15). About 67% of this loss occurred upon clearing and burning forest vegetation, $< 4\%$ via burning crop residues, and the remainder during near-annual burns of savanna, Sahel, and subdesert systems.

Of the 185×10^6 kg N in cleared mature forests, about 43×10^6 kg were removed in the 1978 harvest of $\approx 9.8 \times 10^9$ kg of industrial roundwood (FAO 1979e; assumes a mean wood density of 0.65 [F. Bernhard-Reversat, *personal communication*]). Of that harvested, 2.4×10^9 kg was exported (FAO 1979e), representing a nitrogen loss to the region of $\approx 11 \times 10^6$ kg. The remaining roundwood was presumably consumed within the region, with conversion to NO_x upon burning the probable eventual fate of the 33×10^6 kg N contained therein.

Gaseous losses of N as nitrous oxide (N_2O) and N_2 via denitrifiers in West African soils are probably $\approx 1100 \times 10^6$ kg/yr. Little attention has been paid to denitrification in upland West African soils; as is the case in temperate regions, denitrification in most of the region's systems appears to be a potentially important but poorly quantified nitrogen cycle process.

Volatilization losses of ammonia (NH_3) from unfertilized soils in West Africa are probably low, on the order of 100×10^6 kg N for 1978. Because ammonia volatilization is not likely to be an important source of nitrogen loss in unfertilized systems with a soil pH below 7 or an intact plant canopy (Denmead et al. 1976), significant local losses of ammonia from uncultivated systems probably occur only in parts of the Guinea savanna, the Sahel, and the subdesert.

Ammonia can also be volatilized from commercial fertilizers and manure, although in West Africa relatively little is lost during commercial fertilizer applications because nitrogen fertilizers are not often applied to West African crops. In Nigeria, for example, where natural gas for fertilizer feedstock is readily available, only 1.5 kg/ha of nitrogen were expected to be applied in this form to cultivable land in 1978 (FDA 1977). Suggested fertilizer application rates for most crops (Singh and Balasubramanian 1980a) exceed this figure by two orders of magnitude. Consequently, ammonia losses from surface applications of urea and inorganic nitrogen fertilizers ($\approx 13 \times 10^6$ kg N; Table 16) are relatively minor.

TABLE 9. Nitrogen turnover and uptake in major perennial crops. N uptake is the sum of regional values for primary harvest + harvest residue + litterfall + throughfall + net accretion in biomass. Regional litterfall and throughfall values are based on crop extents in Table 8; all biomass values but primary harvest are dry mass basis. PH:HR is the pri-

Crop	Annual N turnover									
	1° harvest removed			Residue removed			Nonwoody litterfall		Woody litterfall	
	N content			N content			Biomass (10 ³ kg/ ha)	N content		Biomass (10 ³ kg/ha)
	Biomass (10 ⁹ kg) ²	(%)	(10 ⁶ kg)	PH:HR	(%)	(10 ⁶ kg)		(%)	(kg/ ha)	
Coffee	0.22	1.4 ³	3.0	0.35 ⁴	0.39 ⁵	2.4	0.14 ⁶	1.5 ⁷	2.1	0.04 ⁸
Cacao	0.76	3.4 ¹⁰	26	1.0 ¹¹	1.6 ¹¹	12	0.38 ⁶	1.4 ²	5.3	0.7 ⁸
Citrus	0.34	0.12 ¹²	0.4	<0.1	na	<0.1	0.91 ¹³	1.6 ¹³	14.2	0.6 ⁸
Rubber	0.18	0.57 ¹⁴	1.0	<0.1	na	<0.1	5.8 ¹⁵	1.2 ¹⁶	71.7 ¹⁷	1.93 ¹⁵
Oil palm	0.43	1.3 ¹⁹	5.6	0.06 ²⁰	0.18 ²¹	14	7.7 ²²	0.90 ²²	68.9	<0.1
Coconut	0.61 ²³	1.3 ²⁴	8.0	2.3 ²⁵	1.4 ²⁴	3.8	7.7 ²⁶	0.90 ²⁶	69	<0.1
Total			44			32				

¹ Turnover plus net accretion in biomass; accretion = (standing biomass N [from Table 8])/(average plant lifetime); assumes no significant net regional N loss by tree or stand replacement. Plant lifetimes are 30 yr for coffee (Purseglove 1968), 30 yr for cacao and citrus, 40 yr for rubber, and 60 yr for oil palm and coconut.

² FAO (1980a).

³ IBAN (1936).

⁴ Boyer (1973) with beans = 5% moisture (IBAN 1936).

⁵ Bressani et al. (1972) in Elias (1979).

⁶ Estimate based on leaf turnover of 60%/yr; see Table 8 for leaf biomass.

⁷ Estimate based on 75% pre-abscission % N.

⁸ Pruning estimate (wood biomass of 10%/yr).

⁹ From Table 8.

¹⁰ Jacob and Uexküll (1963), Adams (1962); 2.4–4.4% N, *n* = 2.

¹¹ Adams (1962), Boyer (1973), IBAN (1936); 0.81–2.3% N, *n* = 2.

¹² Ayers and Branson (1973), IBAN (1936), Smith and Renner (1954); 0.06–0.16% N.

¹³ Wallace et al. (1951), assuming 100 trees/ha.

¹⁴ Beauflis (1955), Shorrocks (1965b), Rosenquist (1966, in Webster and Wilson 1980); 0.47–0.70% N, *n* = 6.

¹⁵ Shorrocks (1965a), including thinned trees.

¹⁶ Shorrocks (1965b).

¹⁷ Includes 1.6×10^3 kg N from fruit-fall of 0.15×10^3 kg/ha at 1.06% N (Shorrocks 1965a, b).

¹⁸ Shorrocks (1965a).

¹⁹ IBAN (1936).

²⁰ Georgi (1931), Johnson and Raymond (1954).

²¹ Based on total fruit % N = 0.27 (Tinker and Smilde 1963, Georgi 1931, de Geus 1973).

²² Georgi (1931).

²³ Whole nut less husk.

²⁴ de Geus (1973), based on nut + husk N content and 10% husk moisture.

²⁵ Child (1974), Purseglove (1975); 0.61–0.75, *n* = 2.

²⁶ As for oil palm (Pillai and Davis 1963 in Child 1974).

²⁷ Regional total N turnover for each crop = 10⁶ kg in residue removed plus [(10⁶ ha areal extent from Table 8) × (kg/ha in nonwoody litterfall + kg/ha in woody litterfall + kg/ha in throughfall)].

TABLE 10. Fate of nitrogen turned over by major perennial crops.

Crop	1° harvest		2° harvest ¹		Litter ²	
	Consumed	Exported ³	Burned	Returned	Burned	Returned
	Nitrogen content (10 ⁶ kg)					
Coffee	<0.1	3.0 ⁴	1.2	1.2	0.2	13
Cacao	2.8	23	6.1	6.1	16	43
Citrus	0.4	0.0	<0.1	<0.1	<0.1	0.5
Rubber	0.3	0.7	<0.1	<0.1	1.1	11
Oil palm	2.6	3.0 ⁵	6.8	6.8	33	42
Coconut	7.8	0.1	1.9	1.9	9.0	12
Total	14	30	16	16	59	121

¹ FAO (1979g, 1980b).

² Assumes all woody litter and 50% of oil palm and coconut leaf litter burned for fuel (100% burn efficiency).

³ Biomass from FAO (1979b) and % N from Table 9.

⁴ 1978 exports exceeded 1978 production (FAO 1979b); production value (Table 9) used here.

⁵ Includes 1.1×10^6 kg N exported as oil palm, coconut, and other oil cakes.

TABLE 9. Continued.

mary harvest : Harvest residue ratio. na = not available.

Annual N turnover				Annual N uptake ¹
Woody litterfall		Through-fall N (kg/ha)	Regional total N ²⁷ (10 ⁶ kg)	
N content (%)	(kg/ha)			Regional total (10 ⁶ kg/yr)
0.5 ⁹	0.2	10	13	19
0.8 ⁹	5.6	10	60	107
0.44 ⁹	2.6	10	0.6	1.1
0.45 ¹⁶	8.7	10 ¹⁸	12	19
na	<0.1	10	75	102
na	<0.1	10	21	34
			181	282

Nitrogen losses from manure deposited on soil surfaces are by comparison considerable; $\approx 220 \times 10^6$ kg were lost by this pathway in 1978 (Tables 15 and 16). We estimate, using livestock mass extrapolations (Table 16), that $\approx 136 \times 10^6$ kg were lost via extensively grazed livestock; this figure compares relatively well with the 125×10^6 kg estimated to be lost from grazed systems in Table 15. Humans account for $\approx 31\%$ of the manure nitrogen produced in the region, vs. 47% for cattle and 11% for sheep and goats, but because only $\approx 20\%$ of human excrement is available for volatilization on the soil surface (Singh and Balasubramanian 1980a), humans are a minor direct ammonia source.

Nitrogen is also lost by NO₂ and NO emissions from soils, though this NO_x-N flux remains very poorly

understood in general. Makarov (1969) and Kim (1973) estimated fluxes of 0.3–7.0 and 1.7–4.0 g·m⁻²·s⁻¹, respectively, for temperate soils. If these N loss rates are extrapolated to 90 d of equivalent activity per year (0.03–0.71 kg·ha⁻¹·yr⁻¹), and to all of nondesert terrestrial West Africa (418 × 10⁶ ha), then 13–304 × 10⁶ kg could have been lost by this pathway in 1978. Some portion of this may be returned via wet precipitation to locations near the point of origin.

We have estimated hydrologic losses of nitrogen from West Africa using Niger River fluxes, since more complete data are unavailable. On average, ≈ 2.5 kg of mineral-N and 1.7 kg organic-N were lost per hectare of the 209 × 10⁶-ha Niger River watershed in 1978 (Table 17). This watershed includes portions of all vegetation zones, so that this mean loss estimate may be a reasonable figure for the entire region less desert and subdesert areas. Extrapolation of this N discharge rate suggests that $\approx 1500 \times 10^6$ kg/yr were lost to marine systems by river flow in 1978.

Although on a local scale, erosion, runoff, and leaching N-losses can far exceed our estimated 5.1 kg·ha⁻¹·yr⁻¹ regional average (e.g., Fournier 1967, Lal 1977, Roose 1980), most local erosion and runoff losses probably represent redistributions of nitrogen within the region, and high solute losses in wet areas are offset by low rates of loss in drier regions. Some of the nitrogen redistributed by erosion may be immobilized in sediments of lakes and behind recently constructed dams, and may thus be effectively withdrawn from the terrestrial cycle, but the extent of such sedimentation is not presently known.

TABLE 11. Nitrogen in secondary producers and human consumption of secondary producers in West Africa in 1978. na = not available or not applicable; LM = live mass.

Component	Standing pool				Human consumption	
	Pop'n ¹ (10 ⁶)	LM each (kg)	LM total (10 ⁹ kg)	N total ² (10 ⁶ kg)	LM total ³ (10 ⁹ kg)	N total (10 ⁶ kg)
Human	132	55	7.3	7.2	na	na
Livestock						
Cattle	30	250 ⁴	7.6	7.6	1.06	1.1
Sheep	30	25 ⁴	0.76	0.8	0.19	0.2
Goats	48	19 ⁴	0.90	0.9	0.34	0.3
Swine	3.2	100 ⁴	0.32	0.3	0.17	0.2
Asses	2.2	140	0.31	0.3	<0.1	<0.1
Horses	1.0	165 ⁴	0.17	0.2	<0.1	<0.1
Camels	1.2	200	0.25	0.3	<0.1	<0.1
Poultry	178	2	0.36	0.4	0.47	0.5
Wild vertebrates	na	na	0.1	0.1	<0.1	<0.1
Inland fish	na	na	5.0 ⁵	5.0	0.5 ⁶	0.5
Total				23		2.8

¹ FAO (1979a).² All animals assumed to be 0.1% N on a live mass basis.³ Based on dressed mass (FAO 1979a) and dressed mass : live mass ratios of 0.43 (cattle), 0.50 (sheep), and 0.49 (goats) (FAO 1971) and 0.50 (all others).⁴ FAO (1971).⁵ Standing stock assumed = 10 × annual catch.⁶ FAO (1979c).

TABLE 12. Vegetation biomass and nitrogen contents in noncultivated West African systems. Footnotes follow Table 13; na = not applicable.

System	Leaves, flowers and fruits		Wood		Roots		Litter
	Biomass (10 ³ kg/ha)	N (%)	Biomass (10 ³ kg/ha)	N (%)	Biomass (10 ³ kg/ha)	N (%)	Biomass (10 ³ kg/ha)
Lowland rain forest							
Early successional	5.7 ¹	2.2 ¹	72 ¹	0.26 ¹	26 ¹	0.69 ¹	7.4 ¹
Mid-successional	6.5 ²	2.2 ²	117 ²	0.26 ²	31 ²	0.47 ²	5.6 ²
Mature	10 ⁴	2.2	467 ⁵	0.50 ⁶	57 ⁷	0.58	5.0
Semideciduous forest							
Early successional	5.2 ¹¹	1.6 ¹²	28 ¹³	0.55 ¹⁴	11 ¹⁵	1.1 ¹⁵	10.2 ¹⁶
Mid-successional	5.6 ¹⁹	2.5 ¹⁹	112 ¹⁹	0.32 ¹⁹	14 ²⁰	0.9 ²⁰	5.6 ¹⁹
Mature	16 ²²	2.0 ²³	150 ²⁴	0.37 ²⁵	25 ²⁶	0.86 ²	3.9 ²⁷
Derived savanna grassland							
Early successional	8.2 ³⁰	1.1 ³¹	2.4 ³²	0.81 ³³	2.7 ³⁴	0.66 ³⁵	1.2 ³⁶
Late successional	4.8 ³⁹	1.4 ⁴⁰	28 ⁴¹	0.35 ⁴²	28 ⁴³	0.63 ⁴⁴	2.8 ⁴⁵
Guinea savanna woodland							
Early successional	9.6 ⁴⁸	0.35 ⁴⁹	0.0 ⁴⁷	na	8.9 ⁵⁰	0.33 ⁵⁰	1.8 ⁵¹
Late successional	5.7 ⁵⁴	0.42 ⁵⁵	27 ⁵⁶	0.17 ⁵⁷	4.0 ⁵⁸	0.34 ⁵⁹	1.4 ⁶⁰
Sahel Bushland							
Grazed, fallow	1.1 ⁶²	1.1 ⁶³	1.7 ⁶⁴	0.64 ⁶³	3.0 ⁶³	1.0 ⁶³	<0.1 ⁶³
Subdesert grassland							
Grazed, unused	0.1	1.1	0.2	0.64	0.3	1.0	<0.1
Total							

Soil nitrogen

The bulk of the nonatmospheric nitrogen in West Africa is in the soil. Approximately $4\text{--}15 \times 10^{12}$ kg reside in this pool to 150 cm depth (Table 18), although the proportion of this nitrogen that actively cycles in the soil-plant system is not known with certainty. West African soil nitrogen pools vary by soil groups (Fig. 5) from $<0.1 \times 10^3$ to $>70 \times 10^3$ kg/ha, though most soils fall in the $5\text{--}40 \times 10^3$ kg/ha range. Variation within groups can be as great as a factor of 15 or more (FAO-UNESCO 1977, Asamoah 1980), and reflects variation in topographic relief and land use history.

Most soil nitrogen is in organic forms; mineral-N commonly makes up $<2\%$ of total soil N, although NH_4^+ -N fixed in clay lattices has been reported to comprise 12–33% of total soil nitrogen to 150 cm in at least four Nigerian profiles (Moore and Ayeke 1965). Kudeyarov (1980) has suggested that this fixed N may be more active than commonly presumed.

It is not possible to estimate regional nitrogen mineralization rates with precision based on these data. Many authors (e.g., Hainnaux et al. 1980, Penning de Vries et al. 1980b, Wetselaar 1980) have pointed out that rates vary widely and independently of total per-

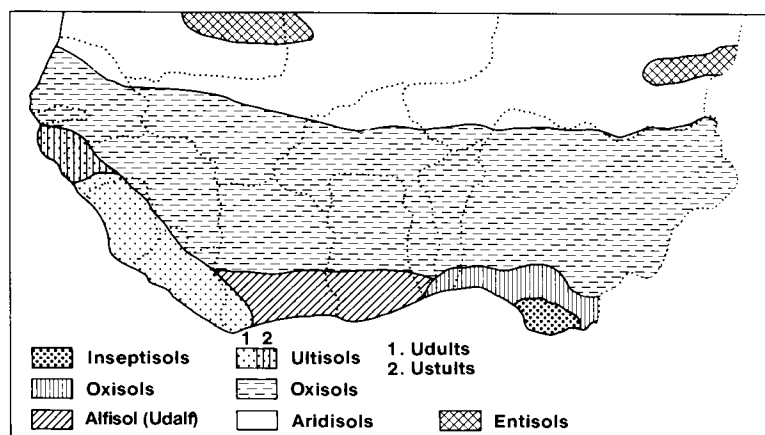


FIG. 5. Major soil groups in West Africa (from Okigbo 1980). See Table 18 for nitrogen contents.

TABLE 12. Continued.

Litter	Standing deadwood		Total N	
	N (%)	Biomass (10 ³ kg/ha)	Local (10 ³ kg/ha)	Re- gional (10 ⁹ kg)
1.1 ¹	2.5 ¹	0.18 ¹	0.6	15.6
1.4 ²	17 ²	0.21 ²	0.7	2.3
1.3	70 ⁸	0.2 ²	3.1	2.5
1.4 ¹⁷	0.9 ¹⁸	0.3 ¹⁹	0.5	14.4
1.3 ¹⁹	92 ²⁰	0.3 ²⁰	1.0	3.2
1.4 ²⁸	121 ²⁶	0.34 ²⁶	1.5	1.2
0.96 ³⁷	<0.1 ²⁹	na	<0.1	0.9
0.88 ⁴⁶	<0.1 ⁴⁷	na	1.0	8.3
0.25 ⁵²	<0.1	na	0.7	2.2
0.34 ⁶¹	<0.1	na	4.5	10.5
0.55 ⁶³	<0.1 ⁶³	na	0.2	1.9
na	<0.1	na	<0.1	0.5
				63.5

cent nitrogen and that current understanding and methodologies preclude accurate predictions of rates even within given vegetation/precipitation zones. Nevertheless, for most West African systems mineralization rates are likely to be between 2 and 10% of total soil N per year (de Rham 1970, Bernhard-Reversat 1974, 1977b, 1981, 1982, Jones and Wild 1975, Greenland 1980, Singh and Balasubramanian 1980a, Wetselaar 1980); within this range, higher rates are likely to occur in forested sites and in sites recently cleared, lower rates in savannas and grasslands, and low to moderate rates in the Sahel and in systems cropped for >2-3 yr.

THE WEST AFRICAN NITROGEN BALANCE

The overall N balance in West Africa (Fig. 6) portrays a cycle dominated by inputs from both precipitation and N₂ fixation in noncultivated systems; by outputs via fire, hydrologic fluxes, and denitrification; and by internal immobilization of nitrogen in growing vegetation. The degree to which our budget balances (within 1%) is striking, particularly since each of the listed fluxes was calculated independently of the others. Because many of our estimates for these fluxes are

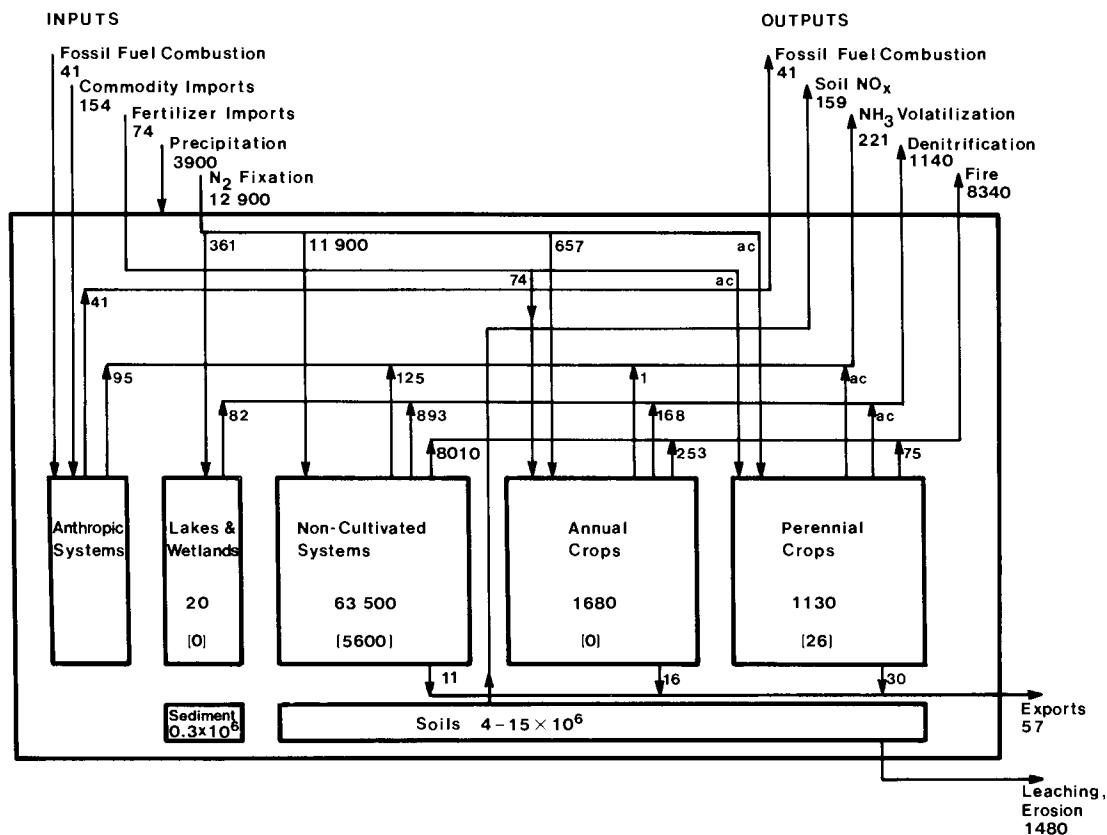


FIG. 6. The overall nitrogen cycle in West Africa in 1978. Flux values are 10⁶ kg/yr. Pool values (in boxes) are 10⁶ kg. Values in brackets within boxes represent N immobilization (10⁶ kg/yr). ac = included in Annual Crop flux.

TABLE 13. Nitrogen turned over and immobilized in vegetation in noncultivated systems.

System	Litterfall (nonwoody)			Litterfall (woody)			Root decomposition	
	Biomass (10 ³ kg/ha)	N content		Biomass (10 ³ kg/ha)	N content		Biomass (10 ³ kg/ha)	N content (%)
		(%)	(kg/ha)		(%)	(kg/ha)		(%)
Lowland rain forest								
Early successional	4.8 ⁶⁵	1.6 ⁶⁵	77	0.3 ⁶⁵	0.7 ⁶⁵	2.1	0.9 ⁶⁵	0.7 ⁶⁶
Mid-successional	5.5 ⁶⁵	1.6 ⁶⁵	88	0.4 ⁶⁵	0.7 ⁶⁵	2.8	1.1 ⁶⁵	0.5 ⁶⁶
Mature	8.5 ⁶⁸	1.6 ⁶⁹	136	1.7 ⁷⁰	0.72 ⁷¹	12	1.9 ⁶⁶	0.6 ⁶⁶
Moist semideciduous forest								
Early successional	2.3 ⁶⁵	2.1 ⁶⁵	48	2.7	0.6	16	0.3 ⁶⁵	1.1 ⁶⁶
Mid-successional	2.5 ⁶⁵	2.1 ⁶⁵	53	11	0.6	66	0.5 ⁶⁵	0.9 ⁶⁶
Mature	7.0 ⁷⁴	2.1 ⁷⁴	147	15 ⁷⁴	0.60 ⁷⁴	88	0.8 ⁶⁶	0.9 ⁶⁶
Derived savanna grassland								
Early successional ²⁹	23	0.49	113	0.3	0.2	0.6	1.3 ⁶⁵	0.6
Late successional	14 ⁷⁵	0.62 ⁷⁶	84	3.3 ⁷⁶	0.21 ⁷⁶	6.9	14 ⁷⁷	0.63 ³⁸
Guinea savanna woodland								
Early successional ⁴⁷	7.7	0.44	34	<0.1	0.2	<0.1	4.3 ⁷⁸	0.3 ⁷⁸
Late successional	4.6 ⁷⁹	0.53 ⁸⁰	24	2.6 ⁸¹	0.21 ⁸²	5.5	2.0 ⁷⁸	0.3 ⁷⁸
Sahel bushland								
Fallow, grazed	1.6 ⁶³	0.5	8	0.16 ⁶³	0.64 ⁶³	1.0	2.3 ⁶³	1.0 ⁶³
Subdesert grassland								
Unused, grazed ⁶⁴	0.2	0.5	1	<0.1	0.6	0.1	0.2	1.0
Total								

¹ Based on 5-yr-old lowland rain forest (1850 mm annual precipitation) in Zaire (Bartholomew et al. 1953).

² Based on 18-yr-old lowland rain forest as in note 1.

³ Based on lowland rain forests in Ivory Coast: Banco Plateau (2100 mm precipitation), Banco Valley (2100 mm), and Yapo (1740 mm) (Bernhard-Reversat 1970, 1972, 1975a, 1977, Bernhard-Reversat et al. 1978). Banco Valley sites are not included in standing biomass estimates.

⁴ 8.0–9.0 × 10³ kg/ha, *n* = 2; plus 1.5 × 10³ kg/ha of liana roots. See footnotes 3 and 9.

⁵ 425–480 × 10³ kg/ha, plus 15 × 10³ kg/ha lianas. See notes 3 and 9.

⁶ Estimate based on woody litter % N (see note 71).

⁷ Huttel (1975), Bernhard-Reversat et al. (1978; see note 3). Does not include tap roots but does include 7.5 × 10³ kg/ha lianas (see note 9).

⁸ Estimate based on percent of wood dead (13%) in mid-successional forest.

⁹ Includes vine biomass based on 24 × 10³ kg/ha total vine biomass (from note 3 but not Banco Valley site) and 1:10:5 estimated leaf: wood: roots biomass ratio.

¹⁰ Based on (a) 6-yr-old forest in southern Nigeria (1830 mm annual precipitation; Nye and Hutton 1957) and (b) 6-yr-old forest in western Nigeria (1300 mm; Jaiyebo and Moore 1964).

¹¹ 5.2–5.3 × 10³ kg/ha, *n* = 2; see note 10.

¹² 1.2–2.0 % N, *n* = 2; see note 10.

¹³ 27–28 × 10³ kg/ha, *n* = 2; see note 10.

¹⁴ 0.3–0.8% N, *n* = 2; see note 10.

¹⁵ Nye and Hutton (1957).

¹⁶ 6–14 × 10³ kg/ha, *n* = 2; see note 10.

¹⁷ 1.1–1.8% N, *n* = 2; see note 10.

¹⁸ Estimate based on percent of wood dead (3%) in early 2° lowland rain forest.

¹⁹ Based on 20-yr-old Ghana forest (1520 mm precipitation; Nye 1958).

²⁰ Estimate based on percent of wood dead in mature forest.

²¹ Based on (a) 20+ yr old successional forest in Ghana (1500 mm precipitation; Nye 1958), and (b) 40–50 yr old forest in Kade, Ghana (1650 mm; Greenland and Kowal 1960).

²² 6–26 × 10³ kg/ha, *n* = 2; see note 21.

²³ 1.9–2.7% N, *n* = 2; see note 21.

²⁴ 112–188 × 10³ kg/ha, *n* = 2; includes total lianas if given separately; see footnote 21.

²⁵ 0.3–0.5% N, *n* = 2; see note 21.

²⁶ Greenland and Kowal (1960).

²⁷ 2.3–5.6 × 10³ kg/ha, *n* = 2; see note 21.

²⁸ 1.3–1.5% N, *n* = 2; see note 21.

²⁹ Based on 4 derived savannas 1, 2, 3 and 4 yr old in Ghana (890 mm precipitation; Nye 1958).

³⁰ 3–13 × 10³ kg/ha, *n* = 4; see note 29.

³¹ 0.67–2.3% N, *n* = 4; see note 29.

³² 0.1–10 × 10³ kg/ha, *n* = 4; see note 29.

³³ *n* = 1; see note 29.

³⁴ 1.9–3.9 × 10³ kg/ha, *n* = 3; see note 29.

³⁵ 0.58–0.8% N, *n* = 4; see note 29.

³⁶ <0.1–4.6 × 10³ kg/ha, *n* = 4; see note 29.

TABLE 13. Continued.

Root decomposition N content (kg/ha)	Throughfall N (kg/ha)	Biomass accretion N (kg/ha)	Total N uptake	
			Local (kg/ha)	Re-gional (10 ⁹ kg)
6.3	30 ⁶⁷	114 ¹	229	6.2
5.5	34 ⁶⁷	39 ¹	170	0.2
11	52 ³	<0.1	211	0.2
3.3	4 ⁶⁷	70 ⁷²	141	4.0
4.5	4 ⁶⁷	24 ⁷³	152	0.5
7.2	12 ⁷⁴	<0.1	254	0.2
7.8	1	3.8 ⁷²	126	0.8
87	1	<0.1	179	2.9
13	1	8 ⁷²	56	1.8
6.0	1	<0.1	37	4.4
24	<0.1	<0.1 ⁶³	33	1.0
2.0	<0.1	<0.1	3	0.2
				22.5

³⁷ $n = 1$; see note 29.

³⁸ Based on 10-yr-old mature derived savanna in Ghana (890 mm precipitation; Nye 1958) and 5 derived savannas at Lamto, Ivory Coast (≈ 1300 mm; Menaut and Cesar 1979). Biomass values are maximum annual values, and leaf:litter ratio is assumed to be same at time of maximum biomass as at time of $\approx 60\%$ maximum. Litter includes herbaceous biomass only.

³⁹ $1.5-8.41 \times 10^3$ kg/ha, $n = 8$; from references in note 38 and Isichei and Sanford (1980) for Olokomeji, Nigeria (1230 mm) derived savanna, with assumption that maximum standing biomass is $\approx 50\%$ of total annual leaf litterfall (Menaut and Cesar 1979; and Oguntala 1980 for Olokomeji, Nigeria).

⁴⁰ 0.6-2.1% N, $n = 2$; Nye (1958; see note 38) and Isichei and Sanford (1980; see note 39).

⁴¹ $<0.1-54 \times 10^3$ kg/ha, $n = 6$; see note 38.

⁴² Nye (1958); see note 38.

⁴³ $21-43 \times 10^3$ kg/ha, $n = 5$; Menaut and Cesar (1979; see note 38).

⁴⁴ Nye (1958).

⁴⁵ $1.2-4.6 \times 10^3$ kg/ha; see note 38.

⁴⁶ Oguntala (1980).

⁴⁷ Based on (a) 1-yr-old unburned fallow savanna at Oyo, Nigeria (1200 mm precipitation; Egunjobi 1974) and (b) < 6 yr old *Imperata* savanna in Ghana (Nye 1958).

⁴⁸ $4-50 \times 10^3$ kg/ha, $n = 2$; see note 47.

⁴⁹ 0.3-0.4% N, $n = 2$; see note 47.

⁵⁰ Nye (1958); see note 47.

⁵¹ $0.6-3.0 \times 10^3$ kg/ha, $n = 2$; see note 47.

⁵² 0.2-0.3% N, $n = 2$; see note 47.

⁵³ Based on two Guinea *Andropogon* savannas 6-20 and 20+ yr old in Ghana (1500 mm precipitation; Nye 1958).

⁵⁴ $2-13 \times 10^3$ kg, $n = 5$; based on references in note 53 and (a) southern Guinea high grass savanna woodland at Old Oyo, Nigeria, (b) northern Guinea lowgrass savanna at Kainji Lake, Nigeria, and (c) northern Guinea *Isobelinia* woodland savanna at Kainji Lake, Nigeria (Isichei and Sanford 1980).

⁵⁵ 0.2-0.6% N, $n = 5$; based on same sites as in note 54.

⁵⁶ $<0.1-54 \times 10^3$ kg/ha, $n = 2$; see note 53.

⁵⁷ Nye (1958); see note 53.

⁵⁸ $3.8-4.2 \times 10^3$ kg, $n = 2$; see note 53; does not include woody vegetation.

probably only correct to a factor of two, however, the very small difference between outputs plus immobilization and inputs appears fortuitous, and the overall balance should be interpreted with care.

To a substantial degree, nitrogen fluxes in rangelands, forests, and other noncropped areas dominate the regional budget. For example, N_2 fixation in cultivated areas appears to be only $\approx 5\%$ of that in noncultivated regions, and over 96% of the nitrogen that is lost via fires in West Africa in 1978 appears to have occurred in noncultivated regions. Nevertheless, a large proportion of these losses is indirectly the result of cultivation: cultural practices drive both the establishment of early successional bush fallows and eventual land clearing; both of these processes lead to conditions highly favorable for specific nitrogen cycle fluxes. Almost half of the nitrogen fixed in noncultivated systems, for example, appears to be fixed in early successional (0-6 yr old) forests (Table 2).

⁵⁹ 0.3-0.39% N, $n = 2$; see note 53.

⁶⁰ $1.2-1.6 \times 10^3$ kg/ha, $n = 2$; see note 53.

⁶¹ 0.3-0.39% N, $n = 2$; see note 53.

⁶² Includes tree leaves: 89 kg/ha; see note 63.

⁶³ Based on grazed Sahel savanna at Fete Ole, Senegal (200-300 mm precipitation; Bille 1977).

⁶⁴ Subdesert fluxes and pools assumed to be 10% of those in Sahel.

⁶⁵ Direct data unavailable; flux assumed to be same proportion of that in mature systems as was biomass in Table 12, and N content same as for mature system.

⁶⁶ No data available; assumes 30-yr root turnover rate for mature forests (Jordan and Escalante 1980) and root litter N content same as for root biomass N (Table 12).

⁶⁷ No data available; estimate assumes proportion of throughfall in nonmature vs. mature is same as for leaf biomass (Table 12).

⁶⁸ $8-9 \times 10^3$ kg/ha, $n = 3$; includes reproductive-tissue litter; see note 3.

⁶⁹ 1.3-1.8% N, $n = 3$; includes reproductive-tissue litter; see note 3.

⁷⁰ $1.1-2.6 \times 10^3$ kg/ha, $n = 3$; see note 3.

⁷¹ 0.6-0.8% N, $n = 3$; see note 3.

⁷² (Living biomass N minus litterfall, throughfall, and root decomposition N) divided by 4 yr (forests) or 2 yr (savannas).

⁷³ Based on amount immobilized in early successional vs. late successional lowland rain forest.

⁷⁴ Based on 40-50 yr old successional forest at Kade, Ghana (1650 mm precipitation; Nye 1961).

⁷⁵ $7-19 \times 10^3$ kg/ha, $n = 6$; based on Menaut and Cesar (1979) and Isichei and Sanford (1980) as in note 39.

⁷⁶ Isichei and Sanford (1980); see note 39.

⁷⁷ $10-19 \times 10^3$ kg/ha, $n = 5$, for herbs; plus 0.2×10^3 kg/ha for woody roots if assume decomposition = production (Menaut and Cesar 1979).

⁷⁸ Direct data unavailable; flux assumed to be same proportion of biomass as in derived savanna, and N content same as in root biomass (Table 12).

⁷⁹ $4-7 \times 10^3$ kg/ha, $n = 4$; Dommergues (1963) for southern Guinea savanna at Mokwa, Nigeria (1180 mm precipitation) and Isichei and Sanford (1980) as in systems in note 54.

⁸⁰ 0.5-0.6% N, $n = 3$; Isichei and Sanford (1980).

⁸¹ $0.7-6.7 \times 10^3$ kg/ha, $n = 4$; see note 79.

⁸² Isichei and Sanford (1980).

TABLE 14. Nitrogen in West African lakes. Local units are mg/L (water column) and mg/ha (sediments to 30 cm). na = not available.

Component	Local N concentration			Regional mass (10 ⁹ kg)
	Mineral	Organic	Total	
Water column	0.06*	0.04	0.10	0.02†
Sediments	na	na	90‡	318†
Total				318

* For Lake Volta: Okali and Attionu (1974) report 0.02–0.06 mg/L; Obeng (1975) reports 1.1 mg/L.

† Based on total area (8.0 × 10⁶ ha) and volume (0.5 × 10¹² km³) of West African lakes (UNESCO 1978; FAO 1979a); seasonal maximum area is assumed for Lake Chad.

‡ To depth of 30 cm assuming sediment density of 2.0 g/cm³ and 1.5% N (range for temperate lakes: 0.1–4.0% N; Macgregor and Keeney 1975).

In contrast to nitrogen cycles in temperate regions, direct anthropic/industrial sources and sinks of nitrogen in West Africa are minor. Fertilizer nitrogen in West Africa in 1978 (14 × 10⁶ kg produced plus 74 × 10⁶ kg imported) and nitrogen produced during fossil fuel combustion (41 × 10⁶ kg) together were a small fraction of the nitrogen produced biologically ≈ 12 800 × 10⁶ kg; this contrasts sharply with estimates for global fluxes that show anthropic sources of fixed nitrogen approaching the importance of biological sources for the planet as a whole (CAST 1976, Söderlund and Svensson 1976). Keeney (1979) estimated that in Wisconsin in 1974, nitrogen fertilizer inputs alone were ≈ 30% of inputs from biological N₂ fixation.

TABLE 15. Annual gaseous nitrogen losses from West Africa via fire (NO_x-N volatilization), NH₃-N volatilization, and denitrification (N₂O-N and N₂-N emission). * na = not available.

System	Fire		Denitrification		NH ₃ volatilization	
	Local (kg/ha)	Regional (10 ⁹ kg)	Local (kg/ha)	Regional (10 ⁹ kg)	Local (kg/ha)	Regional (10 ⁹ kg)
Lowland rain forest						
Cleared ¹	na	2.8 ²	20 ³	0.10	na ³	<0.01
Successional	<0.1	<0.01	10 ⁴	0.3	<0.1 ⁵	<0.01
Mature	<0.1	<0.01	20 ⁴	<0.01	<0.1 ⁵	<0.01
Moist semideciduous forest						
Cleared	na	2.7 ²	20 ³	0.10	na ³	<0.01
Successional	<0.1	<0.01	10 ⁴	0.3	<0.1 ⁵	<0.01
Mature	<0.1	<0.01	20 ⁴	<0.01	<0.1 ⁵	<0.01
Derived savanna grassland						
Fallow, grazed	14 ⁶	0.3	1 ⁷	0.02	<0.1	<0.01
Guinea savanna woodland						
Fallow, grazed	13 ⁸	1.9	1 ⁷	0.2	0.6	0.07
Sahel bushland						
Grazed, fallow	6 ⁹	0.2	1 ¹⁰	0.03	0.6 ¹¹	0.02
Subdesert grassland						
Grazed, unused	0.6 ¹²	<0.1	0.1 ¹²	<0.01	0.5 ¹³	0.04
Wetlands						
Lakes	<0.1	<0.01	10 ¹⁴	0.08	<0.1 ¹⁵	<0.01
Cultivated systems						
Forests ¹⁶	na	na	5 ¹⁷	0.08	<0.1 ¹⁵	0.01
Savanna	na	na	2 ¹⁹	0.08	<0.1 ¹⁸	0.01
Sahel	na	na	1 ¹⁰	<0.01	<0.1	0.01
Lowland rice	na	na	5 ²⁰	<0.01	1 ²¹	<0.01
Total cultivated		0.3 ²²		0.2		<0.01
Total		8.3		1.1		0.1

* Gaseous losses from fertilizer and manure are included in Table 16, and losses from other NO_x sources are included in text. Regional N losses (10⁶ kg) are based on system extensions (Fig. 3).

¹ Assumes 5% of all mature forest, 10% of all mid-successional growth, and 17% of all early successional growth was cleared in 1978; thus 5.0 × 10⁶ ha of lowland rain forest and 5.2 × 10⁶ of semideciduous forest is presumed to have been deforested in 1978.

² See Table 12 for N in each system type; assumes that 95% of nonharvested biomass in forests is burned upon clearing (Vitousek et al. 1980); harvested biomass = industrial roundwood production (FAO 1979e), with 60% assumed to have been taken from mature lowland rain forest and 40% from mature semideciduous forest.

³ Denitrification + leaching N losses = 50 kg·ha⁻¹·yr⁻¹ (Vitousek et al. 1980); estimate assumes that denitrification in cleared forest is 1.4 × denitrification in successional sites since leaching + denitrification in cleared sites is ≈ 1.4 × that in successional sites (Vitousek et al. 1980).

⁴ Vitousek et al. (1980): N losses of <20 kg·ha⁻¹·yr⁻¹; Greenland (1962): "measurable"; mature forest soils assumed to denitrify at rates close to those of cleared forest (Robertson and Tiedje 1984).

TABLE 16. Ammonia volatilized from commercial fertilizer and manure. LM = live mass. na = not applicable.

Source	N production		NH ₃ volatilized	
	By local LM (kg·kg ⁻¹ ·yr ⁻¹)	Regional (10 ⁶ kg/yr)	Proportion (%)	Total N (10 ⁶ kg/yr)
Commercial fertilizer ¹				
Urea-N	na	21	30 ²	6.1
Inorganic N	na	68	10 ³	6.8
Manure				
Human	0.09 ⁴	653	2 ⁵	13
Extensive livestock	0.14	1364	10 ⁶	(136) ⁷
Farmyard animals	0.15 ⁸	135	50 ⁹	68
Native animals	0.14	10	10 ⁶	1.0
Total manure				82
Total				95 ¹⁰

¹ FAO (1979*f*) and assuming urea-N = 23% of all commercial N-fertilizer consumed (IFDC 1977).

² M. Ganry (*personal communication*).

³ Singh and Balasubramanian (1980*a*).

⁴ From Table 11.

⁵ Söderlund and Svensson (1976); assumes 20% deposited on soil surface (Singh and Balasubramanian 1980*a*).

⁶ Healy et al. (1970).

⁷ Includes cattle, sheep, goats, camels, and 50% of horses and asses; included in Table 15 as NH₃ volatilized from grazed systems and calculated here as check only (see text; also see footnote 10).

⁸ Loehr and Hart (1970).

⁹ Eriksson (1959*a*) in Söderlund and Svensson (1976).

¹⁰ Does not include NH₃ volatilized from extensive livestock. See note 7.

DISCUSSION

There are two major justifications for synthesizing elemental cycles at the regional, subcontinental level: to better estimate terrestrial fluxes to global pools and thereby improve predictions of the effects of anthropic disturbance on climate, radiation balances, and other global processes; and to identify fluxes in particular

systems that play key roles in the nitrogen economies and consequently the productivities of those systems.

Of major concern to atmospheric chemists are the fluxes of trace gases to the atmosphere from terrestrial sources. Such gases, among them methane, carbon monoxide, nitrous oxide (N₂O), and other nitrogen oxides (NO_x), influence atmospheric chemistry and earth

←

⁵ Main internal transfer except on cleared sites (Vitousek et al. 1980, Denmead et al. 1976); losses from cleared sites included in leaching losses.

⁶ N losses of 13–15 kg·ha⁻¹·yr⁻¹, *n* = 2; Isichei and Sanford (1980); assumes annual burn cycle (Penning de Vries et al. 1980*b*); Vidal and Fauche (1962): 20 kg·ha⁻¹·yr⁻¹; Nye and Greenland (1960): 28; Singh and Balasubramanian (1980*a*): 25; Penning de Vries et al. (1980*b*): 14.

⁷ Wetselaar (1980): N loss of 0 kg·ha⁻¹·yr⁻¹; Penning de Vries et al. (1980*b*) and Jones and Wild (1975): "low"; Greenland (1962): "low" (young successional vegetation) to "measurable" (late successional).

⁸ N losses of 12–14 kg·ha⁻¹·yr⁻¹, *n* = 3; see footnote 6.

⁹ Penning de Vries et al. (1980*b*) = N losses of 3 kg·ha⁻¹·yr⁻¹; Vidal and Fauche (1962): 10 kg·ha⁻¹·yr⁻¹; assumes 2-yr burn cycle (Penning de Vries et al. 1980*b*).

¹⁰ Penning de Vries et al. (1980*b*): N losses of 0 kg·ha⁻¹·yr⁻¹; Hahn and Junge (1977): ≈1 for Cape Verde desert and ≈0.5 for vegetated sand dunes if 5:1 N₂O:N₂ ratio is assumed; Jones and Wild (1975): "low."

¹¹ Greenland (1980); Woodmansee et al. (1978) = N losses of 0.5 kg·ha⁻¹·yr⁻¹; West and Skujins (1977): 1; Penning de Vries et al. (1980*b*): 1+; Wetselaar (1980): 0.0.

¹² Assumed to be 10% of Sahel fluxes.

¹³ West and Skujins (1977): N losses of 1 kg·ha⁻¹·yr⁻¹; Wetselaar (1980): 0 kg·ha⁻¹·yr⁻¹.

¹⁴ Keeney et al. (1971) and Chen et al. (1972): N losses of 12 kg·ha⁻¹·yr⁻¹ for Wisconsin lake sediment; NAS (1978): 8 kg·ha⁻¹·yr⁻¹ for Florida lake.

¹⁵ Patrick and Mahapatra (1968).

¹⁶ Less the area in rice.

¹⁷ Ayanaba and Veldkamp (1980): N losses of ≈0 kg·ha⁻¹·yr⁻¹; Hainnaux et al. (1980): <20; Greenland (1962, 1980): "low."

¹⁸ Greenland (1980).

¹⁹ Singh and Balasubramanian (1980*a*): N losses of 0 kg·ha⁻¹·yr⁻¹; see note 17.

²⁰ Ayanaba and Veldkamp (1980): N losses of 0 kg·ha⁻¹·yr⁻¹; Garcia (1974): 0; for fertilized rice, Denmead et al. (1979): 120–240 kg·ha⁻¹·yr⁻¹ if 5:1 N₂O:N₂ ratio is assumed; Reddy (1982): 100.

²¹ Greenland (1980), Reddy (1982).

²² From Table 7.

TABLE 17. Nitrogen lost in leaching, runoff, and erosion from West Africa, based on Niger River fluxes.

Component	Flux
Niger River watershed	
Annual flow (10^9 m ³ /yr)	218 ¹
NO ₃ ⁻ -N (g/m ³)	2.4 ²
NH ₃ ⁺ -N (g/m ³)	0.014 ³
Sediment yield (10^9 kg/yr)	35 ⁴
Watershed area (10^6 ha)	209 ⁵
N discharge (kg/ha)	
NO ₃ ⁻ -N + NH ₄ ⁺ -N	2.5
Organic N	1.7 ⁶
Region	
N loss (10^9 kg/yr)	1.5 ⁷

¹ Ledger (1969): 221×10^9 m³/yr; Leopold (1965): 192; Livingston (1963): 292; Martins (1982): 168.

² Livingston (1963): <0.25–0.5 g/m³; Imevbore (1970): 0.6–8.6; van Bennekom et al. (1978): 0.1.

³ van Bennekom et al. (1978).

⁴ NEDECO (1959): 21×10^9 kg/yr; Grove (1972): 38; Sarntheim and Walger (1974): 60; Martins (1982): 19.

⁵ Livingston (1963): 205×10^6 ha; UNESCO (1978): 209×10^6 ha.

⁶ Assumes 1% mean N content.

⁷ Based on total West Africa area (606×10^6 ha) less sub-desert (72.6×10^6 ha) and desert (180×10^6 ha) areas; see Fig. 3.

radiation balances far out of proportion to their abundance (Crutzen 1983), and concentrations of many appear to be increasing. Nitrous oxide fluxes have received particular attention since the mid-1970's, when it was suspected that agricultural fertilizers might indirectly contribute substantial amounts of N₂O to the atmosphere (CAST 1976, NAS 1978).

Recent evidence from temperate sites suggests that N₂O fluxes are also related to the successional status of natural vegetation (Melillo et al. 1983, Robertson and Tiedje 1984), globally a far more important source of N₂O than agriculture (Duxbury et al. 1982, Banin et al. 1984). If N₂O fluxes in tropical successions are also high after clearing and in old-growth communities, then tropical deforestation and widespread changes in the lengths of crop fallow periods may also be increasing global fluxes. However, we calculate, based on West African data, that such changes in tropical land use are likely not contributing significantly to increased N₂O fluxes, and that fluxes may in fact be lower now than in the past. In Table 19 we present relative estimates of denitrification fluxes (N₂ + N₂O) from rain forest at three successional stages, and extrapolate to regional fluxes now vs. fluxes in the precolonial period based on likely changes in the extents of these successional stages. If certain assumptions underlying these estimates are correct, i.e., if denitrification is highest in cleared and mature forest and if land use distributions are reasonably accurate, and if the proportion of denitrification gas product that is N₂O does not change systematically in any given succession, then present N₂O fluxes from West African rain forests may be only 50–75% of precolonial fluxes.

Atmospheric concentrations of N₂O at present appear to be increasing 0.2–0.4% per year globally (Weiss 1981, Kahlil and Rasmussen 1984). If the calculations above are correct, this increase is perhaps being significantly attenuated by shifts in tropical land use. This attenuation, however, if present, will not likely persist. With mature forests disappearing and with continued

TABLE 18. Soil N pools (to 150 cm depth). Soil classification follows the FAO system; for approximations to FDA system see Asamoia (1980) and Fig. 5. Data from FAO-UNESCO (1977) and Asamoia (1980) unless otherwise noted.

Soil type	Extent (10^6 ha)	N content by depth (%)				Total N*	
		0–20 cm	20–50 cm	50–100 cm	100–150 cm	Local (10^3 kg/ha)*	Regional (10^{12} kg)
Acrisols	41	0.06–0.69	0.04–0.06	0.04–0.05	0.02–0.04	7.1–28	0.3–1.1
Cambisols	8.7	0.20–0.49	0.02–0.05	0.01–0.03	0.01–0.03	8.4–22	<0.1–0.2
Ferralsols	21	0.1–1.0	0.06–0.29	0.04–0.07	0.02–0.04	10–42	0.2–0.9
Gleysols	10	0.09–0.12	0.03–0.18	0.02–0.14	0.01–0.14	6.5–34	<0.1–0.3
Lithosols	94	0.02†	0.02†	0.02†	0.01†	3.8	0.4
Fluvisols	14	0.05	0.02	0.02†	0.01†	4.7	<0.1
Luvisols	96	0.05–0.76	0.02–0.11	0.02–0.06	0.02–0.05	5.5–36	0.5–3.5
Nitisols	21	0.02–0.49	0.02–0.65	0.01–0.05	0.01–0.03	3.9–49	<0.1–1.0
Arenosols	85	0.04–0.8	0.02–0.8	0.01–0.02	0.01–0.02	4.6–67	0.4–5.7
Regosols	58	0.006	0.005	0.005	0.007	1.4	<0.1
Vertisols	5.6	0.04–0.48	0.02–0.24	0.22	0.12	26–47	0.1–0.3
Planosols	2.1	0.03–0.05	0.02	0.004	0.003	2.3–3.0	<0.1
Xerosols	60	0.07	0.06	0.04	0.02†	9.3	0.6
Yermosols	81	0.32	0.023	0.01†	0.01†	12	1.0
Solonchaks	0.7	0.08	0.07	0.04†	0.02†	8.0–9.0	<0.1
Azonal‡	2.8	0.0001†	0.0001†	0.0001†	0.0001†	0.1	<0.1
Total	602						3.8–15

* Assumes mean bulk density of 1.6 g/cm³ for soils >85% sand, 1.5 g/cm³ for those >50% sand, 1.4 g/cm³ for >10% sand, and 1.2 g/cm³ for <10% sand.

† Estimated.

‡ Rock debris and salt flats.

TABLE 19. Estimated denitrification fluxes ($N_2 + N_2O$) from West African rain forests before widespread changes in land use relative to likely present-day fluxes. See also Table 15.

Biome, land use	Local N flux (kg/ha)	Present regional		Earlier regional	
		Extent (10^6 ha)	N flux (10^6 kg/yr)	Extent (10^6 ha)	N flux (10^6 kg/yr)
Lowland rain forest					
Cleared	15–25	5	75–125	1	15–25
Successional	1–10	25	25–250	15	15–150
Mature	15–25	1	15–125	15	225–375
Total			115–400		255–550

population pressures resulting in more frequent clearings of mid-successional forests, N_2O fluxes from rain forest regions may now be increasing towards pre-colonial levels. Measurements of N_2O fluxes under successional vegetation in tropical regions would greatly help to clarify these trends.

We were surprised by the overwhelming importance of fire as a vector of nitrogen loss in West Africa; almost 75% of all nitrogen lost is volatilized from burning biomass. Two-thirds of this loss occurs when high-biomass rain forest vegetation is cleared. Because fire is an integral part of the widespread bush fallow cropping system, this rate of loss is not likely to decline significantly in the foreseeable future, and probably will increase, in fact, as population pressures reduce fallow periods. Concomitantly, N immobilization by mid-successional vegetation will decrease.

Fire has important implications at both the regional and local scales. Trace gas release (Crutzen et al. 1979) and carbon aerosol loading of the atmospheric boundary layer (Seiler and Crutzen 1981) may have widespread climatic effects. Locally, the nitrogen (≈ 700 kg/ha) that is available for loss when successional rain forest is burned (Table 12) is a substantial loss relative to crop uptake rates that are probably only 10–20% of this amount per year. Any management practice that could reduce this loss (by inhibiting sprouts and pests by some means other than fire, and thereby allowing slash to remain on site to decompose slowly) could significantly improve the availability of nitrogen to subsequent crops.

Overall, the generality of our West Africa model depends to a large degree on climatic (especially rainfall) fluctuations. Our reservoir and flux values reflect normal precipitation regimes; under other conditions both absolute and relative values will differ. Under drought conditions, for example, inputs from precipitation and N_2 fixation, outputs via denitrification and leaching, and biological immobilization will markedly decline, while nitrogen lost via fire may be substantially elevated. The converse may be true in unusually wet years, although precipitation nitrogen inputs will likely not differ much from normal years. Even in the absence of climatic changes, however, population changes will dramatically affect overall fluxes. As illustrated above for N_2O , moderate changes in land use can dramati-

cally alter regional balances, and land use is driven by population pressure. In particular, shorter fallow intervals will enhance many of the loss vectors and perhaps lead eventually to a regional balance that shows a net loss of nitrogen. Such an effect may be occurring now if total soil nitrogen is not in the regional steady state assumed in this synthesis. In the absence of detailed soil information, it appears at present that the region is receiving about as much nitrogen as is lost each year.

There is considerable room for improvement for most of the N-cycle estimates presented in our budget. Particularly needed are better estimates of land use categories and direct measures of N_2 , N_2O , and NO_x fluxes in noncropped systems. Also needed are various flux measurements for similar systems at different stages of secondary succession; these measures are especially critical for evaluating the impact of increasing population pressures on atmospheric processes and on nitrogen loading of coastal and pelagic marine systems.

ACKNOWLEDGMENTS

We are indebted to the librarians at the Swedish University of Agricultural Sciences library, whose ability to locate sometimes obscure documents made much of this work possible, and to a number of scientists in West Africa and elsewhere who willingly shared unpublished data. We also thank E. Wishinsky for help with compiling several of the tables. D. R. Keeney read and made helpful comments on an early draft. Principal financial support was provided by a SCOPE-Andrew H. Mellon Foundation postdoctoral fellowship to G. Philip Robertson.

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