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Plant Ecology in West Africa
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CHAPTER 5

Savanna

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1. Definition of savanna

1. Vegetation

Fosberg (1961), in an attempt to set up a standard, international set of ecological terms, called savanna any 'closed grass or other predominantly herbaceous vegetation with scattered or widely spaced woody plants' and subdivided this into tall savanna, in which the herbaceous cover is at least 1 m high, and low savanna in which it is less. Savanna is separated from 'steppe' on the basis of the herbaceous cover being closed in savanna but not closed in steppe, the latter thus including 'desert scrub'. This is essentially a broad growth-form definition and is unsatisfactory on two counts; savanna as now generally conceived of has a cover predominantly of grass, not of any other herbaceous material; savanna may or may not have woody plants, and if they are present they may be either scattered or fairly dense.

Other attempts to define savanna by its vegetation have been made. Beard (1967) reviews the terms agreed upon at Yangambi by the Scientific Council for Africa South of the Sahara (CSA, 1956). These are more elaborate and exact than the simple definition stated above but also broadly depend on growth form, together with structural features. Savanna is described as a 'formation of grasses at least 80 cm high, forming a continuous layer dominating a lower stratum. Usually burnt annually. Leaves of grasses flat, basal, and cauline. Woody plants usually present.' This is divided into savanna woodland — 'trees and shrubs forming a canopy which is generally light'; tree and shrub savanna — 'savanna as defined, with trees and shrubs scattered'; and grass savanna — 'trees and shrubs generally absent'. Steppe is defined: 'Open herbaceous vegetation, sometimes also with woody plants. Usually not burnt. Perennial grasses usually less than 80 cm high, widely spaced. Leaves of grasses narrow, rolled, or folded, mainly basal. Annual plants very often are abundant between perennials.' Formations associated with savanna are also defined. Woodland:

'Open forest; tree stratum deciduous of small or medium-sized trees with crowns more or less touching, the canopy light; grass stratum sometimes sparse, or mixed with other herbaceous and suffrutescent vegetation. Sometimes evergreen or partly evergreen.' Thicket: 'Shrubby vegetation, evergreen or deciduous, usually more or less impenetrable, often in clumps, with grass stratum absent or discontinuous.' Scrub: 'Open shrub-land, as opposed to closed thicket.' A major difficulty here is the lack of a clear functional separation between 'savanna woodland' and 'woodland'.

2. *Climate*

Not all definitions of savanna, however, have been based on vegetation. Jaeger (1945) followed by Troll (1952) attempted to define savanna on climatic grounds with little reference to vegetation. 'Humid savannah' encompasses the climatic zone of tropical summer rain with a dry period of from 2.5 to 5 months; 'dry savannah', the regions of summer rain with a dry period of from 5 to 7.5 months; and 'thorn-scrub savannah', the regions with a dry period of from 7.5 to 10 months. Troll has pointed out that savanna always reflects a combination of edaphic, biotic, and anthropogenic factors, and therefore includes all forms, from treeless grasslands to forest. This definition of savanna rather mixes causative factors and appearance.

Trewartha (1954) in his modification of Koppen's world map, also views savanna fundamentally from the aspect of climate; he classes as tropical savanna areas with a distinct alternation of wet and dry seasons with rain in the summer generally exceeding 600 mm and sometimes up to 2000 mm. Walter (1973), however, in a world-wide review of savanna, places the approximate boundary of tree savanna at 400 mm, stating that at below this level only grass or grass and small woody plants occur.

His views (Walter, 1971, pp. 238–239), are similar to those of the early German plant geographers Schimper and Drude, as he looks upon savanna as 'the natural homogeneous zonal vegetation of the tropical summer rain zone showing a closed grass cover and scattered, individual woody plants, either shrubs or trees. This climatically conditioned savannah probably occurs in Africa only in areas with rainfall below 600 mm and corresponds to the "thorn-scrub" of Jaeger.' Where anthropogenic factors are important he uses the term 'secondary savannah'. He excludes 'woodland' and considers 'parkland savannah' (grassland with widely spaced trees, often selected for their economic importance) to be a mosaic of different communities. His climatic savanna is, then, comparable to the Sahel in West Africa which, however, does not always have a continuous cover of grass. Furthermore the grasses are predominantly annual and often patchy in distribution.

3. *Soil*

Still other workers have attempted to demarcate savanna according to edaphic considerations. Thus one of the conclusions of the 1964 IGU–Unesco symposium in Venezuela as reported by Adejuwon (1970) was that there are 'natural savannas which can be considered as edaphic climaxes.

It is certainly obvious in any West African region of forest margin or savanna that patches of open vegetation and forest or woodland occur in relation to soil character. Chachu (pers. comm.) and Milligan (1979) have pointed out how frequently the vegetation of the Kainji Lake National Park region in north-western Nigeria seems to be determined by soil depth. Associated with shallow soil are decreased moisture availability, increased leaching of nutrients, and increased soil temperature, all of which affect vegetation.

Ramsey and de Leeuw (1965a, b) have studied vegetation and soil parent material in northern Nigeria and have concluded that 'only in extreme cases does the parent material of the soil influence the composition of the arboreal vegetation and then mainly through the soil–water relationship'. Ahn (1970), however, reported that the geological boundary between Pre-Cambrian Birrimian formations and sandstone appears to determine the position of the forest–savanna boundary in Ghana. Hall (1977) has clearly demonstrated a demarcation of forest type and species composition in relation to broad soil type (tropical ferruginous–ferralitic).

However, such soil–vegetation relationships, as well as relationships between climate and soil and vegetation, obviously confuse cause and result: a definition of savanna should describe the physical thing that we are going to call 'savanna' rather than list the factors which we believe have brought it about.

4. *A synthetic definition*

From published descriptions of savanna and direct observation of savanna in West Africa, a definition may be arrived at: seasonal tropical vegetation in which there is a closed or nearly closed cover of grasses at least 80 cm high with flat, usually cauline, leaves; usually burnt annually; trees and shrubs at various densities most often present.

The fundamental quality which provides whatever physiognomic, structural, and physiological unity the concept of savanna may have is the presence of a nearly continuous ground cover of grass. Recently Menaut (1983a) has suggested that the most useful characterization of savanna is the ratio between above- and below-ground woody and grass biomass. Such a characterization would not only be useful on a local basis but also on a world-wide basis.

Seasonality, while having climatic implication of a wet and dry period, also implies physical change of the vegetation: the grasses mature, dry, and brown;

many of the trees and shrubs are deciduous. Annual burning indicates that we would not expect to find any considerable amount of dead vegetation accumulating on the ground. The use of the terms 'tree' and 'shrub' indicates that woody plants of at least two height classes are normally present. Trees are understood to be woody plants which at maturity are at least 3 m high, while shrubs are less than 3 m high. (It is more satisfactory to use height as a criterion rather than such often-times stated, but in practice ambiguous, criteria as 'having only one or several stems emerging from the ground'.)

For a discussion of the abiotic environment associated with such vegetation, see section III, below.

II. Fundamental processes of savanna systems

1. Stability as a functional aim

The definition of savanna adopted above is rightly based on gross observable features of the vegetation and necessarily ignores the functional dynamics of savanna as an ecosystem type. Before any discussion of the causes of savanna and before detailed description of West African savanna types and before consideration of their study and management, it may be helpful to summarize briefly the main processes of savanna as a system.

How much of a *system*, in the strict sense, savanna is may be debated, but if any assemblage of plants remains for an appreciable period of time, there must be a satisfactory relationship between the plants of the assemblage and between the plants and the abiotic environment and to this extent a *system* may be said to exist. This is not really saying anything except that if a group of plants survives, its survival must be possible. It is possible, however, to go further and agree that such assemblages are not static in species abundance and composition but change over time, the rate of change being inversely proportional to the adaptive fitness of the individual plants to each other and to their environment of animals, soil, and climate. In other words, environmental pressure and variation in organisms, brought about by immigration and by phenoplastic and genotypic variability, act together in such a way that the most successful forms (i.e. the forms most productive of propagules able to establish themselves and in turn reproduce) of the most successful species replace less successful forms or/and less successful species.

If, barring change in environment, plants are continually being replaced by better adapted ones, the rate of change will decline until it is so slow that the system is more or less stable (using 'stable' to mean 'constant' or 'unchanging'). But a complicating factor spoils this simple picture: each plant species, indeed each individual plant, changes the environment to varying degrees and in varying ways; thus the only condition under which a stable system can develop is that of the development of an assemblage of perfectly adapted plants which do not further change the environment.

The dynamics of the savanna ecosystem thus depend upon the stability of the abiotic environment and the level of adaptive fitness of the plants in that environment.

The climate of West Africa in recent geological times has been relatively unstable or 'capricious' as Livingstone has termed it in a recent review (1975). No part of the African continent has escaped serious climatic change during the past 20 000 years. During the Holocene, 10 000 – 7000 BP, there was great forest expansion, although the continent was never covered with moist forest, and large areas of grassland were present in East Africa very long ago. Dry conditions existed before the period of moist forest expansion (about 13 000 BP) and a gradual drying again occurred from 5000 to 3000 years BP. Livingstone considers the present biota to represent a lag concentrate of species that were able to persist through drier and cooler conditions than those of today. Thus, in the savanna, dry-adapted plants have been gradually infiltrated by some plants adapted to somewhat moister conditions. During the last 1000 years or less, much of the savanna has been subject to annual dry-season burning and in very recent times (perhaps only during the last 300–400 years) to extensive clearing and farming. Annual burning has constituted a stabilizing pressure by selecting species of a certain physiological/morphological fire-resistant type, and by tending to limit vegetation in number of individuals and to control the size-class distribution of individuals. On the other hand, cultivation, and to a lesser extent livestock grazing and browsing, not being regular in occurrence, have been destabilizing in effect. The repeated disturbance of natural vegetation at irregular intervals has destroyed much of the vegetation and has opened the area for immigration of colonizers or weeds, temporary inhabitants which are supplanted by other species when the disturbance is discontinued. It is thus obvious that any piece of savanna will vary in composition and structure according to its history of land use. Such local variations may be ignored for the time being and an attempt made to generalize the tendencies of change leading towards stabilization, and to the major processes of a more or less stable savanna vegetation.

2. *Mineral cycling*

Crucial for an assemblage of plants which long survives is efficient mineral cycling. If essential minerals in available form are present in finite supply and are not made available for reuse, the community will decline in productivity and eventually starve to death. The tropical climate of high temperature which increases the rate of mineralization of organic matter in the soil and of heavy seasonal rain which may bring about erosion, runoff, and leaching conspires to make tropical soils especially vulnerable to deterioration. In West African savanna regions, cultivated crops decline drastically in yield after only three or four years, because there is almost no nutrient cycling in a maize or millet or guinea-corn field. Surviving plant assemblages must avoid this. The main factors in nutrient conservation and cycling which allow a community of plants to persist are a multilayered canopy cover to lessen the impact of rain, a close network of roots to absorb nutrients as soon as they go into solution to prevent their loss by leaching or runoff, and adequate litter fall and decomposition to return nutrients to the soil for reuse. The ideal savanna would, then, have at least two strata of woody plants and a cover of grass and forbs.

Typical Guinea savanna may roughly be described as having an A stratum of large trees at least 7 m in height and a B stratum of woody plants less than 7 m high. Tree canopy cover in northern Guinea savanna in Nigeria ranges, on an average, from about 25 to 35 per cent. (Such cover means a density of trees at least 30 cm in girth at breast height of from 0.010 to 0.020 m $^{-2}$.) Woodland in this region ranges from about 50 to 80 per cent in canopy cover (with a tree density of from 0.040 to 0.20 m $^{-2}$). Southern Guinea may have slightly more canopy cover but is often essentially the same in cover as northern Guinea. In the derived or transition zone, tree cover may be higher in woodland which approaches forest in structure. The herbaceous cover during the rainy season in all regions is well over 200 per cent, often over 400 per cent, being composed of several layers.

The extent of the root network can be approximated by measurement of below-ground biomass. The most precise figures available are those of Cesar and Menaut (1974) for derived savanna in Ivory Coast for eight categories of vegetation, ranging from grass savanna with less than 1 per cent cover by woody plants to woodland with over 50 per cent woody cover. The seasonal mean below-ground biomass was reported to vary from 10.1 t ha^{-1} (1010 g m^{-2}) to 19.0 t ha^{-1} (1900 g m^{-2}), with the ratios of above-ground/below-ground biomass ranging from 0.22 to 0.51. Variation over the year was considerable, with maximum below-ground biomass as high as 28.8 t ha^{-1}. Isichei (1979) has estimated below-ground biomass in derived and Guinea savanna in Nigeria. At the peak period of herbaceous standing crop (October–November) total below-ground biomass ranged from 1322 to 4334 g m^{-2} in derived savanna and from 402 to 1972 g m $^{-2}$ in Guinea Savanna.

Somewhat more information is available for dead material above ground and litter fall. Total standing dead matter above ground in the Ivory Coast study ranged from 0.28 to 0.67 t ha $^{-1}$ (28 to 67 g m^{-2}). Leaf litter fall has been reported by Isichei to range from 63 to 317 g m $^{-2}$ yr^{-1}, and wood litter fall from 223 to 387 g m^{-2} yr^{-1} in derived savanna; 118 to 241 g m^{-2} yr^{-1} leaf fall and from 70 to 672 g m^{-2} yr^{-1} wood fall in Guinea savanna. Hopkins (1966) has reported 90 g m^{-2} yr^{-1} leaf fall in derived savanna (Olokemeji Forest

Reserve, Nigeria), and Collins (1977) has reported 239 g m^{-2} yr^{-1} leaf fall and 139 g m^{-2} yr^{-1} wood fall in Guinea savanna.

As important as the amount of litter fall is the rate of disappearance of the litter. If litter is collected in plastic bags, termites and the larger soil fauna are excluded and disappearance is brought about mainly by bacteria and fungi. This, however, gives an unrealistic estimate of disappearance. Collins (1977) has estimated that the termite, *Macrotermes bellicosus*, alone removes 60.1 per cent of the annual wood fall and 2.9 per cent of the leaf fall in his study area in Nigerian Guinea savanna (an area with a very high density of this termite). The fungus-growing Macrotermitinae were reported to remove 35.5 per cent of the annual leaf litter fall in this region. Isichei (1979), working in Guinea savanna further north, as well as derived and southern Guinea savanna, estimated litter disappearance under completely natural conditions with the litter unenclosed. His reported disappearance rates may be somewhat too low because he was not able to collect data at frequent enough intervals, but they give an extremely good idea of the rapidity of litter disappearance in savanna. Using the exponential growth equation, as suggested by Olson (1963):

$$N_t = N_0 e^{-rt}$$

where N is the litter remaining after time t and N_0 the litter at the beginning of the time interval; rates, r, estimated on a yearly basis were found to range from 1.68 to 4.62 (mean 2.72) for leaf disappearance, with the highest rate of disappearance in northern Guinea where termites were abundant. This means that on the average, 50 per cent of the annual leaf fall disappears within a little over three months. The values of r for wood disappearance were much more variable, probably being more dependent on termite density, and ranged from 0.32 to 1.16 (mean 0.59). Thus, 50 per cent of the annual wood fall disappears in about one and a half years.

Some idea of the amount of nutrients returned with litter is obtained by examination of Isichei's figures for nitrogen content of litter: leaf litter contained from 0.81 to 1.22 per cent nitrogen (mean 0.98 per cent) while wood litter ranged from 0.50 to 0.61 per cent nitrogen (mean 0.57 per cent) by weight of oven-dried material.

3. A nitrogen model

As stated at the beginning of this section, if an assemblage of plants is to survive, nutrients must be conserved and cycled so that a nearly constant level of availability is maintained. Figure 5.1 illustrates nitrogen stocks and flows in savanna woodland (as a composite of the early burnt plot in derived savanna at Olokemeji Forest Reserve and a 1 ha research plot in northern Guinea

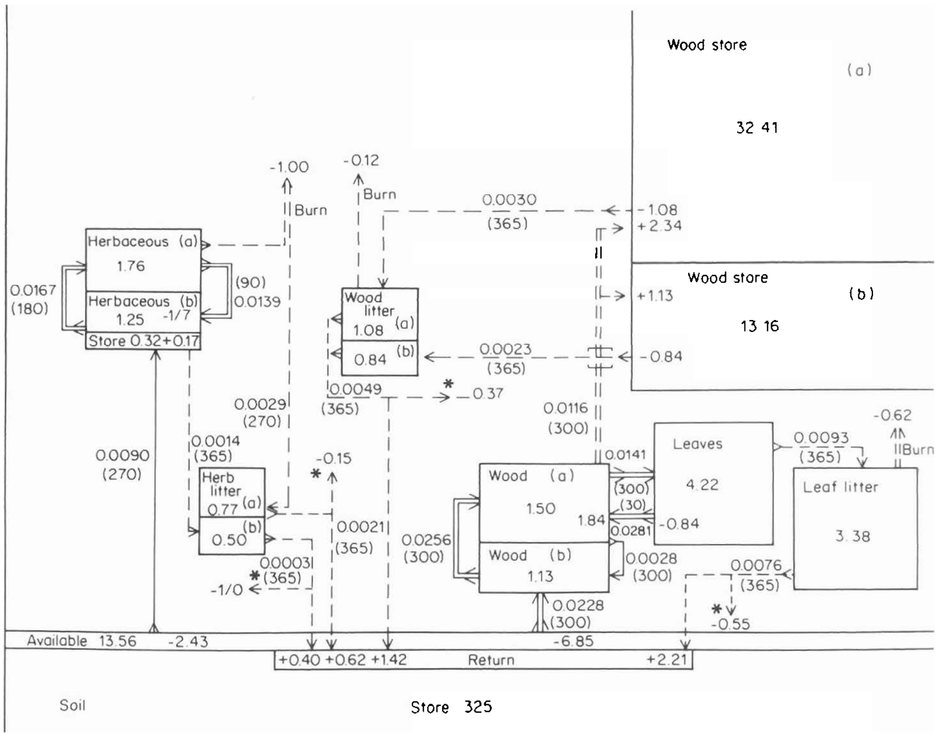

Fig. 5.1. Compartment model of estimated stocks and flows of nitrogen in woodland savanna (composite of the early plot in derived savanna of Olokemeji Forest Reserve, western Nigeria, and *Isoberlinia–Afzelia* woodland in Kainji Lake National Park, north-western Nigeria). *Notes*: (1) Values in brackets indicate number of days in the year a flow is operative; (2) arrows indicate direction of movement of nitrogen; (3) compartments are approximately proportional in size and values are in g N m^{-2} yr^{-1}; (4) decimal values beside flow lines indicate nitrogen flow rates in g m^{-2} day^{-1}; (5) a = above ground; b = below ground; (6) the soil returns shown are estimates of nitrogen reaching the soil after loss of nitrogen by nitrification and ammonification during litter decomposition.

savanna, Kainji Lake National Park, both Nigeria). From soil analyses, Isichei estimated that the soil sink to a depth of 45 cm holds about 325 g N m^{-2}. From tissue and soil analyses and from controlled nutrient feeding studies (Opakunle, 1978) he has estimated that 2.5 per cent of the soil nitrogen becomes available each year for plant uptake. All of this is taken up by the vegetation in this model. Woody vegetation stores 45.6 g N m^{-2} and adds 3.5 g N m^{-2} in new wood each year, while returning 3.6 g N m^{-2} in litter and dead below-ground material. The herbaceous biomass takes up 2.4 g N m^{-2} annually, loses 1 g m^{-2} by volatilization with burning, and returns 1.3 g m^{-2}

in litter and dead below-ground material. This means that a deficit of about 1 g N m^{-2} yr^{-1} is incurred. Such a situation represents as nearly a balanced system as one is apt to find — there is always some 'leakage' of nutrients in any cycle. Open savanna shows a greater deficit. Isichei's composite model indicates that only 61 per cent of the available soil nitrogen is taken up by the vegetation; 39 per cent is subject to leaching, runoff, and use by micro-organisms. Woody vegetation utilizes 2.2 g N m^{-2} and returns 1.8 g m^{-2}, while herbaceous vegetation takes up 2.3 g m^{-2}, loses 1.4 g m^{-2} from burning, and returns 1.1 g. The debit balance is 1.6 g N m^{-2}, yr^{-1} plus up to 5.3 g N m^{-2} not taken up from the soil by higher plants and possibly lost.

These model estimates, while crude, illustrate that the most efficient mineral uptake and cycling occurs in woodland, and that considerable annual loss ('leakage') may occur in more open savanna. Such loss may, however, be made up by inputs. Both woodland and open savanna will receive nutrients in rain. West African savanna, for example, probably receives between 0.39 and 0.75 g N m^{-2} yr^{-1} (Adeniyi, 1982), with the most likely mean value about 0.45 g m^{-2} (Jones and Bromfield, 1970). Further addition comes from N_2-fixation by free-living soil micro-organisms (*Azotobacter* and *Clostridium*), from *Rhizobium*–Leguminosae associations and from the loose association between grass roots and the bacteria *Azospirillum lipeferum* and *A. brasilense*. An additional input for open savanna is N_2-fixation by soil crusts of blue-green algae (largely *Scytonema*) which may fix from 0.33 to 0.92 g N m^{-2} yr^{-1} (Isichei, 1980).

Of nutrients other than nitrogen, only sulphur is subject to loss through volatilization by burning; the others are returned to the soil in ash as well as by litter (ash is, however, most often moved by wind and early rains away from its site of origin). All nutrients are present in considerable amounts in rain-water. Most often limiting in West African savanna is phosphorus; most easily leached in cultivated land is potassium.

4. *Energy utilization*

Just as it may be argued that a community of plants tends to develop such that mineral cycling improves in efficiency, it may be argued that a community develops towards increased efficiency of energy utilization. Ecological efficiency, *E*, may be defined:

$$\frac{Y}{I} = E$$

where *Y* is yield of dry matter and *I* energy input — light in the case of plants, food in the case of animals (Conrad, 1977).

The logic of this argument is simple: if there is any unused light — i.e. any light not reflected back into space or absorbed — such light represents a free resource for primary producers, part of an unfilled niche. Because of plant competition and reproductive expansion, any unfilled niche tends, in time, to become filled. Thus, as shading occurs from the growth of large plants, smaller plants with low light compensation points enter the system.

Working in a region of northern Guinea savanna in Nigeria, where the mean daily global radiation during the growing season (May to November, about 200 days) is approximately 16 242 kJ m^{-2} day^{-1}, Isichei found the mean dry-matter production in open grassland savanna to be 725 g m^{-2} yr^{-1} and in a nearby woodland, 1295 g m^{-2} yr^{-1}, representing ecological efficiencies of 0.4 and 0.70 per cent respectively.

As has been seen, savanna woodland is more efficient in mineral cycling; it can now be seen that it is more efficient in energy utilization. This strongly suggests that savanna, if undisturbed except by annual burning, will tend to develop into woodland savanna (see Figs. 5.2 and 5.3).

III. Causes of savanna

It has long been argued that savanna is *caused* by something, the 'something' sometimes held to be climate (low moisture availability for at least part of the

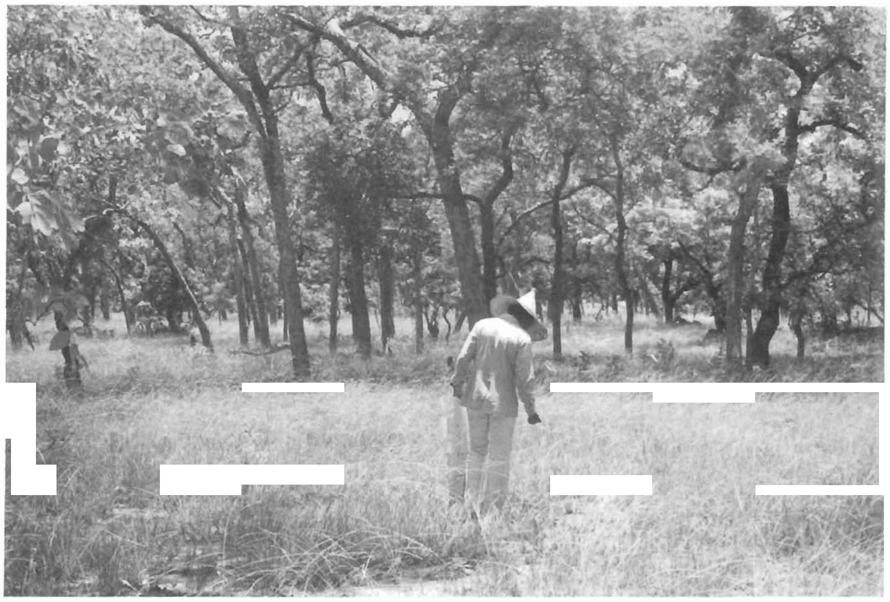

Fig. 5.2 Woodland savanna: *Isoberlinia–Afzelia*, Kainji Lake National Park, northwestern Nigeria. (Photograph W. W. Sanford.)

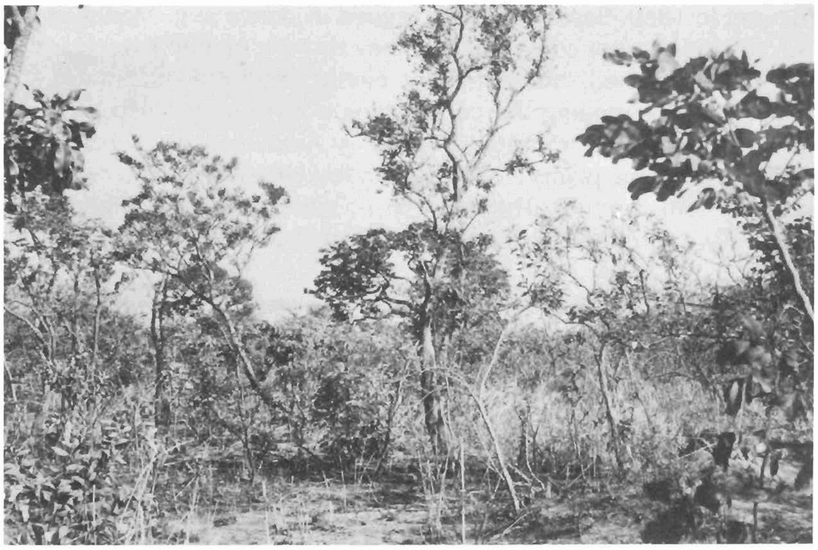

Fig. 5.3. Juvenile bushland (*Burkea–Detarium–Terminalia avicennioides* Savanna) Kainji Lake National Park, north-western Nigeria. (Photograph by W. W. Sanford.)

year), sometimes soil (shallow or/and infertile soil) or, a more recent favourite, anthropic disturbance, especially burning. We will examine these hypothetical causes, although stating at the outset that we do not believe savanna has *a cause* but rather than this broad vegetation system develops in response to a cluster of interacting factors.

1. Climate and soil

Causation by climate or/and soil is usually linked with the old climax or poly-climax theory. According to the classical view of Clements (1916), still favoured by some geographers, vegetations develop directionally through a number of successional phases until a stable and ecologically balanced system, the climax, is achieved. Successions are held to be convergent, all ending up in a state determined by climate according to the climax theory, or by climate, soil, and possibly other factors such as anthropic disturbance according to the poly-climax theory.

As the introductory remarks to section II, above, indicate, we do not subscribe to any simple view of succession and climax. In the first place, vegetation varies over time species by species. Such an individualistic understanding of community change, sometimes considered modern and controversial, was, as Horn (1975) points out, already accepted as common knowledge by Thoreau in 1860. Secondly, there is good evidence (e.g. Matthews, 1979) that successions do not converge, that they strongly tend to diverge.

It cannot be argued, however, that climate and soil do not have great importance in determining the composition and structure of vegetation. As already indicated, the moisture regime is fundamental. It hardly needs expatiation that some plants are adapted to low moisture or/and extended dry periods and some are not. The question is, rather, can the definite structure which we have described as savanna be definitely associated with the moisture regime?

Taking Keay's (1959a) savanna zonation for Nigeria as an example, definite ranges of the ratio of annual precipitation/potential evapotranspiration can be seen in Table 5.1.

Table 5.1

Vegetation zone	Precipitation/evapotranspiration ratio
Derived savanna	0.75–1.0
Southern Guinea savanna	0.65–0.88
Northern Guinea savanna	0.40–0.66
Sudan savanna	0.21–0.40
Sahel (thorn scrub)	< 0.21

But this hardly answers the question, as Keay may have as likely defined the zones by climate as the vegetation of the zones may have been determined by climate.

From the definition of savanna (Section 1.4, above), it is clear that moisture availability must be seasonal, that a dry season must be long enough and severe enough for most herbaceous vegetation to dry thoroughly to ground level. The major problem is whether or not a grass cover would develop in response to such a climatic regime rather than a dry forest — without appreciable grass. This question at once brings soil and topography into the picture. Riverine or gallery or riparian forests (or woodlands) are frequent in savanna regions. Such bands of vegetation follow the course of seasonal or perennial streams and often approximate to rain forest in structure and physiognomy. Grass is often absent. Such vegetation is, however, largely restricted to the more humid Guinea savanna, although trees and shrubs are taller and denser along watercourses even in semi-arid regions. The species composition of such woodlands, while containing species found in rain forest, is distinctive, not mirroring rain forest but rather containing a few widespread forest species (e.g. *Anthocleista vogelii, Antiaris africana, Ceiba pentandra,* *Cola gigantea*), together with larger savanna trees (e.g. *Vitex doniana, Khaya senegalensis*) and trees found only along streams in either forest or savanna (such as *Berlinia grandiflora, Irvingia smithii, Pterocarpus santalinoides*). It is likely that the water-table, soil fertility, and atmospheric humidity in such relatively narrow bands along streams, often in steep valleys, approximate the abiotic environment of seasonal forest regions, and that such vegetation would not survive at a distance from the stream whether or not there was anthropic disturbance.

More intriguing are patches of dry forest, usually dominated by *Diospyros mespiliformis*, found in the midst of Guinea savanna on more or less level ground away from streams. (Fig 5.4). Our recent examination of such dry forests in northern Guinea savanna in Nigeria shows that *Diospyros* saplings of all size classes develop under *Diospyros* canopy, while other species are rare; thus the next generation is very apt to have the same composition and structure as the present one. Such one-species-dominated forests appear to conform to classical views of climax (especially as defined for tropical rain forest by Connell, 1978). While moisture availability is probably a contributing factor to the development of such vegetation patches, soil depth (associated with moisture availability and nutrient store) and character are perhaps more important. Even in the absence of disturbance, the requirements of *Diospyros* when occurring in drier regions (as opposed to rain-forest areas) seem to be specialized enough to preclude the spread of such dry forests over any extensive area.

Superficially similar, except for the presence of a grass stratum, are fairly dense woodlands dominated by *Isoberlinia* spp. or by *Isoberlinia* and *Afzelia africana*. Our observations so far, however, lead us to conclude that such woodlands may not be replaced by the same species composition in the next generation.

Less obvious than the variation in savanna brought about by such woodland patches is the gradual variation in structure and species composition with toposequence: the vegetation at the top of a hill is different from that on the lower slopes or at the base. Such variation is often associated not only with drainage and water-table but also with soil structure, almost impenetrable ironstone often lying sufficiently near the surface to restrict root development.

It is apparent, then, that soil characters — depth, structure and texture, fertility — strongly influence vegetation on a local scale. This still does not answer the question of whether or not savanna would develop in response to soil and climate without anthropic interference. The conclusion of the 1964 IGU–Unesco symposium in Venezuela, referred to above (section I.3) was that: (1) savanna is not a climatic climax; (2) a majority of the units of this vegetation can be considered as anthropic — existing because of the activities of man; (3) there are also natural savannas that can be considered as edaphic climaxes. Acceptance of this without considerable reservation seems rash. It is

Fig. 5.4. *Diospyros mespiliformis* with a dense undergrowth of saplings growing on an old termite mound in *Isoberlinia-Afzelia* woodland, Kainji Lake National Park, northwestern Nigeria. (Photograph by W. W. Sanford.)

known that extensive grasslands, probably fitting our definition of savanna, existed in East Africa long before there was either burning to any extent or cultivation at all (Livingstone, 1975). Furthermore, such grasslands were too extensive to be edaphically developed. A much more reasonable approach is that of Sarmiento and Monasterio (1975) who put forth a holocentric interpretation of savanna as a broad ecosystem type, the multiple factors leading to its development varying in different climatic–vegetation zones. They point out that in regions of rain forest in tropical rainy climates (such as tropical America, where they worked), the type of forest (species composition, structure, physiognomy) clearly varies with the rainfall regime; and where the rainfall is variable from year to year or is slightly low or where the dry season is prolonged, savanna vegetation may develop and supplant forest in local areas of sandy soil, senile soils of latocolic evolution, or on very shallow soils. In drier tropical forests, savannas develop first in areas of poorer and/or shallower soils, but with extreme drought stress they may develop even over fertile soils. Thus savannas are seen to develop in response to a dynamic interplay of soil and climate — and species available for establishment. Clearly, burning may augment any of the conditions tending to bring about savanna development and may lead to its extension.

Menaut (1983a) has recently reviewed probable causes of savanna and concluded that the superior adaptation of grasses to extreme seasonality and low or/and variable moisture supply largely accounts for grass formations replacing or occurring with woody formations. He points out that at the regenerating stage woody plants and grasses are in competition and grasses have the advantage in infertile soils and regions of drought stress. Medina (1983) has also emphasized the importance of adaptation to low soil nutrient status of many grasses.

That all West African savanna represents a replacement of forest is questionable. As Livingstone (1975) has pointed out, Africa was never covered by forest, although there was great forest expansion 10 000–7000 years BP so that much of West Africa may have been forested and this may have been replaced by savanna during subsequent drier periods. For about the last 3000 years, however, moister conditions have prevailed and savanna regions have become hospitable to a somewhat wider range of plants.

2. *Anthropic disturbance*

The question of whether or not savanna as defined would be present except in patches, where poorer soil and climate worked together for its development, without anthropic disturbance has still not been definitely answered. If savanna is undisturbed it moves towards woodland, would such woodland have a grass cover and fit our definition of *savanna* woodland or would grass disappear and the vegetation be dry forest?

Menaut (1977), working in Ivory Coast, reports that woodland savanna cannot normally develop unless the area has had some fire protection, but once this has been afforded 'transformation of an open shrub savanna into a dense savanna woodland seems irreversible whatever might be the future of the plots without any major climatic change'. Extensive savanna woodlands in West Africa which are annually burnt and yet still remain woodland bear out Menaut's latter contention. The question remains, however, whether grass would disappear from such woodland if burning ceased.

The Olokemeji Fire Plots in derived savanna of south-western Nigeria were established in 1929–30. The fire-protected plot is now without grass and is a regrowth forest. This does not provide us with information as to what would happen in Guinea or Sudan savanna. The Red Volta Fire Plots in north-eastern Ghana are on the border of northern Guinea and Sudan savanna with a mean annual rainfall of c. 1100 mm. They were established in 1947 and the most recent report (Brookman-Amissah *et al.*, 1980) shows that in 1977 the fire-protected plots had a density of trees at least 30 cm in girth of 0.02 m^{-2} which is comparable to the density of many areas of annually burnt savanna in Nigerian northern Guinea savanna. These plots had a grass biomass (182 g m^{-2} dry matter) greater than that of the late burnt plots and greater than that of the annually burnt plots at the border of northern Guinea and Sudan savanna in north-western Nigeria as monitored by the Nigerian Man and Biosphere team in 1979 (Sanford *et al.*, 1982b). Whether or not grass will continue in this plot cannot be known. It will depend on which is able to withstand full canopy shading better: grass species or woody plant saplings. Results of our current research indicate that several species of annual grasses (e.g. *Pennisetum pedicellatum, P. subangustum, Brachiaria* spp.) and a few perennials (.e.g. *Andropogon tectorum, A. gayanus, Beckeropsis uniseta*) tolerate or prefer some shade and will continue growth under full canopy if the canopy is high. Small woody plants, however, and grasses are serious competitors. Thus, whether or not grass will continue in the fire-protected plot will probably depend on the size-class distribution of woody plants. At present, 84 per cent of the woody plants are less than 30 cm in girth in the Ghana plots; a stable situation for Guinea savanna is 82 per cent of plants less than 40 cm in girth (Sanford *et al.*, 1982a). The Ghana plot does not appear to be far from a stable distribution, and canopy shading by the larger trees may limit expansion of the percentage of saplings. Ultimately, whether or not grass continues, and whether or not the density of small woody plants will be limited and more or less stable, will depend upon an interplay of soil, climate, and species composition of the area.

If land is cleared and cultivated, then abandoned to nature, the process of vegetational change, termed 'secondary succession', begins. In humid regions of rain-forest potential, such an open area is first dominated by annual forbs (e.g. *Ageratum conyzoides, Synedrella nodiflora, Spigelia anthelmia*), annual sedges such as *Mariscus alternifolius*, and annual grasses such as *Brachiaria* *deflexa*. Perennial forbs then begin to increase in number. In one of our tests in south-western Nigeria the mean number of species in five 2500 m^2 plots was 19.6 the first year and 21.8 the second year with the mean rooted shoot density per square metre increasing from 123 to 273 and the percentage of broad-leaved plants increasing from 47.0 to 86.8. With further time, annual grasses such as *Pennisetum subangustum* and perennials such as *Panicum maximum* and *Rottboellia exaltata* dominated some plots while in others the broad-leaved *Melanthera scandens* and *Ipomoea involucrata* remained most abundant. In all cases the broad-leaved composite *Eupatorim odoratum* became dominant and nearly the sole species four or five years after the succession began, to be gradually replaced by woody plants (first *Trema orientalis* and *Musanga cecropioides*). Only if the cleared area is annually burned will grasses continue to dominate after the third or fourth year. In such cases, *Andropogon tectorum* often becomes dominant in deep fertile soils and *Monocymbium ceresiiforme* and *Loudetia* spp. in shallow soil.

In drier, more northern regions, the pattern of succession is quite different. Annual grasses dominate the first year with only a scattering of forbs (such as *Blumea aurita, Borreria* spp., *Combretum sericeum*). The only detailed record available for an appreciable period of time is for the north-eastern Ghana fire plots, referred to above, where grass continued to be dominant in the fire-protected area. The number of species of forbs, after 30 years of protection, was 20 compared to 16 in the early burnt and 15 in the late burnt area. These results suggest that climate without burning may bring about predominantly grass as the herbaceous vegetation in drier regions, but that in moister regions burning is necessary. In all cases either anthropic disturbance or cultivation or intense burning or locally very poor or shallow soil prevent savanna from moving towards woodland savanna as opposed to open or bush savanna. (Fig. 5.5).

IV. Effects of fire

1. *Time of burning and general effects*

Although burning has already been mentioned as a frequent contributory cause in the development and extension of savanna, it is necessary to discuss its effects further as it is almost invariably a management practice throughout West Africa. How long burning has been regularly practised is unknown. Man probably evolved in East African grasslands very long ago, but his transition from hunting and gathering to farming began only about 10 000 years ago (Washburn, 1978) and burning before and considerably after that must have been very rare. It is of course true that burning may result from natural causes, but we have never accepted as in any way likely Rose Innes's (1972) too often quoted suggestion that fires may start from sparks caused by boulders rolling

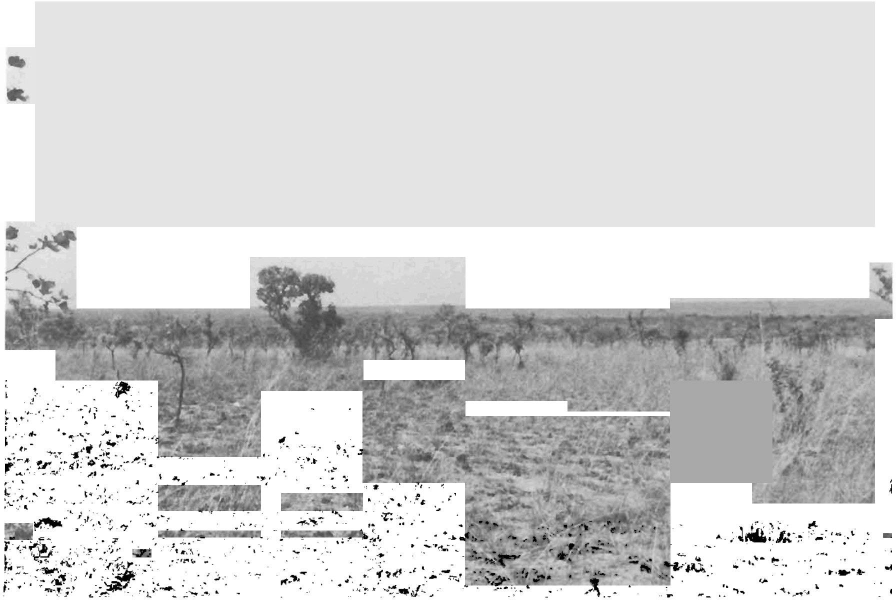

Fig. 5.5 A region of northern Guinea savanna where cutting and burning over the years have led to a degraded Shrub Grassland. (Photograph by W. W. Sanford.)

down slopes. Lightning does, on occasion, cause fires, but as Walter (1971, p. 239) remarks, fires caused by lightning are much less frequent than those caused by man and usually do not spread very far in natural woodland.

Savanna is most often burnt, as Menaut (1977) remarks, in the middle of the dry season — that is, usually during January, although some burning begins in mid or late December and extends through February. In areas of cattle migration, burning occurs shortly after the arrival of herds from more northerly ranges. As vegetation in the north dries and streams and water-holes evaporate, livestock move into more humid areas, first making use of crop residues and areas of still green grass along stream beds. Then, as drying continues, the savanna is burnt to clear away dead standing material and to stimulate new growth (flushing) of the grass. Tentative work by Opakunle, unpublished, indicates that either burning or clipping at ground level and removal of grass will bring about flushing but burning is more effective. (See Fig. 5.6).

Such savanna burning besides removing, on the average, about 82 per cent of the herbaceous above-ground biomass (Isichei and Sanford, 1980) causes leaf shedding of most trees. This is followed by leaf flush, normally occurring in the late mid dry season (February in the Nigerian Guinea zone). Brookman-Amissah *et al.* (1980) report, for the north-eastern Ghana experiment, that by March, 57 per cent of the trees in the fire-protected plot were in leaf, 76 per cent in the early burnt (burnt four months earlier), and 43 per cent in the late burnt area, as yet unburnt. These data suggest that fire has some stimulating effect on tree flush, perhaps comparable to its effect on grass. That the effect is not brought about alone by difference in species composition is shown by the same difference in flushing time occurring for *Entada africana* and *Combretum glutinosum* which occur in all plots.

2. *Soil*

Soil organic matter is of great importance in improving soil texture and its water-holding capacity, in increasing cation exchange capacity, and in providing nitrogen. Because of high soil temperature, organic material is very rapidly mineralized in the tropics so its concentration in the soil is generally low. In some situations the carbon content of soil at a depth of 30–45 cm is greater than at 0–15 cm. This condition, especially frequent in savanna woodland, may be brought about both by more rapid mineralization of humus near the soil surface, where temperatures are higher, and by the presence at lower levels of increased underground biomass of woody vegetation. Because of mineralization near the surface, litter fall is of surprisingly little importance in adding humus to the soil. Even though only about 18.4 per cent of the year's

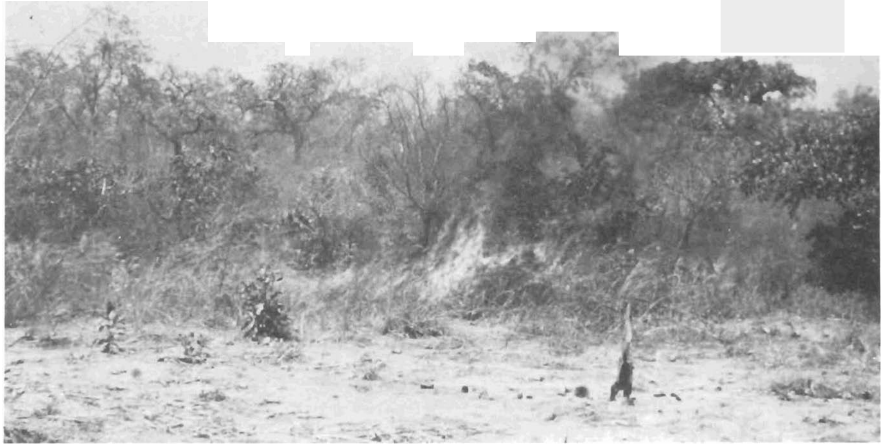

Fig. 5.6 Burning in early January in northern Guinea bushland, northern Nigeria. (Photograph by P. J. Newbould.)

leaf litter fall and 11.7 per cent of the wood fall is burnt by annual fires (Isichei and Sanford, 1980) there is not a significant positive relationship between litter fall and soil organic matter content (although there is between tree density and soil organic content at the 30–45 cm depth). It is very unlikely that organic matter in the upper level of soil is oxidized by the annual fires, as soil temperature at a depth of 2 cm is raised by 14 °C at most and often by as little as 3–4 °C, and then only for a few minutes during burning (Ramsay and Rose Innes, 1963). However, removal of shading material by burning will lead to higher soil temperatures during the remainder of the dry season and this will lead to more rapid mineralization. Brookman-Amissah *et al.* (1980) found a significant decrease of organic matter with burning at the 0–5 cm depth but not at lower depths, although a statistically insignificant trend towards more organic matter beneath fire-protected vegetation can be seen from their data. Moore (1960), working at the Olokemeji Fire Plots 30 years after the commencement of controlled burning, found the humus content of the upper 20 cm of soil higher under early burnt vegetation than under the fire-protected plot, but lower under the late burnt vegetation than under that which was fire protected. His data were not, however, subject to statistical analysis so it is impossible to know whether or not the differences reported are significant. Isichei (1979) has reported soil carbon concentrations of the same plots 50 years after controlled burning began and found the same relationships as Moore at the 0–15 cm depth.

Moore (1960) and Isichei (1979) reported the same trend for soil total Kjeldahl nitrogen at Olokemeji as for carbon except that Isichei found little variation from plot to plot at the 30–45 cm depth. Brookman-Amissah *et al.* (1980) found significant difference only at the 0–5 cm level.

The two elements, carbon and nitrogen, are most likely to be affected by burning as they are volatilized in material burnt and lost from the system. Other nutrients, excepting sulphur, are returned to the soil in the ash, although they may be displaced by wind and water. Considerable attention has been given to nitrogen loss through burning. Values as high as 28.02 kg $\mathrm{ha^{-1}}$ or 0.28 g $\mathrm{m^{-2}}$ (25 lb per acre) for tall grass in the derived zone of Ghana have been reported (Nye and Greenland, 1960, p.54), but Isichei and Sanford (1980) estimate that in natural (unimproved) savanna only about 13 kg $\mathrm{ha^{-1}\ yr^{-1}}$ (range of from 11 to 16 kg $\mathrm{ha^{-1}}$ or from 0.11 to 0.16 g $\mathrm{m^{-2}}$) are lost by burning. Clearly, an equivalent amount must be added to the system if deterioration is not to occur. As we have shown above, considerable input of nitrogen comes from rain and from biological fixation and this explains why there is little if any difference in nitrogen content of the soil with annual burning.

Sanford (1982a) in a review of burning has stated: 'on the whole, climate appears more important than burning in limiting the concentration of organic matter in the soil through its effect on the rate of mineralization. Most soil carbon appears to be derived from underground biomass.' Nitrogen more or less follows carbon.

Burning temporarily raises soil pH slightly. In some soils, especially in the derived savanna, texture may be improved by burning (Fagbenro, 1982) but in others, especially in northern Guinea regions, surface compaction may result, as indicated by the increase in bulk density reported by Brookman-Amissah *et al.* (1980). Considerable redistribution of non-volatile minerals occurs on a micro-scale with wind movement of ash and also some, via rain, on a larger scale. All in all, however, annual burning has little effect on the soil and whatever effects are observed are more dependent on vegetational change brought about by burning than by burning itself.

3. Vegetation

(a) Physiognomy and structure

If one looks at the Olokemeji Fire Plots today, 51 years after the controlled burning experiment started, one sees, regrowth rain forest in the fire-protected plot, while the early burnt plot superficially has the structure and physiognomy of southern Guinea savanna and the late burnt plot looks like northern Guinea savanna. Using only physiognomic characters Isichei carried out principal components analysis of the three Olokemeji plots together with 14 sites including all types of savanna. The results are shown in Figure 5.7. Clear clumping of the Olokemeji plots at the extreme right is seen on the ordination of the first and second axes. These results indicate that while annual burning affects structure and physiognomy of vegetation, 50 years is not enough to turn derived savanna into Guinea savanna.

The characters most affected by burning are shown in Table 5.2 (taken from Sanford, 1980). These characters are useful in classifying vegetation, as will be discussed below. As can be seen from Table 5.3, the percentage of woody legumes increases with burning in derived savanna. This was also true in the north-eastern Ghana experiements. Here the highest percentage of legumes was found in the early burnt plots in 1960, but by 1976 the percentage of woody legume individuals was 73 per cent in the late burnt plots, 66 per cent in the early burnt plots, and 52 per cent in the fire-protected plots.

Of particular interest is the effect of burning on succession and stability in savanna. The demographic changes in woody plant populations at Olokemeji are shown in Table 5.4 (also from Sanford, 1982a). From these results it can be seen that burning, by removal of small saplings, results in a larger mean girth and hence a distinctive size-class distribution. A stable girth size distribution is reached in less time in burnt than in unburnt vegetation, and probably in less time in late burnt than in early burnt vegetation (Sanford, 1982a). One reason for this is the restricted number of species which can survive the more intense

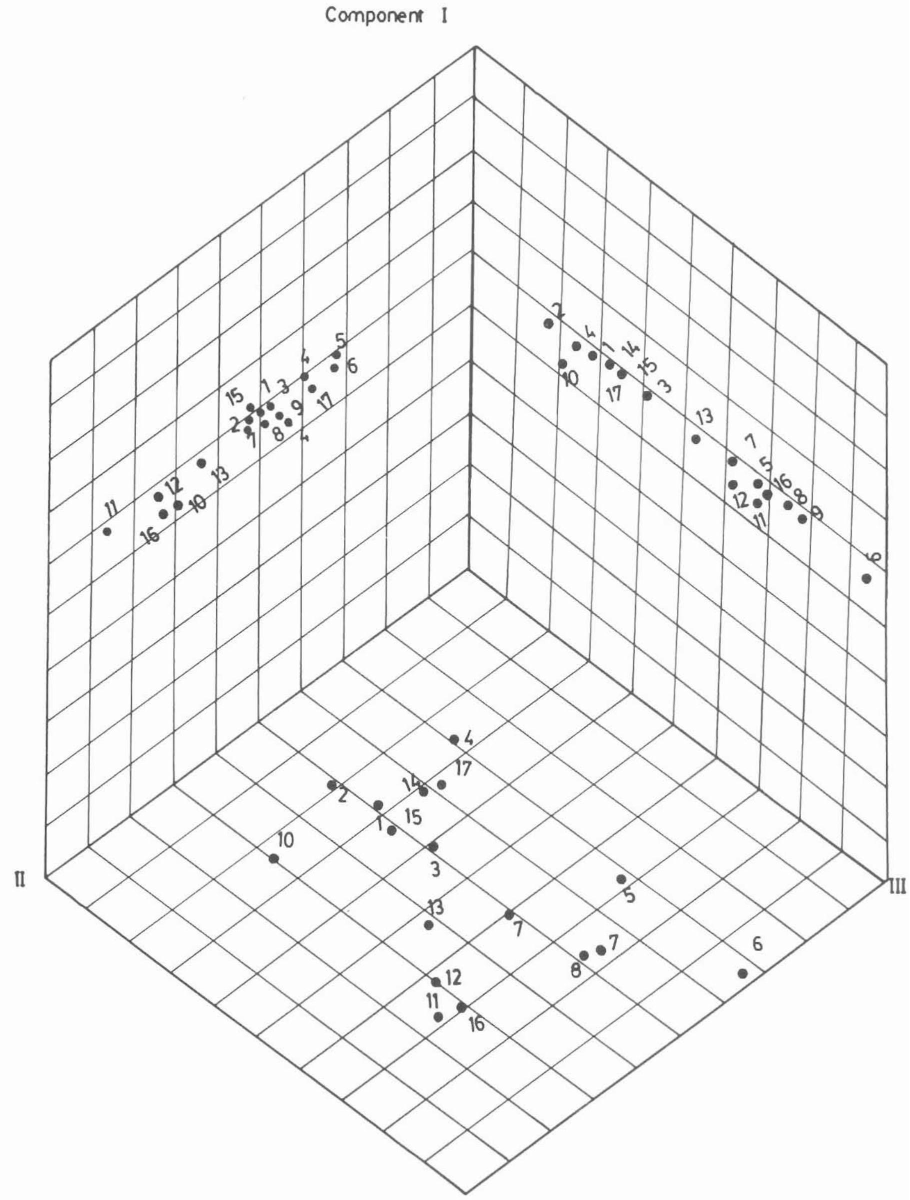

Fig. 5.7. Principal components ordination of 17 savanna sites in Nigeria using characters given in Table 5.2, and listed by site name and location and vegetation type (Keay classification).

(1)	Igbeti: 08°46′N, 04°09′E;	southern Guinea.
(2)	Borgu, Oli River: 10°06′N, 3°38′E;	northern Guinea.
(3)	Borgu, Tungan Giwa: 10°06′N, 3°38′E;	northern Guinea.
(4)	Olokemeji Plot A: 7°26′N, 3°32′E;	derived savanna.
(5)	Olokemeji Plot B: 7°26′N, 3°32′E;	derived savanna.
(6)	Olokemeji Plot C: 7°26′N, 3°32′E;	derived savanna.
(7)	Near Gidan Waya: 09°37′N, 08°24′E;	southern Guinea.
(8)	Near Tungan Giwa: 10°06′N, 3°38′E	northern Guinea.
(9)	Oli River bank: 10°6′N, 3°38′E;	northern Guinea.
(10)	Vom Hills, Plateau: 09°41′N, 08°44′E;	plateau savanna.
(11)	Near Gusau: 13°24′N, 05°10′E;	Sudan savanna.
(12)	Km 313 Sokoto–Zaria Road: 11°07′N, 07°44′E;	Sudan savanna.
(13)	Near Zaria: 11°07′N, 07°44′E;	Sudan savanna.
(14)	Km 132 Kaduna–Jos: 09°55′N, 08°53′E;	Sudan savanna.
(15)	Near Keffi: 10°17′N, 08°40′E;	southern Guinea savanna.
(16)	25 miles N of Sokoto: 13°04′N, 05°16′E;	Sudan savanna.
(17)	Gurara falls near Suleja: 08°12′N, 06°41′E;	southern Guinea.

late burning together with discouragement of the immigration of new species (Fig. 5.8).

Some idea of the relative stability of vegetation may be gained from species diversity estimates, although this relationship is still controversial. It has usually been claimed that diversity increases with successional age and that maximum diversity is associated with climax. North American studies of old fields (e.g. Bazzaz, 1975) have generally shown that there is an initial rapid increase in diversity followed by an abrupt drop (as in the example given earlier, where species diversity increased until an abrupt drop was brought about by dominance of *Eupatorium odoratum*), then a slow rise (in our example as woody plants began to supplant *Eupatorium*). Odum (1969), however, has suggested that theoretically species diversity should decline somewhat at climax, and Connell (1978), at least for tropical forest, has presented evidence that at climax the vegetation is dominated by one or a few most successful species so diversity is low. This is in logical agreement with May's (1973) contention that increased diversity confers increased fragility upon a system — at least as mathematically modelled.

Species diversity, evenness, and richness are shown for the Olokemeji and Red Volta (Ghana) Fire Plots in Table 5.5 (Sanford 1982a from data of Isichei, 1979, and Brookman-Amissah *et al.*, 1980). Increased evenness is probably positively related to increased stability, and a tendency for evenness to increase with burning is clear in both data sets. Species diversity, on the other hand, is consistently highest in fire-protected plots as is species richness.

(b) Life-form

Considerable controversy has been engendered concerning the effect of late and early burning on the proportion of perennial to annual grasses. Examina-

Table 5.2. MAB-3: Field data sheet. Physiognomic/Structural Savanna Vegetation Survey

Site: .... Locality: .... Date: .... Enumerator: ....

Attribute	Rank			
	1	2	3	4
A. Tree height and canopy				
1. Canopy: no closure; patchy cover; *c.* 50% closure; almost complete closure				
2. Trees over 10 m: none, very few; 10–25%; 25–50%; over 50%				
3. Trees/shrubs 3–6 m: (rank as above)				
4. Trees/shrubs under 3 m: (rank as above)				
5. Trees/shrubs under 3 m: mostly scattered; some in clumps or thickets; moderately clumped; extensive thickets				
B. Leaf/leaflet characters of woody elements				
6. Compound: none, very few; 10–25%; 25–50%; >50%				
7. Less than 5 cm long (rank as above)				
8. Over 10 cm long (rank as above)				
9. Pubescent, hairy or glaucous (rank as above)				
10. Tip acuminate (rank as above)				
C. Tree/shrub habit and appearance				
11. High-branched, first branch over 6 m from ground (rank as above)				
12. Low-branched, first branch less than 2 m from ground (rank as above)				
13. Branches of trees over 5 m tall at an angle of *c.* 45° or less with bole (rank as above)				
14. Branches crooked or twisted (rank as above)				
15. Boles slanting, crooked or twisted (rank as above)				
16. Bark dark and prominently fissured or flaky (rank as above)				
D. Taxonomic features of woody elements				
17. *Elaeis guineenis*: none; few; moderate; many				
18. Leguminosae: none or very few; 10–25%; 25–50%; over 50% of woody plants present				
E. Herbaceous vegetation: life-form and taxonomic features				
19. Grass over 2 m high (rank as above, on cover basis)				
20. Grass under 1 m high (rank as above, on cover basis)				
21. Broad-leaved herbs (rank as above, on cover basis)				
22. Leguminosae: none or very few; 10–25% of broad-leaved herbs present; 25–50%; over 50% broad-leaved herbs present				
23. Cyperaceae: none or very few; some in small patches; moderate amount, spread; many spread or in large patches				

Table 5.2. *(continued)*

Site: .... Locality: .... Date: .... Enumerator: ....

Attribute	Rank			
	1	2	3	4
24. Aloe (rank as above, No. 23)				
25. Succulent Euphorbiaceae (rank as above, No. 23)				
F. Surface soil and topography				
26. Slope: none; gentle slope; moderate; steep				
27. Bare ground: not visible; in few small patches; scattered patches; large patches present				
28. Surface soil: red-brown; light brown; grey; dark grey-black				
29. Surface soil: gravelly; sandy; some clay; much clay				
30. Termite mounds: none; few; moderate; many (all types of above-ground mounds)				
G. The eight (8) most abundant woody plants, in order of abundance				
1.				
2.				
3.				
4.				
5.				
6.				
7.				
8.				
H. The four (4) most abundant grasses, in order of abundance				
1.				
2.				
3.				
4.				
I. Comment				

tion of available quantitative data has led us to conclude that in the relatively moist derived savanna areas, burning time and perennial : annual grass ratios are not significantly related. Isichei has shown that in the late burnt Olokemeji plot about 92 per cent of the yield was of perennial grasses and in the early burnt plot about 91 per cent (both on the basis of dry weight). In drier, more marginal regions there does not seem to be any relationship of the ratio with burning time, but more annuals are found in fire-protected than in burnt areas in the Ghana experiments. Afolayan (1979), working in northern Guinea savanna in Nigeria, has reported a tendency for an increase of perennials with late burning, but statistical significance is lacking.

Table 5.3. A comparison of physiognomic/structural attribute scores of the early and late-burnt fire plots at Olokemeji Forest Reserve with those of the fire-protected plot

Attribute	Attribute scores expressed as percentage of the fire-protected plot score		
	Plot B (early burnt)	Plot A (late burnt)	Difference between A and B
Group I			
Canopy closed	86	53	33
Leaves/leaflets glabrous, glossy	95	75	20
Trees high-branched; above 6 m	85	46	39
Boles/branches ± straight	76	41	35
Bark smooth, light coloured	76	47	29
Leaves/leaflets over 12 cm long	76	76	0
Group Ib			
Branches acutely angled with the bole	100	63	37
Trees over 9 m tall	106	69	37
Leaves compound	150	75	75
Group II			
Bark fissured, dark coloured	133	167	34
Grass over 1.5 m high	271	285	15
Leaves/leaflets pubescent, hairy	100	120	20
Trees branched at above 1.5 m	138	175	37
Branches, boles crooked or twisted	162	188	26
Group IIb			
Woody Leguminosae	220	180	40

Table 5.4. Demography of the three Olokemeji Fire Plots, south-western Nigeria

	Condition in 1976			Population change between 1969 and 1976%			
	Number of individuals	Species	Mean girth	Dead or missing	New individuals	New species	Species extinctions
Plot[a] A	133	14	34.6	12	15	0	14
B	236	24	34.2	11	25	4	8
C	456	33	27.4	15	26	5	18

[a] A—late burnt; B—early burnt; C—fire protected. The percentage of species with dead individuals and no new individuals is 29% in A, 25% in B, and 37% in C.

Fig 5.8. Fire scar on the bole of *Crossopteryx febrifuga* in northern Guinea bushland. Both this species and *Afzelia africana* almost invariably bear fire scars and probably a high percentage of the young saplings are killed by fire. (Photograph by W. W. Sanford.)

Table 5.5. Species diversity, evenness, and richness of the fire plots of Olokemeji, Nigeria, and Red Volta, Ghana

	Diversity		Evenness[a]		Richness
	H'	$e^{H'}$	$(l/C \cdot e^{H'})$	$H'/\log_e N$	Spp. number/ $\log_e$ area
Olokemeji 1976					
Late burnt	2.32	10.2	0.82	0.88	1.88
Early burnt	2.36	10.6	0.59	0.74	3.22
Not burnt	2.82	16.8	0.72	0.78	5.09
Ghana					
Late burnt					
1950	1.70	5.47	0.76	0.68	1.30
1977	1.88	6.55	0.70	0.73	1.41
Early burnt					
1950	1.91	6.75	0.85	0.80	1.19
1977	1.58	4.85	0.62	0.60	1.52
Not burnt					
1950	1.82	6.17	0.79	0.76	1.19
1977	2.58	13.19	0.74	0.74	3.47

[a] C = the Simpson coefficient: $1/\Sigma p_i^2$, where p_i is the percentage of individuals of the ith species; N = total number of species.

Species distribution of grasses appears to be largely controlled by soil fertility and depth, tree canopy cover (i.e. shading), and mechanical disturbance. Some species such as *Loudetia* spp., *Monocymbium ceresiiforme*, and *Schizachyrium exile* can manage in poor, shallow soils, while others such as *Andropogon tectorum* require deep, fertile soils. Species such as *Hyparrhenia* spp. and *Schizachyrium* spp. do best in full sun, while other such as *Andropogon* spp. and *Beckeropsis uniseta* do best in light shade. In general, frequent mechanical disturbance leads to an abundance of annuals and such weedy perennials as *Rottboellia exaltata* and *Sporobolus pyramidalis*.

In summary, annual burning leads to a relatively stable vegetation from the standpoints of structure and size-class distribution of trees and general physiognomy. Species diversity decreases with burning as does species richness, but evenness increases. Various physiognomic characters are influenced by burning, especially canopy closure which is decreased, due to the prevalence of high branching; mean tree height is decreased, mean girth is increased. With burning, species are selected which have smaller leaves; pubescent or glaucous leaves are more common as are compound leaves. Taxonomically, the percentage of woody legumes increases with burning. Time of burning does not appear to influence the proportion of annual to perennial grasses. Grass species distribution is influenced rather by soil, mechanical disturbance, and shading; the latter is, however, strongly affected by the burning regime.

4. *Primary production*

(a) Woody plants

Most data relating burning to primary production consist of stem counts or basal area estimates of woody plants. A few examples make the general trend clear. After 47 years of controlled burning at Olokemeji, the late burnt plot contained 16 per cent of the total number of stems of the three fire plots combined, the early burnt 29 per cent, and the fire protected 55 per cent. An estimation of wood volume (Isichei, 1979), however, gives a different picture: the late burnt plot contained 15 per cent of the total volume of the three plots, the early burnt 48 per cent, and the fire protected 37 per cent. The high volume of the early burnt plot is accounted for by the larger mean girth of the trees in this plot. Other data from derived savanna are those from the fire experiments at Kokondekro in Ivory Coast (reported by Ramsay and Rose Innes, 1963). After 25 years of controlled burning, the late burnt plot contained 17 per cent of the total stems, the early burnt 36 per cent, and the fire protected 47 per cent. These figures are not so different from those from Olokemeji, even though Kokondekro was not initially clear-felled as was Olokemeji. The only detailed data from 'true' savanna are those from the Red Volta (Ghana) Plots. Here, after 27 years, the late burnt plot contained only 7.5 per cent of the stems over 30 cm in girth, the early burnt 15.6 per cent, and the fire protected 77 per cent, indicating a considerably greater effect of burning in the drier region than in the more humid areas.

(b) Herbaceous plants

Other than firewood, the major products of the savanna are livestock fodder, thatching, and mat-fencing materials — all herbaceous. Isichei (1979) has compared herbaceous maximum standing crop in the three fire plots at Olokemeji over a three-year period. The late burnt plot averaged 496 ± 68 g m^{-2} dry weight while the early burnt averaged 400 ± 43 g m^{-2} — not a comfortably large difference, while the fire-protected plot produced virtually no herbaceous crop. The late burnt yearly mean was greater than that of the early burnt two years out of three.

Afolayan (1977, 1978) has compared maximum herbaceous standing crop in savanna of three vegetation types at Kainji Lake National Park, north-western Nigeria, ranging from very open savanna to woodland. The areas had previously been burnt annually, probably in January, for many years. Without clear felling, Afolayan subjected the plots to controlled burning for two years. Grass dry weight ranged from 88 to 264 g m^{-2} in the fire-protected plots, from

110 to 393 g m^{-2} in the early burnt, and from 244 to 622 g m^{-2} in the late burnt plots, with late burnt plots in comparable vegetation always having the greatest yield. Isichei (1979) reported two-year mean values of 324 g m^{-2} for open savanna and 259 g m^{-2} for woodland, both burnt in January. Very interestingly, Afolayan's data allow estimation of grass growth rates, using the exponential equation

$$r = \frac{\log_e N_t - \log_e N_0}{t}$$

and analysis of variance shows significant difference between rates with burning treatment at $P<0.01$. Growth rates were highest in unburnt and early burnt plots (0.49, 0.47) and lowest in late burnt (0.42) where the greatest yield was achieved. Examination of regression equations (time : yield) show that the highest Y-intercept occurs with the late burnt plots, indicating that the most grass is already present at the beginning of the growing season. This initial grass may represent the flush stimulated by late burning, whereas the flush stimulated by early burning may have been unable to withstand the long period before the rains and so dried away. That this might be so is suggested by there being little difference between late and early burning yields in derived savanna (Olokemeji) where, because of moister conditions, early flush may survive until the rains.

On the other hand, Opakunle's current work (unpublished) shows that the growth rate itself is greater at least in the first month in unburnt grass.

The Red Volta (Ghana) data differ sharply from both the derived (Olokemeji) and the northern Guinea (Kainji Lake) data in that the grass biomass (dry weight) is significantly the greatest in the early burnt plots (260 g m^{-2}) and greater in the fire protected (182 g m^{-2}) that in the late burnt plots (144 g m^{-2}). This suggests that in the drier, northern savanna shading may be conducive to grass growth, possibly through amelioration of temperature with consequent reduction of transpiration and respiration (Sanford *et al.*, 1982b).

(c) Summary

Very obviously, fire decreases the density of woody stems and late (intense) burning has a greater effect than early burning. In very humid savanna (as in derived savanna regions) the wood volume may sometimes be greater in early burnt plots than in fire protected ones in early successional stages, as smaller mean girth in the fire-protected area may not be compensated for by the increase in stem density.

The effect of fire on herbaceous production varies greatly with climate. In drier, more marginal regions early burning or even fire protection may result in higher grass yields than late burning. In the southern derived savanna, time of burning makes little difference in yield, but somewhat greater yield is achieved with late burning. In intermediate (Guinea savanna) regions, late burning usually appears to increase grass above-ground biomass, although no results of long-term experiments are available.

V. The Savanna Zones of West Africa

So far, an attempt has been made to define savanna and to review its probable causes. The zonation scheme of Keay (1959) and Aubréville *et al.* (1958) has been consistently used. The most difficult task remains: the attempt to express what is actually meant by these zones.

Papadakis (1965) has published a useful synthesis of the vegetation maps of West African countries. He uses the terms coastal savanna, transition forest (between rain forest and Guinea savanna), Guinea savanna, Sudan savanna, thorny tree or shrub (Sahel) savanna and montane savanna. This differs from Keay, but is in agreement with Chevalier (1900) in not separating Guinea savanna into southern and northern Guinea. Keay argues for this separation in his *Outline of Nigerian Vegetation*, but we have found, at least from the standpoints of management and agricultural potential, that the separation is not particularly useful: in practice it is certainly often difficult to make the distinction except perhaps on purely climatic grounds. (It may be argued that Clayton's (1957) separation of Sudan into sub-Sudan and Sudan savannas is more meaningful, but this has not been found useful in practice either.) Papadakis's use of 'montane' is somewhat looser than we would accept. We find Boughey's (1955) classification for tropical Africa more realistic in which 'montane' refers to vegetation found above 3000 m. According to this usage, montane savanna would be found in West Africa only on Mount Cameroun and on the island of Bioko. Hall and Medler (1975a, b) use the term 'highland' for vegetation above 1220 m (4000 ft). Most West African high areas could thus well be termed either highland or sub-montane savanna and woodland. We find that vegetation changes appreciably even when the elevation reaches only 760 m; this corresponds with the demarcation between Boughey's lowland and foothill zones. The factor largely responsible for change, as one of us has discussed previously (Sanford, 1974) is moisture availability. (It should be realized, however, that the classification of vegetation according to elevation alone is fraught with many of the same difficulties as classifying it according to climate or soil alone.)

1. *Conventional zonation*

Most recently, White (1983) has completed the *UNESCO/AETFAT/UNSO Vegetation Map of Africa* (Fig. 1.1). 'Savanna' is not used at all because the author not only finds its definition lacking in precision but also considers it a foreign word to Africa. (It comes via the Spanish from the language of the

Caribbean Indians and was first used in 1535 by Oviédo to designate clearings in the forest. It is difficult to see that this term is any more foreign to Africa than the English and French terms so widely used.) The approximate equivalents from this most recent work will be added at appropriate points in this chapter.

The conventional zonation most current in West Africa will very briefly be reviewed and then a summary of our suggested, more detailed classification of savanna more or less as we presented it at the Nigerian Man and Biosphere Workshop in New Bussa (Sanford, 1982b) will be proposed.

(a) Guinea Savanna

Southern Guinea and transition or derived savanna are classed by White (1983) as mosaic lowland rain forest and secondary grassland with most of the region being Guineo-Congolian in vegetation with the more northerly region a mosaic of lowland rain forest, *Isoberlinia* woodland and secondary grassland. This implies that the entire region is 'derived' — a position with which we disagree.

The northern Guinea zone is termed Sudanian woodland with abundant *Isoberlinia*.

Guinea savanna (the zone of gallery forest of Rousseau (1932), 'forêt clairierée tropophile', Jacques-Felix, 1950, 1951) is a region of high grass at least 1.2 m tall; characterized by such trees as *Lophira lanceolata, Daniellia oliveri, Parkia clappertoniana, Isoberlinia doka* and *I. tomentosa*, various *Combretum* spp., and *Terminalia* spp. These may be close enough together to form a closed or nearly closed — although light and irregular — canopy (woodland), or scattered (bushland or open savanna), or species of economic use, particularly *P. clappertoniana, Butyrospermum paradoxum* and *Adansonia digitata*, may be scattered at some distance apart in open grassland almost free of shrubs or smaller trees (parkland). Keay (1959a) describes southern Guinea as open woodland with high grasses from 1.5 to 3 m tall, trees up to 12–15 m (rarely up to 30 m) high with rather short boles and broad leaves. The trees *Lophira lanceolata, Daniellia oliveri, Afzelia africana, Hymenocardia acida, Piliostigma thonningii*, and *Vitex doniana* are especially common. The grasses are mainly *Andropogon* spp., *Hyparrhenia* spp., *Schizachyrium* spp., and *Pennisetum* spp. Transition or derived savanna (Fig. 5.9) is intermediate between lowland rain forest and southern Guinea savanna and is considered anthropogenic both in origin and maintenance — in other words, it is largely defined by its presumed cause. This becomes a sticky problem in logic when we consider that southern Guinea savanna is also often thought to be caused and/or maintained by man. One can try to fall back on age and say that derived savanna is more recently anthropogenically formed. In practice, however, the difference is broadly physiognomic and structural, with derived savanna being largely in mosaic patches or in very irregular bands containing a number of forest trees and many oil-palms (*Elaeis guineensis*); the grass, *Andropogon*

Fig. 5.9. Transition or derived savanna, with a dense stand of *Andropogon tectorum* in the foreground and a mixture of small savanna and forest trees in the background. (Photograph by W. W. Sanford.)

tectorum, is especially abundant, and this gradually almost drops out as one proceeds northward into Guinea savanna.

Coastal savanna is in our opinion a form of Guinea or humid savanna closely allied to transition (derived) savanna. Keay (1959b), in his explanatory notes for the vegetation map of Africa south of the Tropic of Cancer, terms this formation 'coastal forest-savanna mosaic' or, in the Ghana region, 'coastal scrub and grassland zone', noting that because of the high atmospheric moisture derived from the nearby sea, the vegetation is somewhat different from inland regions of the same annual rainfall. The species found tend to be a mixture of inland savanna species and forest species. White (1983) terms this 'West African coastal mosaic' occupying an anomalous dry area of the extensive zone of transition between Guineo-Congolian and Sudanian regions. Such vegetation occupies a strip about 25 km wide along the coast from about 1° W to 2° 40′ E, although any exact border is impossible to set as it is continuous with what can be termed typical Guinea savanna (*sensu* Keay, 1959a). (It should be noted that this latter type of vegetation dips southward from western Nigeria through Ghana.) Coastal savanna has been largely determined by the moisture regime in the first place, and secondarily by very long-term grazing, land clearing, etc. The more or less open grasslands extending all the way to the sea in this area long ago very probably contributed to the early rise and power of the kingdom of Dahomey and later to foreign colonization and the slave trade. Savanna is much more hospitable to the deeds of men, whether they be peaceful or violent, than is forest. (And of course man arose from hominoid ancestral animals in the arid and semi-arid savannas of East Africa around Lake Turkana rather than in forested Africa or moist, fertile Mesopotamia.)

The rainfall/evapotranspiration ratio begins to decrease as we move from central Nigeria westward at about Ibadan (ratio of 1.00). South-west of this city, at Pobé on the Nigeria–Republic of Benin border, the ratio is also 1.00 even though this site is much nearer the sea and rainfall generally increases seawardly. The ratio at Ondo, Nigeria, at the same latitude but eastward is 1.49. Lagos, Nigeria, on the sea, has a ratio of 2.10, while Cotonou, Benin, also on the sea, has a ratio of 1.38; further west at Ouidah, Benin, the ratio has dropped to 0.99 and at Lomé, Togo, to 0.89. At Accra, Ghana, the ratio is only 0.70. These ratios correspond to those found in typical derived and southern Guinea savanna zones (see Section III. 1, above). Westward from here, the ratio again rises so that at Takoradi, Ghana, it is 1.36 and at Axim, 2.60.

This strange climatic dip has lead to the vegetational anomaly long termed the 'Dahomey Gap' which is ancient enough to have affected the West African distribution of birds (Moreau, 1966, 1969) and permitted some speciation in plants as well. In general, the coastal vegetation of Ivory Coast is similar to that of Cameroun and the extreme south-east of Nigeria, but a number of differences occur. The Accra plains have a remarkable concentration of endemic and disjunct species (Jeník and Hall, 1976).

East of Accra, there are extensive regions of impacted soils with such poor drainage that low-lying pockets are seasonally waterlogged, while higher ground is occupied by steppe-like vegetation — low grasses, often with rolled or cylindrical leaves, and sparsely scattered small shrubs. Some areas are almost completely bare. Slightly further inland, hills are covered with woody vegetation typical of transition savanna woodland of Nigeria and are surrounded by open grass plains, maintained in such an open condition by semi-nomadic grazing. This is in contrast with the more humid plaints west of Accra where farming is common. Thus the Ghana coastal plains east of Accra are very different from the western portion (often differentiated as the Winneba Plains). The coastal savanna of Benin and Togo varies from littoral sand communities of coconut palms and brackish marshes to scrub vegetation resembling highly disturbed transition savanna.

While the savanna of the coastal regions of Benin, Togo, and central and eastern Ghana have been brought about primarily by the climate and secondarily by man who, acting as positive feedback, has followed this more open vegetation to the sea and made it more open still by his activities, soil has had considerable effect as well. The soils of the Dahomey Gap are in general poor. Both ferrisols and ferrallitic soils occur (Ahn, 1970). The ferrisols tend to be richer and better structured than most tropical soils of comparable depth, while the ferrallitic soils have a low cation exchange capacity and are characterized by advanced leaching and weathering. In the area of lowest rainfall/evapotranspiration ratios, the better ferrisols may possibly somewhat compensate for the unfavorable moisture regime so that small patches of dense vegetation are not uncommon and many forest species manage to survive. Usually, however, forest remnants are associated with topography, occupying valleys which not only accumulate richer, deeper soil but also are sheltered from drying winds. On the other hand, richer soils have lead to more intensive agriculture. That woody vegetation is often almost entirely missing is the result of man's continual interference. The most detailed studies of the vegetation of the Accra plains are those of Jeník and Hall (1976) and Liebermann (1982).

Northern Guinea savanna is more similar to the East African 'miombo' and is a generally open woodland or 'bushland' with grasses somewhat shorter than in southern Guinea savanna. Trees with compound leaves become relatively more abundant. Particularly frequent species are *Isoberlinia doka* and *I. tomentosa, Terminalia avicennioides, Detarium microcarpum, Piliostigma thonningii, Parinari polyandra* and *P. curatellifolia* (=*Maranthes* spp.), *Burkea africana*, many *Combretum* spp. Grasses are mainly *Andropogon, Hyparrhenia*, and *Schizachyrium* spp. (Fig. 5.10).

(b) Sudan Savanna

This zone is not differentiated from northern Guinea by White (1983) but is said to be composed of Sudanian woodland with abundant *Isoberlinia*, Sudanian undifferentiated woodland with islands of *Isoberlinia* and, in the northernmost areas, undifferentiated woodland. Keay's Sahel savanna becomes Sahel *Acacia* wooded grassland and deciduous bushland.

The Sudan zone is termed 'savane typique' and said to be characterized by *Butyrospermum paradoxum* by Rousseau (1932), and 'forêt clairierée tropophile' characterized by *Butyrospermum* and *I. doka* by Jacques-Felix (1950, 1951). It is often open grassland or parkland with scattered *Butyrospermum* or *Adansonia* trees or low woodland or bushland. Grasses are lower, usually under 1.2 m tall. Cultivation is very extensive, particularly of millet and guinea-corn, and this is probably responsible for the greater prevalence of bushland and parkland as opposed to woodland. The lower grasses may also derive from cultivation, often being colonizing weedy species, with annuals abundant. Woody plants are *Acacia* spp., many Combretaceae (especially noticeable is *Guiera senegalensis*), *Piliostigma thonningii* and now *P. reticulatum, Balanites aegyptiaca, Adansonia digitata, Capparis* spp., *Monotes kerstingii*, and *Anogeissus leiocarpus*, which is distributed from the fringing rain forest to Sahel scrub but is often particularly noticeable here as a larger tree, many times in clumps of several. It is interesting to note that *Anogeissus*,

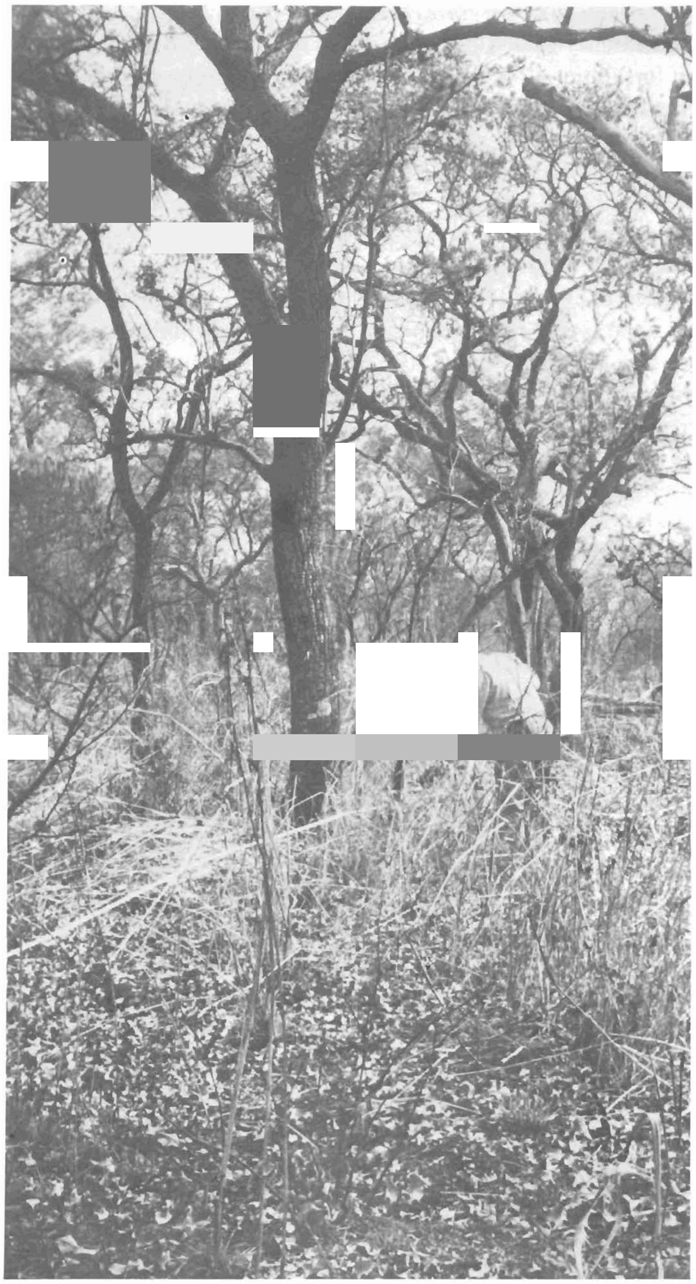

Fig. 5.10. Mature bushland in northern Guinea savanna after January burning. (Photograph by Sheila Jeyifo).

Balanites, Monotes, and occasional *Adansonia* extend into the Sahel area to a limited degree. (It should be emphasized, in case anyone thinks taxonomic descriptions of vegetation zones too easy, that most of the woody species mentioned extend from the derived savanna zone throughout the Guinea savanna and into the Sudan zone but vary in abundance.) (Fig. 5.11).

(c) Upland Savanna

Highland or submontane grasslands (montane elements of White, 1983) are well developed in the Moka area of the island of Bioko, in the western Cameroun highlands and in the Obudu and Mambila plateaus of Nigeria: all of these highlands are related in geological formation, having been formed by volcanic action. In all of the areas, there is sufficient moisture for forest growth and often fertile soil as well, although because of very heavy rainfall leaching is extensive wherever vegetation cover has been removed. Open grassland has apparently been maintained largely by animal overgrazing and cutting and burning by man, but in some local areas, leaching and erosion have been extensive enough in the past to create edaphic grasslands. Species lists of a typical West African highland (the Obudu Plateau, Nigeria) are given by Hall and Medler (1975a, b; see also Hall, 1971). These highland areas are usually open grassland in which the grasses are less than 1 m tall; most common species include *Eragrostis* spp., *Hyparrhenia* spp., *Sporobolus* spp. — espe-

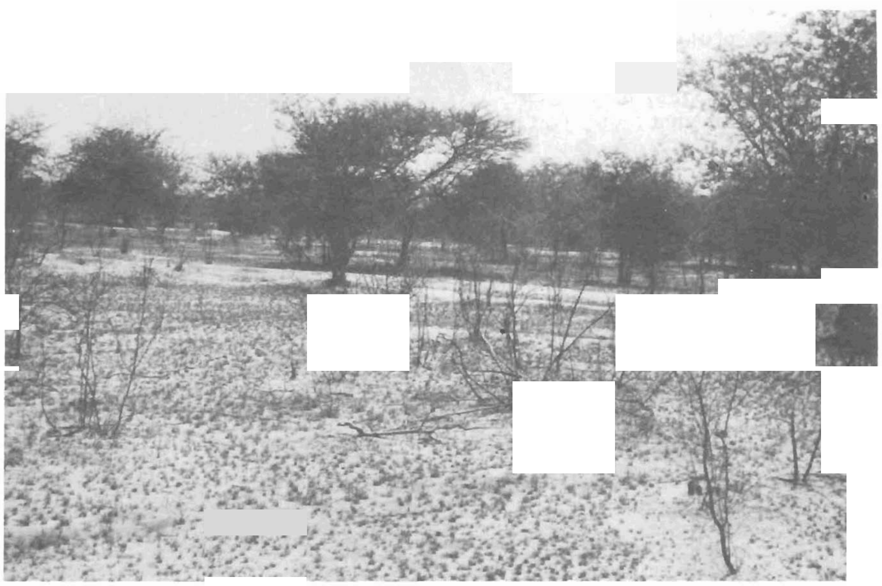

Fig. 5.11. On the border between Sudan savanna and Sahelian scrub, near Maiduguri, north-eastern Nigeria, in early July. (Photograph by W. W. Sanford.)

cially *S. africanus*, with a very few woody plants except in the ravines where forests or woodlands commonly develop. Woodland in such local areas is probably accounted for both by deeper and more fertile soil and by less disturbance from man because of its inconvenience for farming, etc. Tree species found are those of montane and submontane forests. The common temperate zone fern, *Osmunda regalis*, is often found along watercourses where there is no tree shading, and *Pteridium aquilinum*, the temperate zone 'bracken', may occur in extensive, almost closed stands (Fig. 5.12).

(d) A proposed savanna classification

One of us (Sanford, 1982b) has worked out a scheme for savanna classification and mapping which is currently in the experimental stage. The aim is to provide a feasible system from the standpoint of labour input which at the same time provides practical information on a scale of detail suitable for management planning. The conventional zonation terms are retained as the framework, but they are defined climatologically. The second hierarchical step concerns soil and topography; the third, physiognomic and structural features of the vegetation; the fourth, taxonomic features. This scheme is outlined below.

1. Climatic-ecological zone	Length of rainy season (days)	Precipitation/ evapotranspiration
(a) Transition savanna	> 200	0.66–1.0
(b) Guinea savanna	150–200	0.40–0.75
(c) Sudan savanna	110–150	0.21–0.40
(d) Sahel short grassland	< 110	< 0.21

2. Topography and soil

Topography: Broken (i.e. ironstone ridges, inselbergs, small hills and valleys, mountains) with local slopes: (1) steep, (2) moderate, (3) gradual; undulating; plain.

Soil: Ferrallitic (Food and Agriculture Organization ferrasols) (1) yellow-brown; (2) red, ferruginous (FAO ferric luvisols) (1) on sandy parent material, (2) on crystalline acid rocks, (3) non-differentiated. Ferrisols (weakly developed soils and rocky areas) (1) young soils, (2) lithosols, (3) soils on iron-pan crusts. Brown and red soils of arid and semi-arid regions. Volcanic soils or soils with volcanic elements: sand/clay ratio; percentage organic matter (or C).

Fig. 5.12. Montane savanna in the Cameroun Highlands. (Photograph by W. W. Sanford.)

3. Physiognomic and Structural Features of the Vegetation

Overall physiognomy based on woody plant density:

(a) Woodland: Woody plant density — one tree per less than 40 m^2, of which at least 35 per cent are over 30 cm in girth.

(b) Tree savanna: Woody plant density — one tree per from 40 to 100 m^2 of which over 35 per cent are over 30 cm in girth.

(c) Bushland: Woody plant density — one tree or shrub per less than 40 cm^2 of which less than 35 per cent are over 30 cm in girth.

(d) Wooded savanna: Woody plant density — one tree per over 100 m^2 of which over 25 per cent are over 30 cm in girth.

(e) Shrub savanna: Woody plant density of one per from 40 to 100 m^2 of which less than 35 per cent are over 30 cm in girth.

(f) Open or shrub grassland: Woody plant density of one per over 100 m^2 of which less than 25 per cent are over 30 cm in girth.

(g) Permanent or seasonal savanna swamp (subdivided as (a–f) above; see Fig. 5.13).

(These formations are prefixed by 'highland' when found above 1220 m.)

Size-class distribution of woody plants

Each of the seven formations is classed according to the distribution of girth sizes of all woody plants over 1 m high and at least 1 cm in girth (at the

Fig. 5.13. Surface iron-pan with *Loudetia* cf. *arundinacea* growing in crevices, and abnormally luxuriant vegetation growing in the drainage area of the pan (Jos Plateau, Nigeria.)

mid-point if under 3 m in height, at breast height otherwise). (Goodness of fit may be tested by chi-square or G tests).

Mature — 59 per cent of the woody plants from 1 to 20 cm in girth; 21 per cent from 21 to 40 cm; 10 per cent from 41 to 60 cm; 5 per cent from 61 to 80 cm; 3 per cent from 81 to 100 cm; 3 per cent over 100 cm in girth.

Juvenile — if there is significant deviation from the above distribution as increase in number of stems in size classes below 61 cm.

Old — if there is significant deviation from the above distribution as increase in number of stems above 60 cm.

4. *Taxonomic composition of the vegetation*

Each formation is characterized by the two to four most abundant woody plants and by the two to four most abundant grasses.

VI. Management problems

1. *Conservation and improvement of soil fertility*

(a) Clay in the soil

While savanna regions may suffer drought for part of the year, for another part rainfall is so intense that leaching and erosion may occur. Leaching is only prevented by ion-adsorbing properties of the soil and by plant uptake of soluble nutrients and their storage in organic molecules. Soil properties preventing leaching are the presence of clay and organic matter. Clay particles, being negatively charged, hold cations. The most abundant clay in tropical soils is kaolinite, which is, unfortunately, relatively inefficient as a cation adsorber because of its large particle size (up to 1 μm in diameter). Much more efficient are the rarer montmorillonite clays. Jones and Wild (1975) report data from various sources concerning the mean percentage and range of clay in various tropical soils. The two most common soils in West Africa are ferruginous tropical and ferrallitic soils, making up approximately 58 and 10 per cent respectively of West African savanna soil. Both contain only about 9 per cent clay, with a range from 0.0 to 34 per cent. Vertisols are richest in clay (mean 52 per cent, range 22 – 79 per cent, but they make up only about 1.9 per cent of West African savanna soils. The clay of these soils is about 63 per cent montmorillonite, whereas ferruginous and ferallitic soils contain mainly kaolinite.

While clays are helpful in holding ions, they are very fine particled and tend to lead to soil compaction with the result that rain, particularly the first heavy rains of the season, do not penetrate but run off, carrying soil particles and dissolved nutrients. Soils tending to become compacted must be kept well covered by vegetation and/or litter. As mentioned earlier (Section IV.1) burning may increase soil compaction as well as remove plant cover and litter and should, therefore, be carried out cautiously over heavy soils.

Not much can be done to change the clay content of soil. While addition of organic matter is effective in lightening and improving the texture of soils in temperate zones, rapid mineralization makes this relatively ineffective in the tropics. The best means of conserving and utilizing heavy clay soils appears to be to keep them covered with grass under a light, high tree canopy. Leaf fall from the trees will protect the soil after grass burning and underground biomass will add some humus to the soil.

'*Fadama*', seasonally inundated land along streams and in floodplains, contains on an average 24 per cent clay (range 1.5–71.5 per cent) and the clay is often montmorillonite (Jones and Wild, 1975). Primary production is potentially very high in such restricted regions (e.g. Afolayan (1977) reported the maximum standing crop from fadama along the Oli River in Kainji Lake National Park, northern Nigeria, to be 172 per cent of the maximum achieved in nearby woodland savanna and 323 per cent of that achieved in almost adjacent *Burkea–Terminalia* open savanna). Because of this production potential, such restricted regions are increasingly being utilized for agriculture. This has disturbed nomadic and transhumance movements of livestock, as formerly such valley bottoms were grassland refuges for the dry season. Clearly, dry season substitutes for *fadama* grazing must be found (Fig. 5.14).

Fig. 5.14. Savanna marsh along a river. The very tall grass is *Pennisetum purpureum*, 'elephant grass', (Photograph by W. W. Sanford.)

(b) Organic matter in the soil

The importance of organic matter in soil has been discussed in sections II.2 and IV.2, but a few additional comments are needed. The main organic component of soil is humus, a collective term for an amorphous group of colloids containing about 60 per cent carbon and 5 per cent nitrogen. According to Ahn, (1970, p.123), West African savanna soils contain from 1 to 3 per cent organic matter. Micro-variation from metre to metre is often greater than mean variation from hectare to hectare as the presence of unmineralized organic matter so much depends on vegetation, especially trees.

While it has been shown above (section IV.2) that the organic matter content of soil is more dependent on below-ground biomass than on surface litter, litter is extremely important in protecting soil from runoff and erosion and, by shading, lowering soil temperature and so slowing the rate of mineralization. Mulching with crop residue has proved very effective in accomplishing these aims as well as in controlling weeds, but crop residues are becoming increasingly important as livestock fodder, and this trend will continue as pressures against nomadism increase (see section VIII.3, below).

(c) Vegetation cover

(i) In relation to water In section II.2 we showed how important a multi-layered above-ground cover of vegetation and a below-ground root network

are in maintaining an ecosystem. It is the disturbance of such a vegetation system which most frequently leads to deterioration of the soil — often irreversibly. For example, in Ivory Coast savanna, bare soil with a slope of 7 per cent lost from 24 to 32 per cent of the rain as runoff and from 10 477 to 11 770 t km^{-2} yr^{-1} (10.4–11.8 g m^{-2}) of soil; an experiment in Senegal showed 40 per cent loss of rain as runoff from bare soil and 17 per cent loss from rather sparse grassland, with soil loss of 2313 t km^{-2} yr^{-1} (2.3 g m^{-2}) from bare ground and only 488 t km^{-2} yr $^{-1}$ (0.49 g m^{-2}) from the grassland (CTFT, 1969). Relative erosion has been estimated by Roose (1975); if erosion from bare ground is rated 1, erosion from forest is 0.001; from savanna in good condition, 0.01; from palms, coffee, or cocoa with cover plants growing beneath, 0.1; from yams, cassava, 0.2–0.8; from ground-nut, 0.4–0.8; from maize, sorghum, millet, from 0.3 to 0.9 (Fig. 5.15).

Leaching from well-developed savanna is very little, but may be considerable from farmland. For example, in northern Nigeria, with a mean annual rainfall of 1114 mm, leaching losses from grain fields range from 1.6 kg ha^{-1} yr^{-1} of sodium to 2.1 and 4.9 kg of magnesium and calcium respectively, and from 6.3 to 7.4 kg of potassium and nitrogen respectively (Jones and Wild, 1975, p. 141).

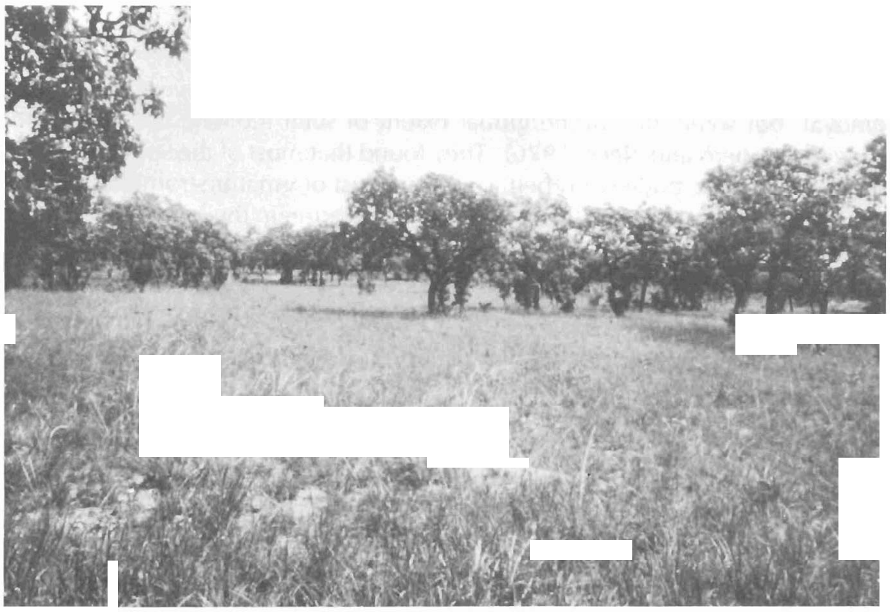

Fig. 5.15. Tree savanna in a *fadama* along the Oli River in Kainji Lake National Park, north-western Nigeria. The large trees are *Terminalia macroptera*. (Photograph by W. W. Sanford.)

The factors which conspire to deplete soil resources are heavy rains (both amount per unit time and drop size are important parameters), land slope and fine soil particle size. Because of the first two factors, highlands may be especially subject to leaching, runoff, and erosion. For example, the Obudu Highlands of eastern Nigeria receive about 4300 mm of rain during 275 days. The soil is leached and acidic. The area is so erosion prone that where grass has been trampled by human footpaths or cattle paths, erosion channels soon start. We have seen some that are yet only the width of the path (about 50 cm) but already 1.5 m deep.

Very often sheet erosion may remove even more soil than gully erosion, but it is not as readily discerned. This is true of lowlands as well as highlands. For example, it has been stated (Brammer, 1962) that erosion was not a serious problem in Ghana, but in 1972, Adu (1972) described erosion in the Navrongo–Bawku area of northern Ghana and estimated that 40 per cent of the land was affected by sheet erosion; as much as 8 per cent of the land in this area had lost both A and B profiles.

(ii) In relation to wind Water is not the only important factor in causing erosion: wind is also a menace. Each year, throughout West Africa, a haze of dust, largely fine diatomaceous earth, is brought down from the Sahara. European explorers and settlers of the eighteenth century referred to this, the harmattan, as 'the smokes', a visually apt term. A small amount of nutrient material is deposited with the dust, but this is of little importance.

Of considerable importance is the wind removal of loose soil from Sahelian and Sudan zones within West Africa. We can find no reliable figures of soil removal, but some idea of the global extent of such removal is given by the study of Prospero and Nees (1976). They found that most of the solid aerosol of the North Atlantic trade wind belt is mineral dust originating from the arid and semi-arid regions of West Africa. Mean concentration in the atmosphere above Barbados, West Indies, during June, July, and August ranged from 6.2×10^{-6} g m^{-3} in 1965 to 26.5×10^{-6} g m^{-3} in 1973. The authors relate this great increase to the Sahelian drought.

2. Conservation of vegetation

(a) Gene conservation

Obvious necessities for conservation of vegetation are the prevention of erosion, runoff, and leaching, the maintenance of watersheds and implementation of efficient mineral cycling (see also section VII.4, below). Other than these, there are the less obvious needs of gene conservation for future use in plant breeding and the conservation of attractive scenery associated with quality of life and recreation.

Plants of savanna areas are often subject to marginal environments as regards moisture regime, temperature range, soil nutrient status, and herbivore and disease predation and thus may possibly provide valuable genetic material for improving resistance and habitat amplitude of economic plants. This is perhaps most obviously true of the Gramineae, most of which have C_4 metabolism and are thus adapted to high temperatures and light intensity. (The first product of CO_2 fixation is a 4-carbon molecule instead of the usual 3-carbon phosphoglycerate; plants having this metabolic pathway do not have appreciable, light-induced respiration and so do not waste carbon substrate under conditions of high light intensity; at the same time the photosynthetic mechanism is less sensitive to heat and so continues to function efficiently at much higher temperatures than is the case with C_3 plants.)

Besides such high-temperature tolerance, savanna plants often show remarkable tolerance of drought conditions and, in some cases, of high soil/water salinity. For example, some hydromorphic soils in northern Nigeria have pH values as high as 9.6 in the middle horizon where there are high concentrations of calcium and sodium salts (Jones and Wild, 1975, p. 41, citing Pullan, 1962). Plants growing in such an environment must be unusually tolerant of high salt concentrations. Areas around Lake Chad are also halomorphic, and with long irrigation many savanna soils may accumulate salts to a toxic level.

An interesting example of insect resistance is found with the mature seeds of tropical American *Mucuna* (Papilionaceae). (Some tropical American *Mucuna* spp. are grown as pasture plants cover crops in West Africa: also there are six species of this genus found in West Africa, one of which, *M. pruriens*, is also found in America.) Several species of this genus have sufficiently high concentrations of L-dopa (3,4-dihydroxy-phenylalanine) in the mature seeds to prevent insect attack (Rehr *et al.*, 1973).

(b) Scenic amenity

Obviously, no one enjoys viewing bare earth for long, but some types of vegetation are more aesthetically pleasing and/or more suited to recreational activities than others. In general, forest and woodland are considered more pleasing than bushland, scrub, or open grassland. As discussed earlier, woodland is the most nearly stable (perhaps 'climax') savanna structure and so is desirable from more utilitarian considerations as well. While it is very resistant to natural environmental fluctuations and even to annual burning, it is, of course, quickly destroyed — and for many, many years — by cutting. Increased firewood demands throughout West Africa are making serious inroads on natural woodland. Even more disastrous is large-scale 'Green Revolution' cultivation. Clearly, it is necessary to determine which areas are suitable for cultivation without endangering future soil fertility through erosion and leaching and which areas should be left as woodland. Unfortunately, such decisions are often made according to criteria far from ecological considerations.

3. Nomadism, transhumance, and settled agriculture

Throughout the savanna regions of West Africa, conflict between traditional patterns of nomadism and transhumance livestock management and settled agriculture is increasing in range and intensity (Figs. 5.16 and 5.17). Man-made lakes such as the Volta in Ghana and Kainji Lake in Nigeria not only flood grazing land but bring about land-use transformation through irrigation over large surrounding areas. Growing populations and increasing demands for a higher standard of living have forced all countries to implement various agricultural expansion schemes and put more land under monoculture and intensive agriculture. Milligan and Sule (1982), of the International Livestock Centre for Africa, have recently discussed this problem. Possible solutions are: (1) settlement of the traditional herdsmen with managed pastures or ranches; (2) restricted movement with supplementary livestock feeding from such agricultural by-products as cottonseed cake, or from hay or insilage prepared from natural savanna grasses; or (3) planned transhumance with natural savanna management. Quite clearly, no one alternative provides a satisfactory solution and all must be judiciously used. From economic and logistic considerations, the third choice will probably be the most extensively applied

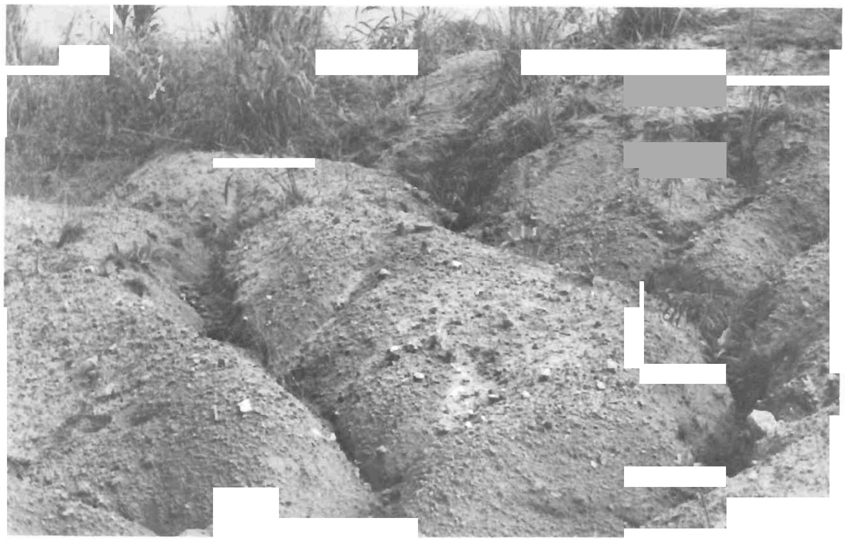

Fig. 5.16. Gully erosion beginning where the grass cover has been removed. (Photograph by A. O. Isichei.)

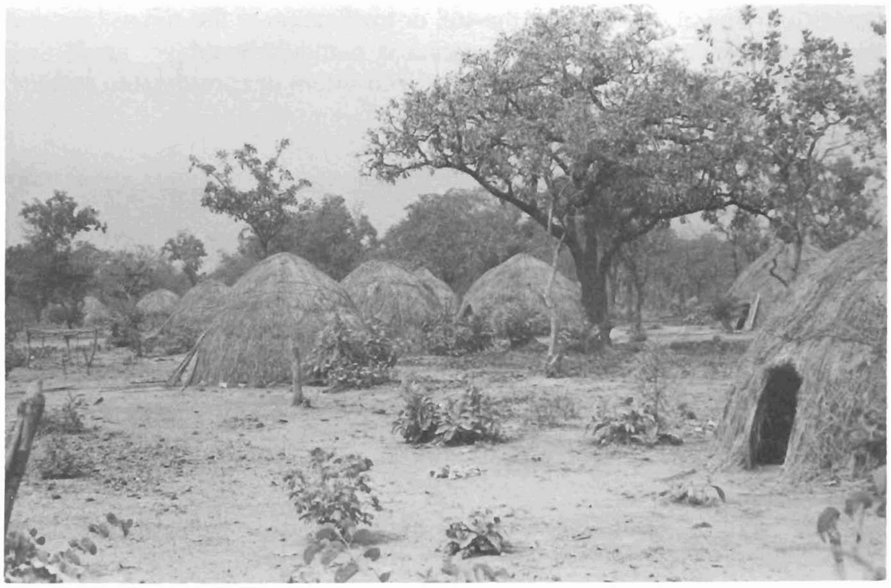

Fig. 5.17. Dry season shelters of Fulani herdsmen in southern Guinea bushland. Modified transhumance is practised with these herdsmen taking their livestock further north soon after the rainy season beings. (Photograph by W. W. Sanford.)

for a long time. Supplementary feeding is, in the case of products such as seed cake, very expensive, and in the case of hay and insilage requiring of labour at times and locations where it is not available. In all cases the logistics of such feeding is a serious constraint. It is very likely, however, that soon the tall grasses of the humid savanna must be utilized more efficiently than at present. Cutting during the mid-growth period (about three to three and a half months after the start of the rainy season, usually late June to mid-July) would provide a large bulk of material with fair protein content. (Protein concentration declines almost exponentially from the period of flushing to the time of maturity and maximum standing crop.) Cutting would induce regrowth and at least two, in some areas three, crops could be harvested for hay or insilage per year. This raises an ecological question requiring urgent investigation: What will be the effect on the soil of such intensive harvesting and removal of nutrients from the system?

4. *Desertification*

A practical definition of desert is any temperate or tropical region where almost no primary production occurs. This situation can be brought about by either drought or mineral depletion of the soil or toxification of the soil as by salt or heavy metal accumulation. The savanna is particularly subject to all three conditions and so must be considered an ecosystem of considerable fragility.

(a) Climatic fluctuation and change

The recent seven-year Sahelian drought in Africa turned the attention of many climatologists to the possibility of climate change, but no clear-cut evidence has yet emerged. Changes several thousand years ago are known (and briefly discussed in section III.1), but more recent changes are problematical. The possibility which has received the most attention is the increase of carbon dioxide in the atmosphere. Gates (pers. comm., 1977) has reported that atmospheric CO_2 is increasing at about 1.0 ppm yr^{-1}. This would result in a doubling of the pre-industrial CO_2 concentration by about 2025–2050 and would lead to an average global temperature increase of about 2.0 C. Such an increase in marginal areas, such as the drier savannas, would result in drought and probable desertification.

Of less controversial importance are the year-to-year climatic fluctuations and possible short-term (most often from 10 to 60 years) cyclic tendencies of rainfall. In areas of marginal water availability, such as the entire Sahelian area and at least part of the Sudan zone, such variation means that in some years crops will fail and available fodder will not be enough to support the livestock population. In effect, such areas are utilized beyond their carrying capacity for some years and 'crash' in other years. The recent Sahelian drought was such a crash. An idea of yearly variation is given by the mean precipitation and standard deviation for 10-day periods at Maiduguri in north-eastern Nigeria on the border of Sudan savanna and Sahelian short grassland (11° 51′ N, 13° 05′ E): the standard deviation averages 114 per cent of the mean rainfall.

(b) Anthropogenic effects

Even more important than climatic fluctuations are the disruptive activities of man. These include burning of vegetation, heavy grazing by domestic livestock, wood-cutting, and cultivation. All of these have been mentioned before so their probable impact on savanna desertification will now be only summarized. Grove (1973) has stated that 'burning of the vegetation is possibly not a very important agency in the process of desertification. . . . An exception to this general rule might be woodland alongside watercourses.' We agree with this assessment, but would like to amplify slightly the exception. The land along watercourses is often steeply sloping so that if vegetation is removed, erosion may be drastic. We have seen very recent evidence of this in the Nigerian Obudu Highlands where recent fires have destroyed woodlands along steep ravines; the topsoil has already nearly disappeared.

Heavy grazing, while extremely serious in many regions of East Africa, is not extensive in West Africa. One reason is the seasonal livestock migration enforced by custom, tsetse-fly, and the unpalatable character of tall grasses as the season progresses (Fig. 5.18). Exceptions do occur in some Sudan regions, in some highland areas (the Jos Plateau in Nigeria, for example), in the Sahelian region in general, and around boreholes in particular. In the latter case, water, brought by modern technology to alleviate chronic water shortage, has brought about intensive settlement near water resulting in overgrazing to such an extent that near-desert surrounds many boreholes. We have seen this from the ground in driving from Maiduguri, Nigeria, to Lake Chad, and a remote-sensing specialist told us how puzzled he was at first by the blank white areas surrounding boreholes. Besides this extreme case of livestock concentration, the changes in land use mentioned in section VI.3 have brought about more intensive grazing of the ever-shrinking free-range areas. In the near future this may lead to desertification in many areas now well covered with vegetation.

The recent increase of firewood cutting has already been mentioned (Section VI.2b). Mortimore and Wilson (1965) have estimated that nearly three-quarters of Kano (Nigeria) city's firewood consumption of some 75,000 t yr^{-1} is brought in by donkey from within a radius of c. 20 km. As Kano and similar cities are

Fig. 5.18. Cattle moving southward into Guinea savanna in January (mid-dry season). The vegetation is mature bushland, near New Bussa, north-western Nigeria. (Photograph by Sheila Jeyifo.)

Fig. 5.19. Firewood collected near Jebba in the southern Guinea zone of Nigeria ready to be transported out. Donkeys are being replaced by lorries and the radius of collection around the large towns grows ever wider. (Photograph by Sheila Jeyifo.)

growing at a rate of from 5 to 10 per cent annually, the firewood problem will become great unless other fuels can be substituted (Fig. 5.19). Once woodland has been cut, its regeneration is difficult. As discussed earlier (Section IV.2), it is probably almost always necessary to provide a considerable number of years of fire protection before woodland can be established. In areas of heavy grazing by either domestic livestock or wild herbivores, an only slightly less long period of fencing is necessary.

The relationship between desertification and cultivation is too obvious to require amplification, although it should be pointed out that the importation of foreign, large-scale agricultural technology is increasing faster than the knowledge of how to manage it. Such management practices as no or minimum tillage, use of legume cover crops, crop rotation, and judicious use of fertilizers will certainly be necessary if disaster is to be avoided.

VII. Coda

Ultimately the fate of the people of West Africa rests upon the fertility of savanna soil. Savanna, covering up to nearly 80 per cent of the land area of many West African countries, must supply most of the food. A few years ago it might optimistically have been believed that no matter what was done to this land, European and American agricultural technology, improved breeds of crops and livestock, massive doses of fertilizer, and frequent spraying with pesticides and herbicides would solve all problems and not only maintain but increase food production. Such blind optimism is still harboured in the minds of a number of politicians, but citizens of developing countries have recently seen the possibility for massive physical loss of soil by water and wind, together with depletion of soluble minerals by leaching; they have seen that new breeds of plants and animals may not be suited to local conditions and that uniformity of breeds anywhere may lead to destruction by pests and disease; they have seen that pesticides and herbicides may have disastrous side-effects besides costing more money than is often available; they have seen that world-wide inflation may make the purchase of sufficient quantities of fertilizers impossible except by the richest countries (which perhaps need them the least); and that the existence of some crucial nutrients is finite. This knowledge is increasingly leading men everywhere to realize that the land and its ecosystems must be handled with the utmost care and that such care can only be learned by the local study of local conditions by men and women who have a tangible stake in the form of children and grandchildren in the future of the land.

References

Adejuwon, J. O. (1970). The ecological status of coastal savannas in Nigeria. *J. Trop, Geogr.*, **30**, 1–10.

Adeniyi, F. (1982). Mineral input in rain free-fall. In W. W. Sanford, H. M. Yesufu and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Proc. Man and Biosphere State-of-Knowledge Workshop: Kainji Lake Research Inst.*, New Bussa, 20–24 April 1980, pp. 352–376. Unesco/Kainji Lake Research Inst., New Bussa.

Adu, S. V. (1972). Eroded savanna soils of the Navrongo–Bawku area, northern Ghana: *Ghana J. Agric. Sci.*, **5**, 3–12.

Afolayan, T. A. (1977). Savanna structure and productivity in relation to burning and grazing regimes in Kainji Lake National Park. Ph.D. thesis, University of Ibadan.

Afolayan, T. A. (1978). Grass biomass production in a Northern Guinea Savanna ecosystem. *Oecol. Plant.*, **13**, 375–386.

Afolayan, T. A. (1979). Change in percentage ground cover of perennial grasses under different burning regimes. *Vegatatio*, **39**, 35–41.

Ahn, P. M. (1970). *West African Soils*. Oxford University Press, London.

Aubréville, A., Duvigneaud, P., Hoyle, A. C., Keay, R. W. J., Mendonça, F. A., and Pichi-Sermolli, R. E. G. (1958). *Vegetation Map of Africa South of the Tropic of Cancer* (Map sheet 1 : 10 000 000). Clarendon Press, Oxford.

Bazzaz, F. A. C. (1975). Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, **56**, 485–488.

Brammer, H. (1962). Soils. In J. B. Wells (Ed.), *Agriculture and Land Use in Ghana*, pp. 88–126, Oxford University Press, London.

Beard, J. S. (1967). Some vegetation types of tropical Australia in relation to those of Africa and America. *J. Ecol.*, **55**, 271–290.

Boughey, A. S. (1955). The nomenclature of the vegetation zones on the mountains of tropical Africa. *Webbia*, **11**, 413–423.

Brookman-Amissah, J., Hall, J. B., Swaine, M. D., and Attakorah, J. Y. (1980). A reassessment of a fire protection experiment in north-eastern Ghana savanna. *J. Appl. Ecol.*, **17**, 85–100.

Cesar, J., and Menaut, J. C. (1974). Analyse d'un ecosysteme tropicale humide: la savane de Lamto (Côte d'Ivoire). II. Peuplement vegetal. *Bull. de liaison des Chercheurs de Lamto*, Numero special, 1974, Fasc. II.

Chachu, R. E. O. (1982). A tentative hypothesis of plant succession in Kainji Lake National Park. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Procs. Man and Biosphere State-of-Knowledge, New Bussa, 20–24 April 1980*, pp. 406–417. Unesco/Kainji Lake Research Inst., New Bussa.

Chevalier, A. (1900). Les zones et les provinces botanique de l'A.O.F. *c.r. hebd. séanc. Acad. Sci.*, Paris, **130**, 1205–1208.

Child, G. S. (1974). *An Ecological Survey of the Borgu Game Reserve*. FAO, Rome.

Clayton, W. D. (1957). A preliminary survey of soil and vegetation in Northern Nigeria. *Regional Res. Station, Samaru, Zaria. Northern Nigeria: Departmental Report.*

Clayton, W. D. (1961). Derived savanna in Kabba province, Nigeria. *J. Ecol.*, **49**, 595–604.

Clements, F. E. (1916). *Plant Succession. An Analysis of the Development of Vegetation*, No. 242. Carnegie Inst. Washington, DC.

Collins, N. M. (1977). Vegetation and litter production in Southern Guinea Savanna, Nigeria. *Oecologia (Berl.)*, **28**, 163–175.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Conrad, M. (1977). The thermodynamic meaning of ecological efficiency. *Amer. Natur.*, **11**, 99–106.

Centre Technique Forestier Tropical (CTFT). (1969). *Conservation des sols au sud du Sahara*, Nogent-sur-Marne, 211 pp. (Techniques rurales en Afrique, No. 12).

CSA (Scientific Council for Africa) (1956). *CSA Specialist Meeting on Phytogeography, Yangambi*, No. 53, p. 35. CCTA, London.

Fagbenro, J. A. (1982). Effects of fire on soil with special reference to Tropical Africa. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Proc. Man and Biosphere State-of-Knowledge Workshop: Kainji Lake Research Inst., New Bussa, 20–24 April 1980*, pp. 128–143, Unesco/Kainji Lake Research Inst., New Bussa.

Fosberg, F. R. (1961). A Classification of vegetation for general purposes. *Trop. Ecol.*, **2**, 1–28.

Geerling, C. (1973). Vegetation map of Borgu Game Reserve. Unpublished; Dept. Forest Resources Management, Univ. of Ibadan, Nigeria.

Grove, A. T. (1973). Desertification in the African environment. In *Drought in Africa*, pp. 33–45. Report of the 1973 Symposium, Centre for African Students, School of Oriental and African Studies, University of London.

Hall, John, B. (1971). Environment and vegetation on Nigeria's highlands. *Vegatatio*, **3**, 339–359.

Hall, John, B. (1975). Fire as an experimental variable at Auno. *Ife Univ. Herbarium Bull.*, No. 10.

Hall, John, B. (1977). Forest-types in Nigeria: An analysis of pre-exploitation forest enumeration data. *J. Ecol.*, **65**, 187–199.

Hall, John, B., and Medler, J. A. (1975a). Nigeria and its affinities. *Vegatatio*, **29**, 191–198.

Hall, John, B. and Medler, J. A. (1975b). The flora of the Obudu Plateau and associated highlands: an annotated species list. *Ife Univ. Herbarium Bull*, No. 9.

Hill, M. O. (1973). Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.*, **61**, 237–249.

Hopkins, B. (1966). Vegetation of the Olokemeji Forest Reserve, Nigeria IV. The litter and soil with special reference to their seasonal changes. *J. Ecol.*, **54**, 687–703.

Horn, H. S. (1975). Succession. In R. M. May (Ed.), *Theoretical Ecology*, Ch. 10. Blackwell, Oxford.

Howell, J. M. (1968). The Borgu Game Reserve of Northern Nigeria. Part 1, *Nig. Field*, **38**, 39–116; Part 2, 147–165.

Isichei, A. O. (1980). Nitrogen fixation by blue-green algal soil crusts in Nigerian Savanna. In T. Rosswall (Ed.), *Nitrogen Cycling in W. African Ecosystems, Proc. SCOPE/UNEP Workshop, IITA, Ibadan, Dec. 1978*, pp. 191–198. SCOPE/UNEP, Uppsala.

Isichei, A. O. (1979). Elucidation of stocks and flows of nitrogen in some Nigerian savanna ecosystems. Ph.D. thesis, University of Ife, Nigeria.

Isichei, A. O. and Sanford, W. W. (1980). Nitrogen loss by burning from Nigerian grassland ecosystems. in T. Rosswall (Ed.), *Nitrogen Cycling in W. African ecosystems, Proc. SCOPE/UNEP, Workshop, IITA, Ibadan, Nigeria. Dec. 1978*, pp. 325–332. SCOPE/UNEP, Uppsala.

Jacques-Felix, H. (1950). Geographie des denudations et degradations du so au Cameroun. *Minist. France outre-mer, Direction Agric. Elev. For., Bull. Sci.*, No. 3, 1–84. Paris.

Jacques-Felix, H. (1951). Regions naturelles et paypagos vegetaux, *Encycl. Afr. Jr. Cameroun-Togo*, 15–29. Paris.

Jaeger, F. (1945). Zur Gliederung und Benennung des tropischen Grasslandgürtels. *Verh. Naturf. Ges. Basel*, 56, 509–520.

Jeník, J., and Hall, J. B. (1976). Plant communities of the Accra Plains, Ghana. *Folios Geobot, Phytotax. Praha*, **11**, 163–212.

Jones, M. J. and Bromfield, A. R. (1970). Nitrogen in rainfall at Samaru, Nigeria. *Nature (London)*, **227**, 86.

Keay, R. W. J. (1959a). *An Outline of Nigerian Vegetation*, 3rd edn. Government Printer, Lagos.

Keay, R. W. J. (1959b). *Vegetation Map of Africa, Explanatory Notes*. Oxford University Press, London.

Liebermann, D. (1982). Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.*, **70**, 791–806.

Livingstone, D. A. (1975). Late Quaternary climatic change in Africa. *Ann. Rev. Ecol. Systematics*, **6**, 249–280.

Matthews, J. A. (1979). A study of the variability of some successional and climax plant assemblage-type using multiple discriminant analysis. *J. Ecol.*, **67**, 255–272.

Medina, E. (1983). Organic matter production of the grass cover in S. American savanna, with emphasis on nutritional aspects. In *Report of Symp. on Savanna and Woodland Ecosystems in Trop. America and Africa: A Comparison, Univ. of Brasilia, Brazil, 2–7 Oct. 1983*, pp. 19–20. Internat. Biosciences Network, Paris.

May, R. M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, New York.

Menaut, J. C. (1977). Evolution of plots protected from fire since 13 years in a Guinea Savanna of Ivory Coast. *Proceedings 4th Intern. Symp. Tropical Ecol.*, Panama.

Menaut, J. C. (1983a). A tentative synthetic approach to the functioning of savanna ecosystems. In *Report of Symp. on Savanna and Woodland Ecosystems in Trop.*

America and Africa: A Comparison, Univ. of Brasilia, Brazil, 2–7 Oct. 1983, pp. 19–20. Internat. Biosciences Network, Paris.

Menaut, J. C. (1983b). The vegetation of African savannas. In F. Bouliere, (Ed.), *Tropical Savannas*. Elsevier, Amsterdam, Oxford, New York.

Milligan, Kevin (1979). An ecological basis for the management of Kainji Lake National Park. Ph.D. thesis, University of Ibadan.

Milligan, K., and Sule, B. (1982). Natural forage resources and their dietary value. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Proc. Man and Biosphere State-of-Knowledge, Workshop, Kainji Lake Res. Inst. New Bussa, 20–24 April 1980*, pp. 190–207. Unesco/Kainji Lake Res. Inst., New Bussa.

Moore, A. W. (1960). The influence of annual burning on a soil in the derived savanna zone of Nigeria. *7th Internat. Congr. Soil Trans.*, **4**, 257–264.

Moreau, R. E. (1966). *The Bird Fauna of Africa and its Islands*. Academic Press, New York and London.

Moreau, R. E. (1969). Climatic changes and the distribution of forest vertebrates in West Africa. *J. Zool. (London)*, **158**, 39–61.

Mortimore, M. J., and Wilson, J. (1965). *Land and People in the Kano Close-settled Zone*. Occasional Papers 1, Ahmadu Bello Univ., Dept. of Geography, Zaria, Nigeria.

Nye, P. H., and Greenland, D. J. (1960). *The Soil Under Shifting Cultivation*. Tech. Commun. No. 51, Commonwealth Bureau of Soils, Bucks, England.

Odum, E. (1969). The strategy of ecosystem development. *Science*, **164**, 262–270.

Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**, 323–331.

Opakunle, J. S. (1978). Nitrogen partitioning in relation to season and nitrogen content of the growth medium in two Nigerian occurring grasses — *Andropogon gayanus* Kunth. and *Schizachyrium sanguineum* (Retz.) Alston. M.Sc. dissertation. Univ. of Ife.

Papadakis, J. (1965). *Crop Ecologic Survey in West Africa*. FAO, Rome.

Prospero, J. M., and Nees, R. T. (1976). Dust concentration in the atmosphere of the equatorial North Atlantic: possible relationship to the Sahelian drought. *Science*, **196**, 1196–1198.

Pullan, R. A. (1962). A report on the reconnaissance soil survey of the Nguru–Hadejia–Gumel area with special reference to the establishment of an experimental farm. *Samaru Soil Survey Bull.*, 18. Inst. Agric. Res., Samaru, Nigeria.

Ramsay, D. McC., and de Leeuw, P. N. (1965a). An analysis of Nigerian Savanna III. The vegetation of the middle Gongola region by soil parent materials. *J. Ecol.*, **53**, 643–660.

Ramsay, D. McC., and de Leeuw, P. N. (1965b). IV. Ordination of vegetation developed on different parent materials. *J. Ecol.*, **53**, 661–677.

Ramsey, J. M. and Rose Innes, R. (1963). Some quantitative observations on the effects of fire on the Guinea Savanna vegetation of Northern Ghana over a period of eleven years. *African Soils*, **8**(1), 41–85.

Rehr, S. S., Janzen, P. H., and Feeny, P. P. (1973). L. Dopa in legume seeds: A chemical barrier to insect attack. *Science*, **181**, 81–82.

Roose, E. (1975). Paper presented at the workshop on *Soil Conservation and Management in the Humid Tropics*, Ibadan, Nigeria, 30 June – 4 July, 1975, as reported in *Tropical Ecosystems*, p. 264, Unesco/UNEP/FAO, Paris.

Rose Innes, R. (1972). Fire in West African vegetation. *Proc. Tall Timbers Fire Ecology Conf.*, **11**, 147–173.

Rousseau, J. A. (1932). Mission d'études forestières dans la region du Nord-Cameroun. *Bull, Agence. Gener. Colonies*, Extrait No. 285, 1766–1823.

Sanford, W. W. (1974). The use of epiphytic orchids to characterize vegetation in Nigeria. *Bot. J. Linn, Soc.*, **68**, 291–301.

Sanford, W. W. (1982a). Savanna burning: A review. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Procs. Man and Biosphere State-of-Knowledge Workshop, Kainji Lake Res. Inst., New Bussa, 20–24 April 1980*, pp. 160–188, Unesco/Kainji Lake Res. Inst., New Bussa.

Sanford, W. W. (1982b). Savanna: an overview. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Procs. Man and Biosphere State-of-Knowledge Workshop, Kainji Lake Res. Inst, New Bussa, 20–24 April 1980*, pp. 3–23, Unesco/Kainji Lake Res. Inst., New Bussa.

Sanford, W. W., Obot, E. A., and Wari, W. (1982a). Savanna vegetational succession: a means of assessment by the distribution of girth size of woody elements. In W. W. Sanford, H. M. Yesufu, and J. S. O. Ayeni (Eds.), *Nigerian Savanna: Procs. Man and Biosphere State-of-Knowledge Workshop: Kainji Lake Res. Inst., New Bussa, 20–24 April 1980*, pp. 418–432. Unesco/Kainji Lake Res. Inst., New Bussa.

Sanford, W. W., Usman, S., Obot, E. A., Isichei, A. O., and Wari, W. (1982b). The relationship of woody plants to herbaceous production in Nigerian savanna. *J. Trop. Agric. (Trinidad)*, **59**, 315–318.

Sarmiento, G., and Monasterio, M. (1975). A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in Tropical America. In F. B. Golley and E. Medina, *Tropical Ecological Systems*, Ch. 6, pp. 223–250. Springer-Verlag, Berlin, Heidelberg, New York.

Thoreau, Hod. (1860). The succession of forest trees. In *Excursions* (1863). Houghton Mifflin, Boston.

Trewartha, G. T. (1954). *An Introduction to Climate*. McGraw-Hill, New York.

Troll, C. (1952). Das Pflanzenkleid der Tropen in seiner abhangigkeit von Klima, Boden und Mensch. *Dtsch Geogr.*, **28**, 35–66.

Walter, H. (1971). *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh.

Walter, H. (1973). *Vegetation of the Earth in Relation to Climate and the Eco-physiological Conditions* (trans. from 2nd edn. by J. Wiesar). English Universities Press, London.

White, F. (1983). *Unesco/AETFAT/UNSO Vegetation Map of Africa*. Unesco, Paris, 356 pp. and map.

Washburn, S. L. (1978). The evolution of man. *Scient. Amer.*, **239** (3), 146–155.