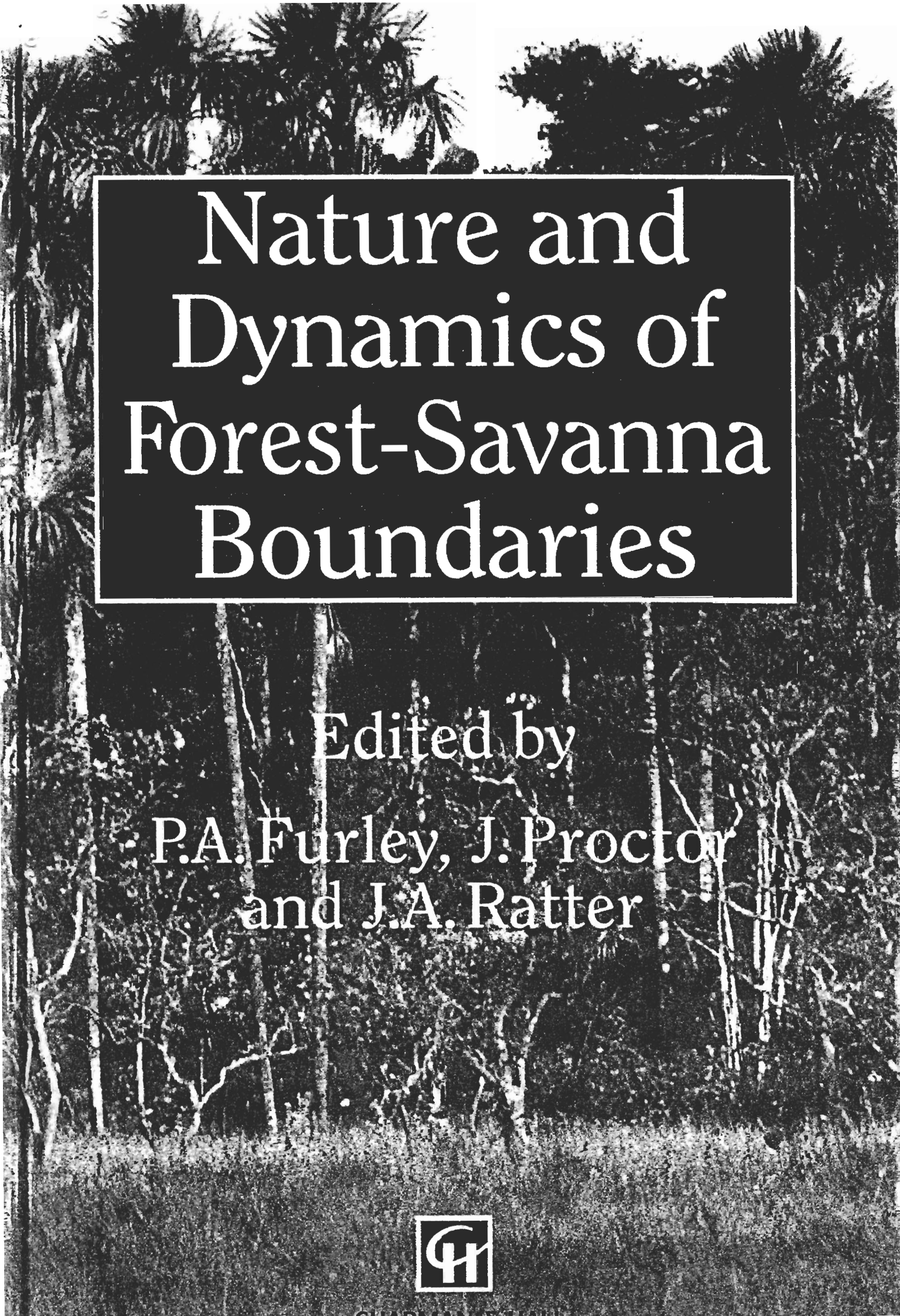

Nature and Dynamics of Forest-Savanna Boundaries

Edited by

P.A. Furley, J. Proctor
and J.A. Ratter

Citar como:

Sarmiento, G. 1992. A conceptual model relating environmental factors and vegetation formations in the lowlands of tropical South America. En: Furley, P.A., Proctor, J., Ratter, J.A. (Eds). Nature and Dynamics of Forest-Savanna Boundaries. Chapman & Hall, London, pp. 583-601.

Nature and Dynamics of Forest–Savanna Boundaries

Edited by

P.A. FURLEY
Department of Geography
University of Edinburgh
UK

J. PROCTOR
School of Molecular
and Biological Sciences
University of Stirling
UK

J.A. RATTER
Royal Botanic Gardens
Edinburgh
UK

CHAPMAN & HALL
London · Glasgow · New York · Tokyo · Melbourne · Madras

1992

30

A conceptual model relating environmental factors and vegetation formations in the lowlands of tropical South America

GUILLERMO SARMIENTO

SUMMARY

1. A resumé is given of previous models relevant to forest and savanna distribution, particularly in South America.
2. Previous works on the classification of South American lowland forests and savannas are considered.
3. The environmental determination of tropical lowland ecosystems is discussed, paying particular attention to climate and soil, as well as to human action and long-term processes. The environmental factors determining the occurrence of forests and savannas in South America operate through the combined effects of drought, water excess and deficiency of nutrients. A preliminary model is presented where tropical lowland formations are placed in environmental space between these three axes. While seasonal water availability has long been considered one of the key factors in the determination of tropical ecosystems, the importance of nutrient shortage has only been appreciated more recently. The role of nutrient stocks in soils and vegetation are considered, emphasizing the sharp differences between forests and savannas in biomass, mineral element allocation and stocks.
4. Replacement of forests by savannas, or vice versa, is also examined as a natural and/or human-induced process (the two operating on different time-scales), that leads to crucial changes in nutrient availability and cycling.

INTRODUCTION

To establish qualitative or quantitative conceptual models that explain and predict how the physico-chemical environment interrelates with the distribution of ecosystems has always been a key objective of biogeography.

Walter (1964, 1973) produced a simple model representing the distribution of vegetation zones on 'an average continent' that gives emphasis to climate. This model shows how the equatorial rainforest is bordered in both hemispheres by a belt of tropical deciduous forest (and moist savannas), whereas a longitudinal band of orographically determined tropical rainforest occupies the equatorial eastern coasts of this ideal continent. The tropical thorn bush (and dry savannas) limit deciduous forest towards the western subtropical zones as a transition to steppes or semi-deserts and hot deserts. According to Walter, within the tropical deciduous forest belt, moist savannas are largely anthropogenic or of edaphic origin. It may be seen then how lowland tropical vegetation could be ordinated from rainforest to desert along a climatic axis of increasing drought, with the possible exception of those savannas not determined by soil or man.

Sarmiento (1968) arranged all plant formations in the Americas within a climatic plane with mean annual temperature and rainfall as the two environmental axes. The aim of that model was to show how each vegetation type, with some exceptions, has a definite trend towards the occupancy of a well delimited area within a bidimensional climatic space. In this space, tropical American savannas occupy a restricted but well defined climatic zone between the tropical rainforest and the deciduous or tropophyllous tropical forest, where annual rainfall ranges from 1200 to 1500 mm and mean annual temperature from 21 to 28 °C. We now know that in this climatic belt, besides tropical savannas, both rainforests and deciduous forests may occur. However, moist savannas appear in this area more frequently than the two tropical forest types.

Walter (1973), on a smaller geographical scale, related the tropical plant formations in India to a gradient of increasing dryness, taking annual rainfall and length of drought as his environmental axes. Each vegetation formation occupies a well defined zone in this space, though dry savannas and thorn bushes overlap within the same area. Box (1981) produced a simple predictive model on the determination of 77 plant-forms by eight climatic parameters, validating the model with 74 sites world-wide. As would be expected, tropical plant-forms, such as rain-forest trees, monsoon deciduous trees, tall tussock grasses, etc., showed wide and overlapping temperature and rainfall ranges, seriously restricting the usefulness of simple climatic parameters to set apart the ecological spaces of these plant-forms.

Sarmiento and Monasterio (1975), in their discussion on factors associated with the occurrence of tropical American savannas, presented a model on the ideal distribution of ecosystems under tropical wet and dry climates, relating plant formations to two environmental axes: soil humidity at the end of the dry season and soil water at the end of the rainy season. The discriminatory power of these two environmental factors was high for most formations but it failed to separate some types of savannas from deciduous forests.

Outside these conceptual models aimed at clarifying the environmental determination of tropical vegetation, little further progress has been attained. The savanna problem in particular has not been satisfactorily solved. In this chapter we want to discuss the determination of South American tropical forests and savannas by climate and soil factors. Besides focusing our attention on the variety of savanna ecosystems in this continent, we will also try to relate neotropical lowland vegetation zones to some broad features of their environments.

ENVIRONMENTAL FACTORS DELIMITING TROPICAL FORESTS AND SAVANNAS

Classification of lowland forests and savannas

Beard (1944, 1955) placed plant formations in five formation series: seasonal, montane, dry evergreen, seasonal swamp and swamp. Apart from the montane series determined by altitude and the woodlands and scrubs characterizing the driest areas, most of Beard's units are moist forests whose variety is related to major environmental gradients. In the case of his seasonal series, ranging from the rainforest *sensu stricto* to the seasonal evergreen, semi-deciduous and deciduous forest, the major environmental gradient is one of increasing seasonal drought, paralleling the change from continually wet to tropical wet and dry climates. On the other hand, dry evergreen formations appear as climax types under constantly subhumid conditions. Seasonal waterlogging determines the seasonal swamp series, while the swamp series corresponds to habitats under permanent water excess. This simple scheme was followed in later studies of tropical American vegetation (Hueck, 1966; Walter, 1973; Schnell, 1987).

Beard's system recognizes only a few non-forest formations: palm and herbaceous swamps in the swamp formation series, and palm marshes and savannas in the seasonal swamp series. Occurrence of savannas is explained by the occurrence of seasonal waterlogging. In our opinion, Beard's model still holds, except perhaps with regard to the ecological explanation of savannas. Later classifications of tropical plant formations, at regional or at continental level, do not provide more detailed interpretations of relationships between environment and vegetation.

The physiognomic-ecological classification of Mueller-Dombois and Ellenberg (1974) divides tropical forests into open and dense formations, further subdividing each type according to seasonality following Beard's terminology. On the other side, their predominantly herbaceous formations include a wide range of vegetation types, such as savannas, steppes, meadows, sedge swamps and salt swamps. Savannas and related tropical and subtropical grasslands are subdivided according to height of grasses and to the distribution patterns and height of woody species. Their comprehensive system may be applied to an ecological interpretation of tropical vegetation units, but this task has not yet been undertaken.

In Brazil, Veloso *et al.* (1975) established an *ecological system* of vegetation classification to be used in the Amazonian region. Three main types of stable formations were recognized: forests, savannas (*cerrados*) and steppes (*caatingas*). Two major forest types were distinguished: open forest and dense forest, the former on hydromorphic soils, the latter on well drained soils; each was subdivided according to seasonality into ombrophyllous, seasonal and deciduous forest. Both savannas and steppes were classified by physiognomic features following the regional names. This system has the obvious advantage over previous classifications that savannas are unequivocally considered as stable plant formations of regional siginificance, as might be expected in a classification of the vegetation of the South American country with the greatest area of savannas. However, this so-called ecological system is only partly based on ecological features, since it considers physiognomy at least as important for recognition of plant formations as habitats and vegetation seasonality.

Rizzini (1979), in his comprehensive treatise on the phytogeography of Brazil, discusses the ecological characteristics of plant species in all major formations in that country: rainforests, dry forests, evergreen sclerophyllous forest (*cerradão*) and savannas. He considers that savannas are determined by soil conditions (drought and scarcity of nutrients) and by recurrent fires.

In order to clarify the environmental conditions associated with savanna ecosystems, it is first necessary to describe the differentiation of some major savanna types. The first basic distinction is between dry and moist savannas which are quite unrelated ecosystems. Moist savannas are the only type found in tropical America, and, as Walker (1985) points out, are more akin to rainforests than to dry savannas. Dry savannas, on the other hand, are floristically and ecologically related to thorn woodlands and to various semi-arid scrubs. Dry savannas are widespread in Africa and Australia but they do not occur in the Americas, since in the neotropics, when rainfall is less than 700 mm per year, low woody formations lacking a layer of perennial grasses (such as the Brazilian caatinga) appear as the regional climax. In subtropical areas of South America, such as the Chaco, mixed or grassy formations occur under semi-arid climates, but these subtropical ecosystems bear little resemblance to the moist neotropical savannas (Sarmiento, 1990).

Within moist savannas, at least three major ecological types have to be distinguished according to soil-water regime, vegetation seasonality and functioning (Sarmiento and Monasterio, 1975; Sarmiento, 1984). In *seasonal savannas* the dominant perennial grasses overcome an extended period of water shortage induced by rainfall seasonality, although water excess is absent or unimportant. In *hyperseasonal savannas* water excess and water shortage occur during each annual cycle. The topsoil becomes water-saturated during the rains, and dries out completely during the dry season. *Semiseasonal savannas* just suffer from an extended period of water excess without any long period of water deficiency, thus approaching the soil-water regime of seasonal marshes (although the waterlogging may not be as pronounced nor as extended as it is in marshes).

These three types of savanna frequently coexist on the topographic and soil catenas of savanna landscapes, with seasonal savannas on the higher positions with coarse, well drained soils (alluvial levées, sand dunes, high plains, etc.), hyperseasonal savannas on silty soils of intermediate topographic positions, and semiseasonal savannas, together with seasonal marshes and swamps, in the bottomlands, with heavy clay soils.

Having thus briefly considered the main ecological types of forests and savannas, we now discuss their environmental boundaries.

DO FORESTS AND SAVANNAS OCCUR IN SIMILAR OR IN DIFFERENT ENVIRONMENTS?

The lowlands of tropical South America, below 1300–1500 m, show a great diversity of climates and soils, as we might expect for an area of about 11.1 million km^2. Given that mean monthly temperatures are relatively constant throughout the year, with annual means, ranging according to latitude and elevation, between 18 and 28 °C, the two most relevant factors inducing climatic variability are total rainfall and its seasonality. Climatic factors, together with parent material, geological history, topography and vegetation are responsible for the characteristics and evolution of the soil profile. Plant formations in turn are related to climate and soil.

Forests and savannas represent alternative possibilities for occupying a given area in the humid, tropical lowlands. Which of these two plant formation actually occurs in any area will depend on the overall habitat conditions.

The conceptual model implicit in the foregoing statements is that forests and savannas occupy different multidimensional ecological spaces, or better ecological hyperspaces, whose n dimensions or axes are the environmental factors acting upon each ecosystem. Under this assumption, both types of ecosystem will not coexist in the same area, unless there are different habitat conditions (e.g. variations in soil type).

Several possibilities may be envisaged concerning these environmental hyperspaces. If their respective hyperspaces do not have common points along some axes, forests and savannas will appear as two systems without any frontier or common border between their environments, even if they overlap along other axes (Fig. 30.1a). This is, of course, a rather extreme assumption concerning the environmental delimitation of these formations. In Fig. 30.1b, the first axis separates forests from savannas, whereas the second axis does not. Another possibility is that if forests and savannas do overlap along all axes, then both hyperspaces will still be partly different but will have a common frontier, or tension area, of environmental indetermination (Fig. 30.1c).

Other conceptually different models depict the cases where the environmental conditions of one type of ecosystem are totally included within the space of the other (Fig. 30.1d,e), or the most extreme case of environmental indetermination occurs when both types of ecosystems share exactly the same ecological hyperspace (Fig. 30.1f). If these last three models approach real situations, then we have to appeal to non-environmental factors as determinants, or to assume that disturbance has been responsible for the existence of forests or savannas. Most probably the truth lies in between, with each system occurring in an exclusive part of the environmental space but with overlapping fields with the other system.

THE DISCRIMINATING POWER OF SOME ENVIRONMENTAL AXES

We shall consider boundaries along certain environmental axes as an initial step in the analysis of forest and savanna environments, taking into account a few important environmental factors, such as annual rainfall, mean temperature, number of dry and wet months, soil fertility, etc.,

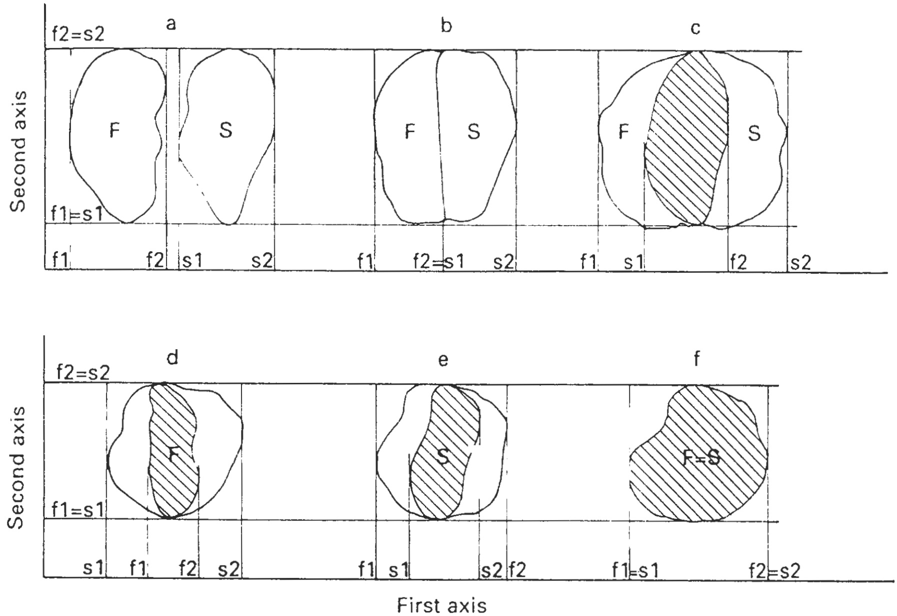

Fig. 30.1 Several possibilities for distribution of forests (F) and savannas (S) in a two-axis environmental space. According to this case, the first axis may or may not separate both types of ecosystems, while the second axis does not show any discriminating power.

in order to assess their power in discriminating the two ecosystems. Climatic data from 84 localities, embracing all South American countries with tropical lowlands and representative of the full range of climatic variation found in this continent, served as a basis for the diagrams, while the boundaries between plant formations reflect both published data and the author's own field experience. The conclusions should be regarded as a preliminary hypothesis.

Figure 30.2 shows the distribution of forests and savannas on the two-dimensional space or plane of annual rainfall and mean temperature. A total overlapping is evident except in the area of highest rainfall (above 2.5 m) where savannas do not occur, leaving only evergreen tropical forests. For the rest, the overlapping represents the coexistence of seasonal savannas and semi-deciduous forests under conditions of intermediate rainfall (1.5–2.5 m), and of seasonal savannas and deciduous forests in the somewhat less rainy areas. With less than 0.6 or 0.7 m of rainfall, already under tropical dry climates xerophytic formations replace deciduous forests and savannas, while below an annual mean tempera-

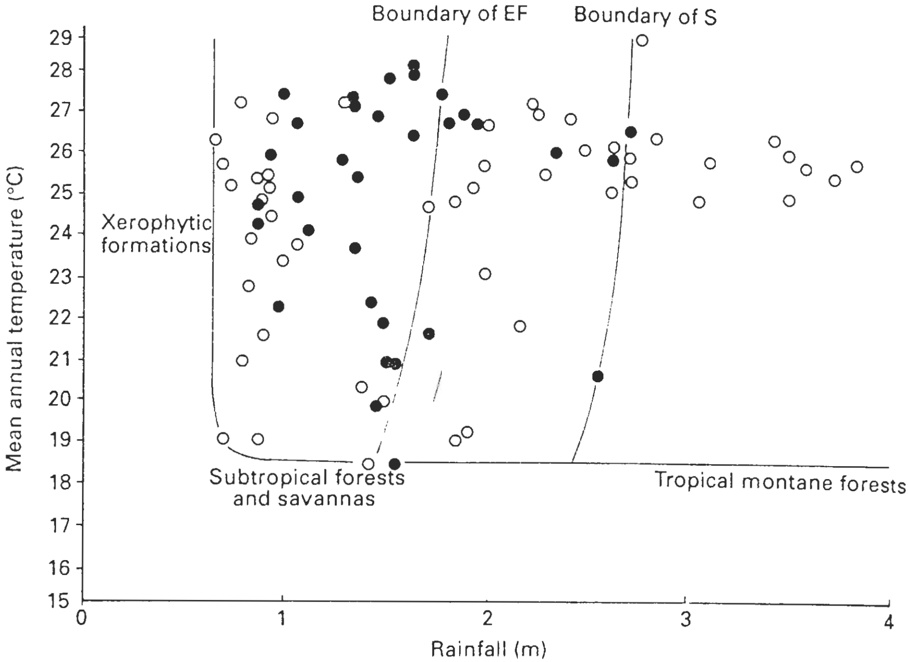

Fig. 30.2 Distribution of forests (○) and savannas (●) in the environmental space whose axes are annual rainfall and mean annual temperature, showing the boundary of savannas towards the wettest climates and the boundary of evergreen tropical forests towards the less rainy climates. EF, evergreen forest; S, savanna.

ture of 18 or 19 °C tropical formations give place either to subtropical ecosystems or to tropical montane forests. To summarize, then, the discriminating or predictive power of the temperature axis to set apart savannas and forests seems to be null, while that of the rainfall axis appears to be quite low.

Considering now the distribution of forests and savannas in the plane determined by annual rainfall and by the number of dry months (taking as 'dry' a month with less than 50 mm rainfall), the almost total superposition in areas of intermediate rainfall can be seen in Fig. 30.3. This overlapping is mainly due to the fact that the environments of tropical semi-deciduous and tropical deciduous forest are indistinguishable from that of seasonal savanna (SS). Figure 30.3 also shows that forests may occur in wetter as well as in drier areas than savannas, and also that neither of these two contrasting formations occurs where the dry season extends for more than eight consecutive months.

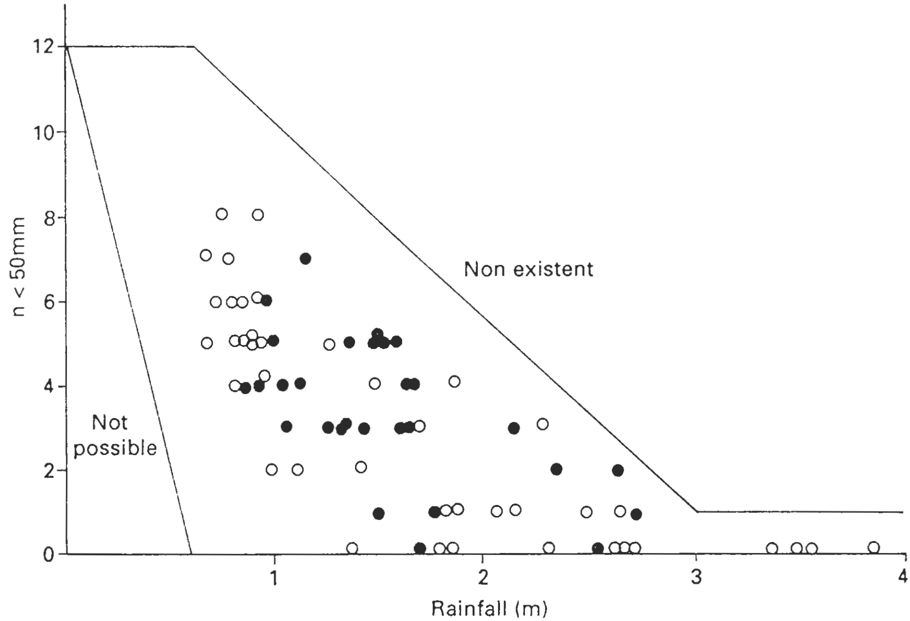

Fig. 30.3 Distribution of forests (○) and savannas (●) in the environmental space determined by annual rainfall and the number of months with less than 50 mm rainfall. Evergreen forests predominate towards the lower-right part, while deciduous forests occupy the upper-left part. SS, seasonal savanna.

If both the number of dry months and of months with water-saturation or waterlogging are taken into account (Fig. 30.4), the savannas become clearly divided into two main ecological types: seasonal savannas where the period of water excess is short or non-existent, and hyperseasonal savannas with both contrasting stresses alternating during each annual cycle. The field of seasonal savannas greatly overlaps with that of deciduous forests and somewhat less with evergreen forests, while swamp forests separate from other formations on this environmental plane.

As a last example of a two-dimensional analysis, the distribution of forests and savannas in the plane given by a climatic axis (number of dry months) and an axis of nutrient availability (sum of exchangeable bases in topsoil) is given in Fig. 30.5. On this plane the habitats of deciduous forests and seasonal savannas separate into a strongly nutrient-deficient area occupied by seasonal savannas and a field with richer soils where deciduous forests occur, while evergreen forests extend throughout the whole range of soil fertility, but only in the less extreme part of the

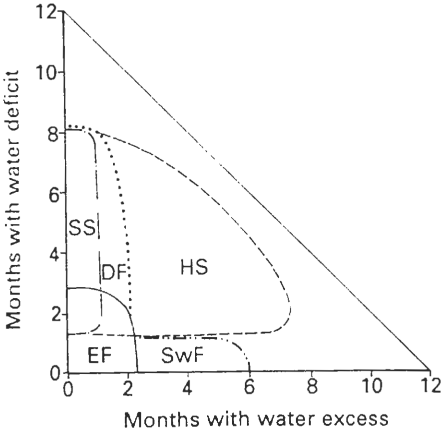

Fig. 30.4 Distribution of tropical lowland ecosystems in the environmental space determined by number of months with water excess and with water deficit. DF, deciduous forest; EF, evergreen forest; HS, hyperseasonal savanna; SS, seasonal savanna; SWF, swamp forest. Note the overlapping of SS and DF.

drought gradient. These few examples clearly illustrate that it is necessary to employ more than two axes to discriminate forest and savanna environments in the lowland tropics.

MODIFICATIONS OF THE ORIGINAL ENVIRONMENTS

The relationships between the physico-chemical environment and tropical biotas are still more complex, since once an ecosystem becomes established, be it forest or savanna, the modifications to the habitat initiated during its development will continue, tending to widen still more the original environmental differences. Thus, for instance, each ecosystem has characteristic patterns of carbon and nutrient balance in the vegetation biomass, of litter production and decomposition, and of soil organic matter accumulation, as well as divergent water budgets produced by differences in such processes as throughfall, stem flow, transpiration, etc. When recurrent fires become a normal ecological event, they also alter plant growth and nutrient cycling (Table 30.1). Consequently, it becomes difficult to know whether environmental conditions in forest and savannas were different before maturity, or whether their environments underwent a secondary, *a posteriori*, differentiation through the action of vegetation and ecosystem processes.

These biologically induced changes in habitats are gradual and accompany the development of each ecosystem, but after a certain time,

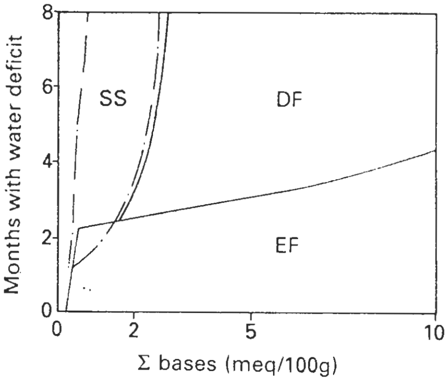

Fig. 30.5 Distribution of tropical lowland ecosystems in the environmental space determined by the sum of exchangeable bases and the number of dry months. On this plane seasonal savannas (SS) become almost entirely separated from deciduous (DF) and evergreen forests (EF).

Table 30.1 Some contrasting characteristics of tropical forests and savannas

	Forests	*Savannas*
Vegetation biomass	Higher stocks of carbon, nitrogen and mineral elements in the biomass. Higher stocks in the aerial parts	Lower stocks of carbon, nitrogen and mineral elements in the biomass. Higher stocks in the subterranean ground parts
Litter accumulation	Litter accumulation and decomposition on the soil surface (leaf litter)	Subterranean decomposition of plant materials (root litter)
Soil organic matter	Concentrated in the topsoil. Occurrence of organic surface horizons. High CEC in topsoil due to SOM	More gradual decrease with depth. Deeper organo-mineral horizons. Lower cation exchange capacity (CEC) in topsoil due to less soil organic matter (SOM)
Fire	Exceptional. It starts vegetation succession	Almost yearly. Little damage to soil and vegetation. It starts regrowth. Losses of volatiles

perhaps thousands of years, the original conditions become strongly altered and many positive feedback mechanisms begin to operate, securing the maintenance of a new equilibrium between the biotic and the abiotic components of the steady-state ecosystems. We will refer again to these changes when discussing the dynamics of the whole landscape in the next section.

ECOSYSTEM REPLACEMENTS: NATURAL AND HUMAN-INDUCED

The occurrence of natural savannas on previously forested areas, without changes in the original environment, does not seem to have been documented anywhere in the neotropics. The palynological record in tropical American lowlands for the Holocene and the Upper Pleistocene (Wijmstra and van der Hammen, 1966; van der Hammen, 1974, 1983) certainly shows almost continuous replacements of forests and savannas in both directions, but at time-scales of hundreds or thousands of years. These replacements have been explained as induced by climatic changes associated with glacial and interglacial periods, or by geomorphological processes operating in the plains that suddenly or gradually modify soil and water conditions. I have no information about forests converted to savannas, or vice versa, during historical times. Certainly, many previously forested areas have been, and continue to be, deforested, but in these cases the secondary plant formations replacing the original forests differ widely from the primary savannas that still persist in neighbouring areas, and they can be easily recognized as man-induced, unstable systems by their composition or structure.

It has already been shown that neither seasonal drought nor water excess or poor soil may be itself explain the alternative occurrence of forests and savannas. Furthermore, tropical forests have been widely converted into secondary grasslands or bushlands, and these successional formations are frequently subjected to the same types of influences in recurrent fires and grazing pressure as the primary savannas. But it is still not known if, given enough time (10–100 years?), these secondary communities under such pressures will evolve into ecosystems similar to primary savannas, or whether they will remain as disclimaxes.

Independently of human action, the natural evolution of forest ecosystems in the long term (10^4–10^5 years) leads to irreversible environmental changes involving water and nutrient cycles that may favour the replacement of long-established forests by savannas. Some of the processes involved in this senescence of the landscape are related to latosolization, podzolization, cuirassment, extreme leaching and depletion of soil cations, etc. Under these conditions of decreasing soil fertility, woody vegetation accumulates in its long-lived biomass a significant part of the total stock of nutrients in the ecosystem, at the same time that the overall stock in the ecosystem decreases. Moreover, one of the consequences of nutrient stress on vegetation seems to be the development of scleromorphic traits in the dominant trees together with an opening of the forest canopy. Both features favour occurrence of natural fires.

These features render the ecosystems quite fragile and less able to recover from natural disturbances, such as occasional fires, and in the long term may lead to the gradual replacement of these extremely oligotrophic forests by savannas that can cope more successfully with poor soils and fires. Probably such processes, operating on white sands and other very poor parent materials in various regions of tropical South America and the Caribbean, produced the present landscapes where highly scleromorphic forests intermix with open woodlands and savanna bushes (van Donselaar, 1965; Hoock, 1971; Rizzini, 1979).

These trends towards *savannization* may be reversed by geological and geomorphological processes that produce a rejuvenation of the landscape. An uplift, for instance, induces a renewal in erosion by running waters that increase availability of nutrients, since new, deep soil layers can be attained by tree roots, favouring in this way the reconversion of savanna areas to forest. Similar changes may be brought about by a climatic change towards increasing rainfall. Such landscapes of contracting savannas and expanding forest appear in various neotropical regions, such as the Venezuelan llanos and the Brazilian cerrados (Sarmiento and Monasterio, 1975; Cole, 1986). In Fig. 30.6, the combined action of all these factors and processes on the equilibrium between forests and savannas is represented in a graphical form.

ENVIRONMENTAL CONSTRAINTS, PLANT RESPONSES AND THE DYNAMICS OF FORESTS AND SAVANNAS

Tropical lowland forests are dominated by tall trees, either evergreen or deciduous. Considering the whole range of plant formations in the broad definition of 'tropical lowland forest' these tall trees may vary widely in height, but even under less favourable conditions the forest canopy reaches at least 12 or 15 m, while on more favourable habitats the canopy may reach 35 or 40 m. As a direct consequence of the enormous size of forest trees, the total above-ground vegetation biomass normally attains 300–500 t dryweight ha^{-1}.

Savannas have a different structural pattern and are always dominated by perennial grasses and sedges, with low trees as the growth-form second in importance. Compared with forest trees, savanna low woody species together with grasses have a much smaller biomass, which usually ranges from a maximum of about 100 t ha^{-1} in woody savannas to less than 20 t ha^{-1} in savanna grasslands (Sarmiento, 1984).

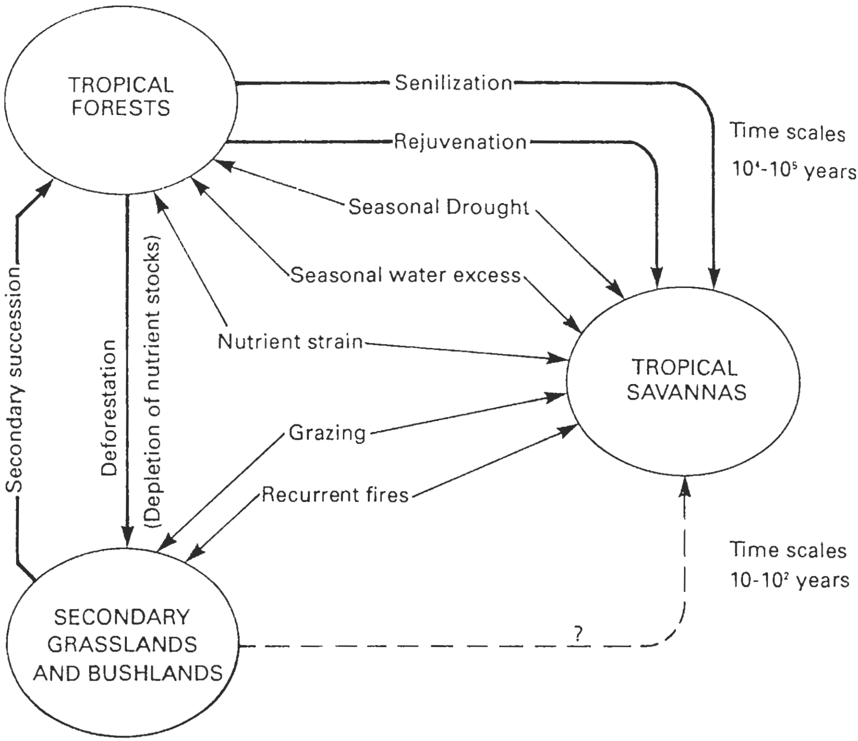

Fig. 30.6 Major factors acting upon tropical forest and savannas, together with processes involved in the conversion of one to another and to secondary formations.

As the total vegetation biomass is about ten times higher in forest than in savannas, the stocks of mineral elements follow this same pattern. Thus for instance, savanna formations in the Venezuelan llanos have in the grass layer (above- and below-ground) about 20 kg ha^{-1} of phosphorus and 60–140 kg ha^{-1} of potassium. The woody biomass in an open savanna woodland has roughly the same quantities. In contrast a semi-evergreen rainforest in the same area contains 290 kg ha^{-1} of phosphorus and 1820 kg ha^{-1} of potassium just in the above-ground biomass (Hase and Folster, 1982).

Finally, in humid tropical forests a direct transference of nutrients from decaying plant parts to roots, via mycorrhizae and decomposing micro-organisms, seems to occur, short-circuiting the mineral soil and securing a most efficient recycling of critical nutrients (Herrera *et al.*, 1978). That is, even if forests and savannas are both subjected to severe nutrient limitations as a consequence of their highly dystrophic soils, forest trees have developed various mechanisms that increase the efficiency of nutrient storage and recycling that tend to create an important stock of mineral elements within the living vegetation. The disruption of these mechanisms may induce the natural replacement of forest by more tolerant savanna ecosystems.

CONCEPTUAL MODELS RELATING VEGETATION TO HABITAT IN TROPICAL AMERICA

A major difficulty in understanding the environmental conditions determining tropical American savannas derives from not having, in previous models, considered nutrient shortage as a constraint acting on species occurring on poor tropical soils. In the first experimental studies on the Brazilian cerrado, occurrence of nutrient-poor soils was recognized to be among the principal determinants of these savannas (Alvim and Araujo, 1952; Arens, 1958, 1963). This interpretation was later extended to the seasonal savannas in tropical America (Sarmiento, 1984).

The seasonal savanna associated with well drained soils stands as a characteristic ecosystem on some of the poorest soils of tropical America. But obviously, if only soil nutrient stocks were considered, many or even most of the neotropical humid forests would overlap with seasonal savannas as ecosystems occurring on dystrophic soils. The points emphasized here are, first, that the whole nutrient capital of the ecosystem must be taken into account, and that this capital is much more important in forest than in savannas because of the storage of mineral elements in the forests biomass. Second, that nutrient cycles are very tight and therefore an impact on nutrient stocks may switch the system towards a new equilibrium, that is from forests, with higher stocks, to savannas, with lower stocks and requirements.

On the basis of the foregoing considerations, tropical American lowland ecosystems were arranged in a three-dimensional space where drought, water excess and low nutrient levels are the three axes of environmental variability (Figs 30.7 and 30.8). Each axis in turn represents a sort of complex gradient resulting from the joint action of simpler factors. This arrangement, although purely qualitative, may serve as a conceptual model, suggesting the principal environmental constraints impinging upon these ecosystems and their species.

Seasonal drought is the main environmental factor determining the deciduous forest and, to a lower degree also, the semi-deciduous forest, whereas the thorn forest and related arid formations occupy the extreme of the drought axis (Fig. 30.7). Nutrient deficiency is the most severe

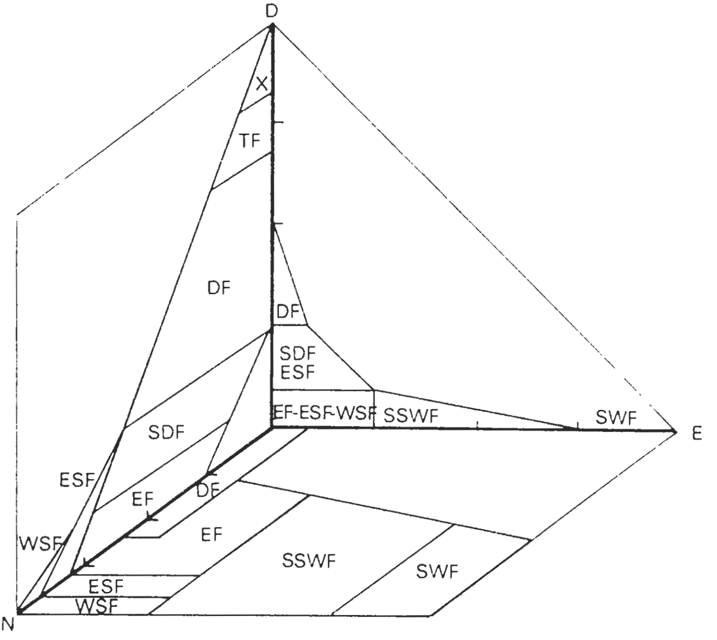

Fig. 30.7 Distribution of lowland tropical forests in the environmental space determined by water excess, drought and nutrient levels. The projections on the three environmental planes are shown. The *E* and *D* axes vary from 0 to 12 months of water excess or drought respectively, while the *N* axis has been divided into four parts corresponding to eutrophic, mesotrophic, dystrophic and hyper-dystrophic soils. DF, deciduous forest; EF, tropical evergreen forest; ESF, evergreen sclerophyllous forest; SDF, semi-deciduous forest; SSWF, seasonal swamp forest; SWF, swamp forest; TF, thorn forest; X, xerophytic vegetation.

environmental constraint in evergreen sclerophyllous forest, as well as in forests and scrubs on white sands. To a lesser degree the tropical evergreen forest, or rainforest *sensu stricto*, as well as the semi-deciduous forest, are also subjected to nutrient limitations. Water excess is the environmental pulse modelling the two types of alluvial Amazonian forests: *várzea* and *igapó*; the former corresponds roughly to Beard's seasonal swamp forest, the latter to his swamp forest.

Savannas occupy different positions in Fig. 30.8, showing how they are simultaneously influenced by more than one major environmental constraint. The locations of seasonal savanna, semiseasonal savanna and hyperseasonal savanna illustrate the role of drought, water excess and nutrients as environmental factors modelling the structural and functional features of these ecosystems. Fire seems to be an unavoidable con-

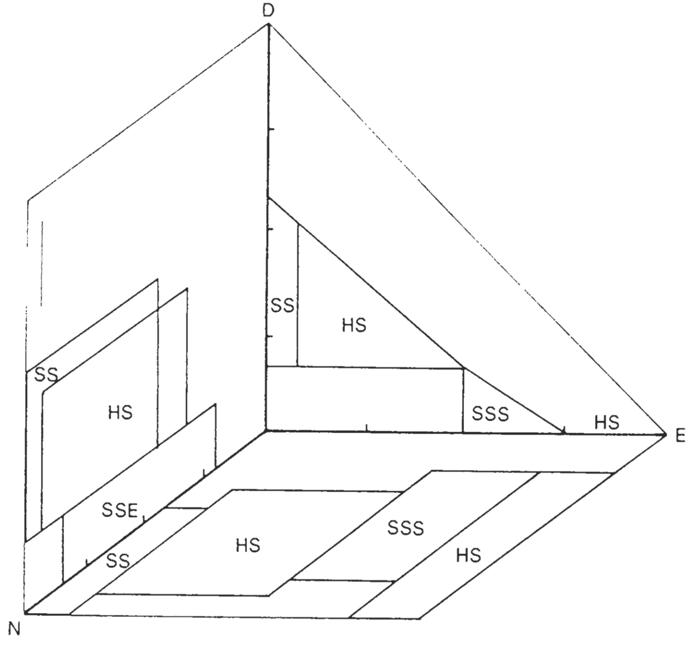

Fig. 30.8 Distribution of tropical savannas in the environmental space determined by water excess, drought and nutrient levels. The projections on the three environmental planes are shown. Notice how the three axes have a joint determination on savanna ecosystems. HS, hyperseasonal savanna; SS, seasonal savanna; SSS, semiseasonal savanna.

sequence of savanna structure and seasonality, reinforcing the effects of drought and nutrients.

When enough quantitative data concerning the environmental features of tropical ecosystems are available, more precise statistical approaches and multivariate analysis will be possible, and then sounder models relating biotic and abiotic characteristics may be elaborated. For the time being, our preliminary approach may operate as a guide to further research.

REFERENCES

Alvim, P. de T. and Araujo, W. (1952) El suelo como factor ecológico en el desarrollo de la vegetación en el centrooeste del Brasil. *Turrialba*, **2**, 153–60.

Arens, K. (1958) O cerrado como vegetaçao oligotrófica. *Bol. Fac. Fil. Ciênc. Letr. USP Botánica*, **15**, 58–77.
Arens, K. (1963) As plantas lenhosas dos campos cerrados como flora adaptada as deficiências minerais do solo, in *Simpósio sôbre o Cerrado*, (ed. M.G. Ferri), Editora da Universidade de São Paulo, São Paulo, pp. 287–99.
Beard, J.S. (1944) Climax vegetation in tropical America. *Ecology*, **25**, 127–58.
Beard, J.S. (1955) The classification of tropical American vegetation types. *Ecology*, **36**, 89–100.
Box, E.O. (1981) *Macroclimate and Plant Forms: An Introduction to Predictive Modelling in Phytogeography*, Junk, The Hague.
Cole, M.M. (1986) *The Savannas. Biogeography and Geobotany*, Academic Press, London.
Hase, H. and Folster, H. (1982) Bioelement inventory of a tropical (semi-) evergreen seasonal forest on eutrophic alluvial soils, western llanos, Venezuela. *Acta Oecologica, Oecologia Plantarum*, **3**, 331–46.
Herrera, R., Mérida, T., Stark, N. and Jordan, C. (1978) Direct phosphorus transfer from leaf litter to roots. *Naturwissenschaften*, **65**, 208–9.
Hoock, J. (1971) *Les Savanes Guyanaises: Kourou*, ORSTOM, Paris.
Hueck, K. (1966) *Die Wälder Sudamerikas*, Gustav Fischer Verlag, Stuttgart.
Mueller-Dombois, D. and Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*, John Wiley, New York.
Rizzini, C.T. (1979) *Tratado de Fitogeografia do Brasil*, Hucitec, São Paulo.
Sarmiento, G. (1986) Correlación entre los tipos de vegetación de América y dos variables climáticas simples. *Boletín de la Sociedad Venez. de Ciencias Naturales*, **113–114**, 454–470.
Sarmiento, G. (1984) *The Ecology of Neotropical Savannas*, Harvard University Press, Cambridge, Massachusetts.
Sarmiento, G. (1990) Ecologia comparada de ecosistemas de sabana en América del Sur, in *Las Sabanas Americanas. Aspectos de su Biogeografia, Ecologia y Utilización*, (ed. G. Sarmiento), Fondo Editorial Acta Cientifica Venezolana, Caracas, pp. 15–56.
Sarmiento, G. and Monasterio, M. (1975) A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in tropical America, in *Tropical Ecological Systems*, (eds E. Medina and F.B. Golley), Springer-Verlag, New York, pp. 223–50.
Schnell, R. (1987) *La Flore et la Végétation de l'Amérique Tropicale*, vol. 1; Masson, Paris.
van der Hammen, Th. (1974) The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, **1**, 3–26.
van der Hammen, Th. (1983) The paleoecology and paleogeography

of savannas, in *Ecosystems of the World, 13: Tropical Savannas*, (ed. F. Bourlière), Elsevier, Amsterdam, pp. 79–108.
van Donselaar, J. (1965) An ecological and phytogeographic study of northern Surinam savannas. *Wentia*, **14**, 1–163.
Veloso, H.P., Goés Filho, L., Barros-Silva, S., Ferreira, H. de C. *et al.* (1975) Vegetaçao, in *Projeto RADAMBRASIL. Levantamento de Recursos Naturais*, vol. 8, Departamento Nacional de Produçao Mineral, Rio de Janeiro, pp. 307–403.
Walker, B.H. (1985) Structure and function of savannas: an overview, in *Ecology and Management of the World's Savannas*, (eds J.C. Tothill and J.J. Mott), The Australian Academy of Science, Canberra, pp. 83–91.
Walter, H. (1964) *Die Vegetation der Erde in Oko-physiologischer Betrachtung. I. Die Tropischen und Subtropischen Zonen*, 2nd edn, E. Ulmer, Stuttgart.
Walter, H. (1973) *Vegetation of Earth, in Relation to Climate and the Eco-physiological Conditions*, English Universities Press, London.
Wijmstra, T.A. and van der Hammen, Th. (1966) Palynological data on the history of tropical savannas in northern South America. *Leidsche Geologische Mededelingen*, 38, 71–90.