Tropical grasslands: dynamics and utilization

William Sanford and Elizabeth Wangari

In 1979, Unesco, UNEP and FAO jointly prepared a major state-of-knowledge report Tropical Grazing Land Ecosystems, *which has been published as No. XVI of the Unesco series 'Natural Resources Research'. A large part of this report was naturally devoted to grasslands. Since then the subject has received considerable attention from both the scientific community and from land managers, including under the MAB Programme. Several important meetings have highlighted concern over grasslands: the Unesco–ICSU symposium on the comparison of savannah and woodland productivity in Africa and tropical America (Brazil, 1983), and the savannah conference and Fourth International Rangeland Congress both held in Australia during May 1984.*

The following article, prepared on the basis of the results of these meetings and of personal international experience, is intend to give a bird's-eye view of some current thinking on tropical grasslands, because of their particular importance for most developing countries and for balancing population, resources, environment and development on worldwide scale.

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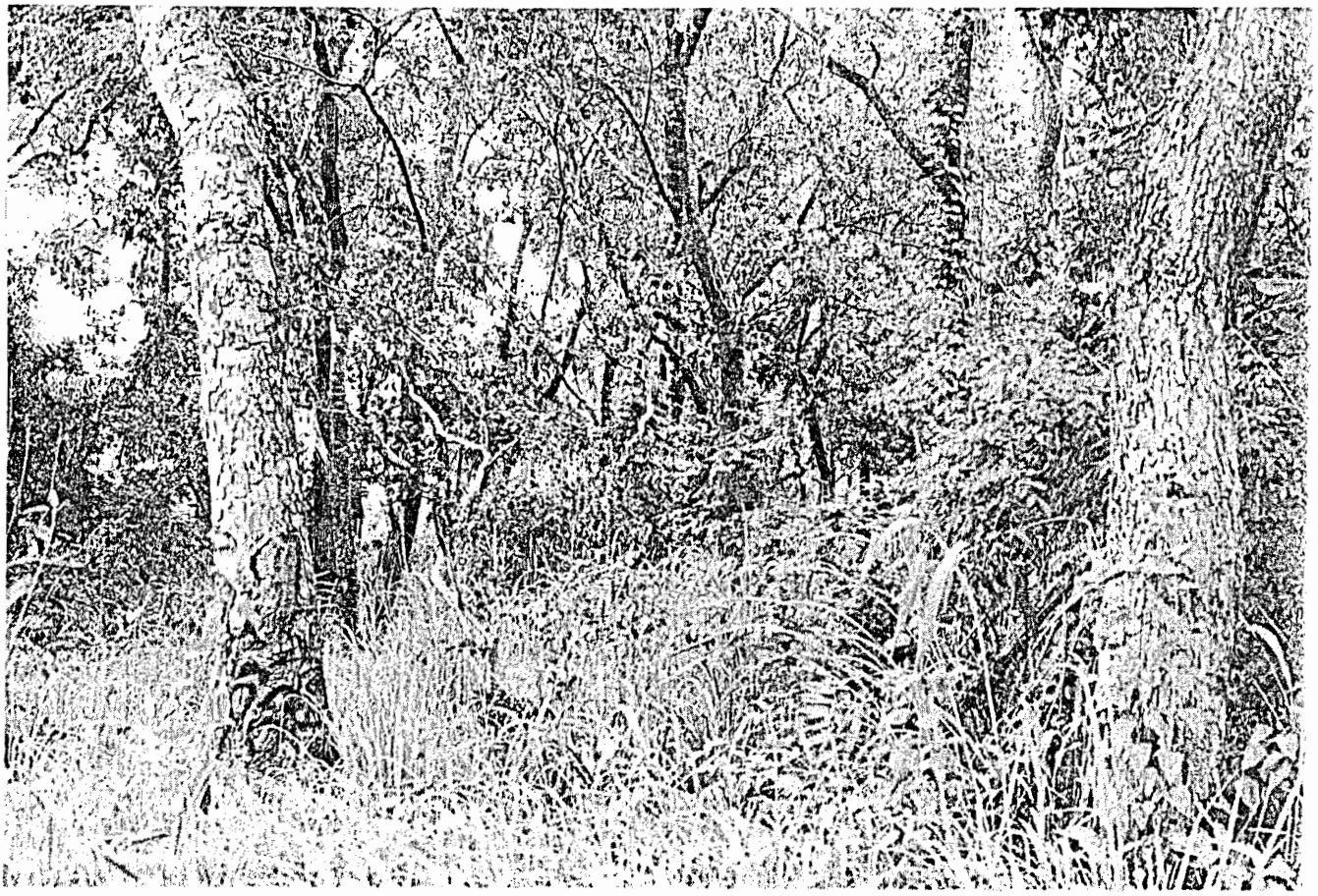

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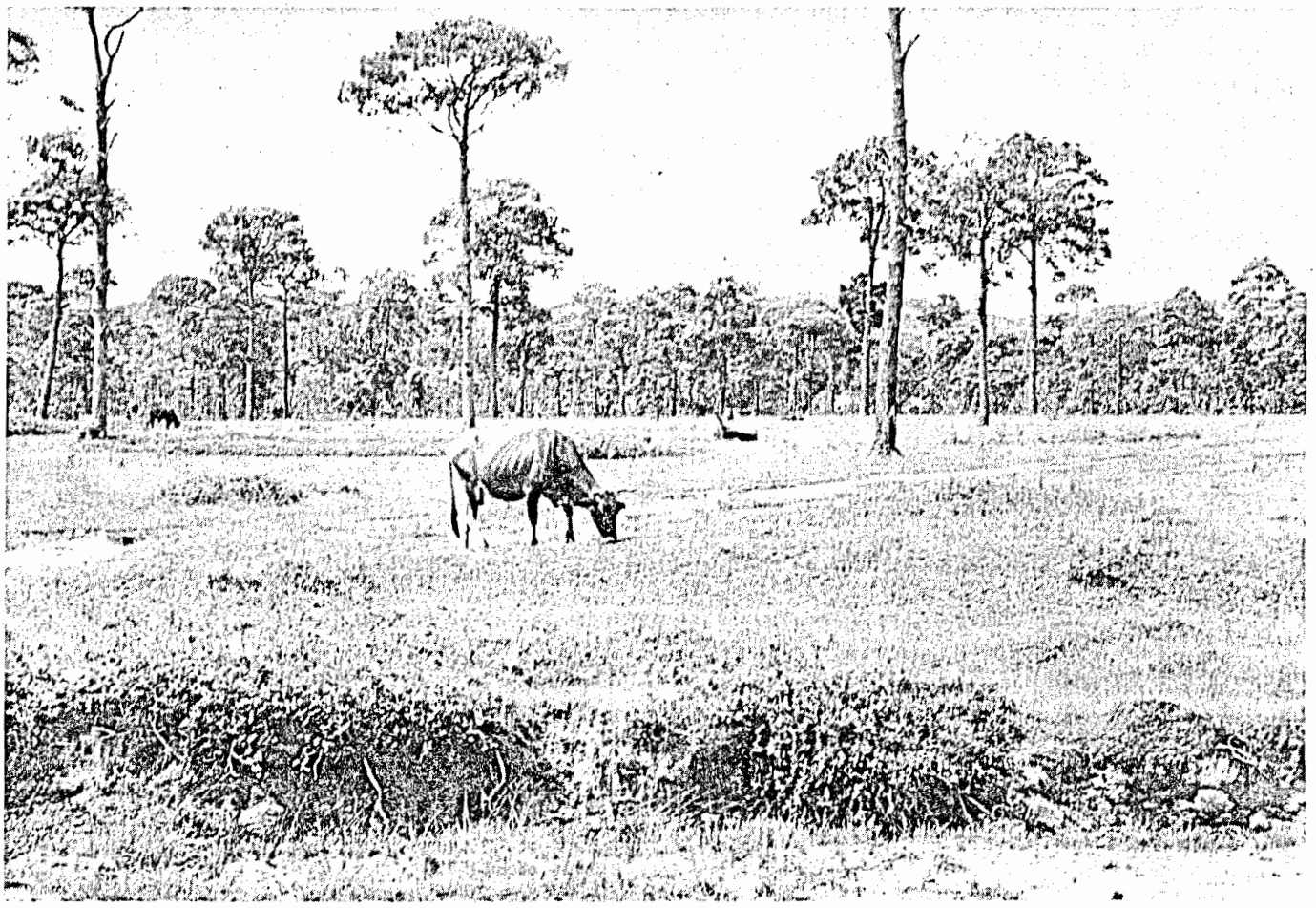

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One characteristic of tropical grasslands is their great variability in terms of landscape, tree density and density of the herbaceous cover itself. Shown here and on pages 14 and 15 are four different kinds of grassland environments:
(a) Sub-humid savannah woodland in Nigeria.
(b) Grassland–forest mosaic in Chiapas State (southern Mexico).

In the tropics, that 40 per cent of the earth's surface lying between the Tropics of Capricorn and Cancer, there are three fundamental types of vegetation: (a) in the driest regions, deserts and arid lands with very little vegetation, scattered and mainly ephemeral, and much bare earth and rock; (b) in the wettest regions, rain-forest of tall woody plants close enough together that their crowns touch or overlap and provide so much shade that little grows beneath them; and (c) in between, a highly complex series of vegetations having a ground cover of grass.

The grass family, formerly Gramineae, now Poaceae, is today recognized as a cosmopolitan assemblage of some 10,000 species, annual and perennial, usually considered to be among the most evolutionarily advanced of plants, with members distributed from the equator to Arctic snows and ranging from tiny creeping plants to treelike bamboos.

Although grasses are so adaptable that we find them nearly everywhere, it is in the 'in-between' vegetation of neither the forest nor desert that they are most widespread forming a nearly continuous ground cover. Some grass-dominated formations are virtually without trees or shrubs and are commonly termed 'grasslands' and are physiognomically and functionally very like the prairies of temperate regions. Other formations have a few scattered tall trees; still others have scattered low trees and shrubs and yet others have trees over 5 metres high, which are close enough together that many of the crowns touch. Such formations merge on the one hand with the tropical forests of wet regions and on the other with the 'steppes' and 'thorn scrub' of arid lands, and occupy about 30 per cent of the earth's surface. Representative estimates for tropical and sub-tropical regions are shown in Table 1.

Table 1. Approximate percentages of representative regions which are grass covered

Region	Percentage grass covered
Africa	42–57
Nigeria	over 70
South Africa	over 50
Asia	6–12
Australia	over 50
South America	80
Brazil	30 *(cerrados* 24)
Venezuela	40

The grass-covered vegetation types of sub-tropical regions are very similar in appearance to those of tropical regions and have probably had a similar evolutionary

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development. Widespread in both the subtropics and temperate regions are 'heathlands'. The terms 'heath', *'heide'*, 'steppe', 'desert', *'wuste'*, 'prairie', *'macchia'*, *'maquis'*, *'garrigue'*, *'tomillares'* and *'phrygarra'* all mean 'waste land', and such formations are ecologically restricted to soils very low in plant nutrients and often subject to periods of impeded drainage, waterlogging, and periods of drought. Where the soil is poorest, plants are mainly shrubby evergreen sclerophylls —plants with small, hard, stiff, narrow leaves. Where the soil is better, grass becomes prevalent and the formation looks much like a low, tropical grass savannah.

'Savannah' is a word of Latin-American origin adopted from the language of the Caribbean Indians, first used in 1535 by Oviédo to describe Venezuelan grassland now commonly called *'llanos'*.

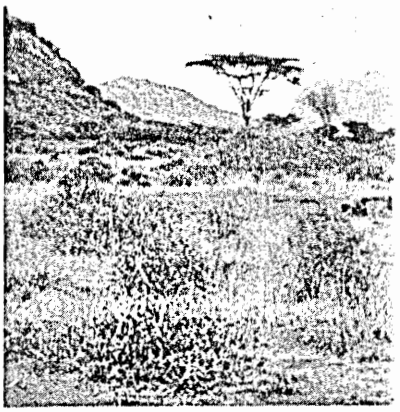
Much argument and many scientific papers have been presented as to what the definition of 'savannah' should be, and yet agreement has not been reached. Very broadly speaking, however, some geographical generalizations may be made. African savannahs are typically tall grass formations, with perennial grasses over 2 metres high forming a dense ground cover and scattered large trees and shrubs much in evidence. However, even in Africa, savannah is extremely variable, with sparse short grasses occurring in the driest regions and dense woodlands found in humid and sub-humid regions. Australian grasslands are perhaps most similar to those of Africa in appearance, and in both continents aridity is a major determinant of plant development. Some regions of Mexico and tropical America, however, appear very similar to African savannah, though the grass is often much lower in height. Grasslands in Asia are most different and are probably more often strictly secondary in formation, having been brought about by forest-clearing and burning by man rather than responses to soil and climate. In the Philippines, extensive grasslands occur in wet areas of impeded drainage and are dominated by the universal weed, spear grass *(Imperata cylindrica)*.

In all grassland regions, 'riverine' or 'gallery' forests occur along stream channels. In humid grasslands, these narrow bands of vegetation may resemble rain forest and contain a number of plant species found in moist forests; in drier regions, the trees are those species occurring in grasslands but they are much taller and closer together than in areas away from water courses. Several conditions may bring about such networks of forest within open grasslands. Sometimes the valleys are so steep-sided as to be almost inaccessible and so have been spared clearing and cropping. In dry regions the valleys provide protection from desiccating winds, and the soil is moister with the water table closer to the surface. Always, the soil is deeper and more fertile in these stream channels; not only have rains carried down soil particles and nutrients from higher ground but both rain and wind have deposited nutrient-rich ash left from grassland burning.

Grasslands are seen to vary greatly in height and density of grass and in presence or absence of trees and shrubs of various sizes at various densities. Significant differences also occur in the proportion of perennial and annual grasses and of grasses and broadleaved herbs. Generally savannahs are classified into sub-types on the basis of tree height and density, grass height and perenniality/annuality.

Primary production, that is the amount of dry matter produced by plants, largely determines the worth of vegetation to man and this varies tremendously both from region to region and from one type of formation to another and even within one formation in response to such micro-environmental differences as shading—exposure, soil depth and moisture, nutrient content, plant species. The above-ground biomass varies from less than 20 g of dry matter per square metre in arid grasslands to over 2,000 g in humid regions. For example: in India, minimum above-ground biomass varies from 0 to 871 g/m^{-2}, maximum from 76 to 3,296 g/m^{-2}; in Uganda representative figures are 59 to 405 g/m^{-2}; and in Panama from 501 to 2,088 g/m^{-2}. The below-ground biomass varies as much, with a marked tendency for an increasing proportion of below-ground production with increasing aridity, although of course the absolute below-ground biomass is always greater in moist regions.

Values from India are representative: in semi-arid regions, 16 to 86 g/m^{-2}; in



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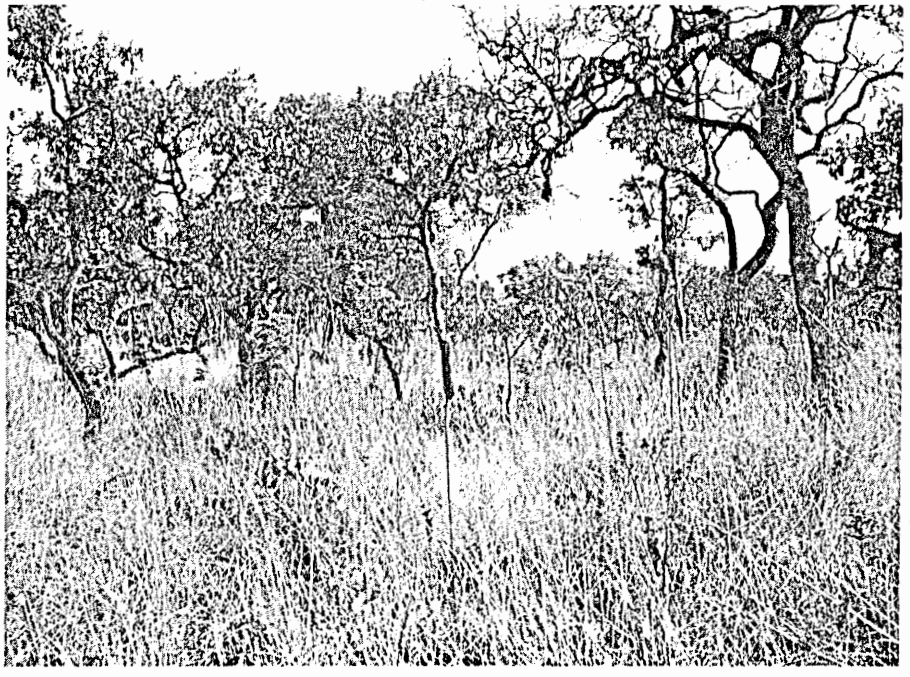
(c) Semi-arid grassland of East Africa.

(d) Cerrado grasslands in Brazil.



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humid regions from 705 to 1,381 g/m^{-2}. The ratio of above/below-ground biomass varies with the season. For example, ratios estimated in Ivory Coast range from 0.34 in the early growing season to 3.21 at peak standing crop.

Despite such great variation in the estimates of net primary production, tropical grasslands are almost invariably at least 1 per cent more efficient than temperate grasslands of regions comparable in moisture and nutrient availability. This is mainly brought about by the special photosynthetic metabolism of tropical grasses, their higher water-use efficiency and their being able to utilize high light intensities.

But even more variable than the structure, composition and productivity of grasslands, are the names applied to them!

In Colombia, ten subtypes of *'llanos'* are recognized, and in Brazil, at least eleven types of wooded grasslands called *'cerrados'* occur.

More open grasslands are termed *'campos'* and semi-arid dry forests or scrub, *'caatinga'*. Other tropical American and Mexican terms for grasslands are *'paramo'* and *'pastizal'*. In East Africa, savannah woodland is called *'miombo'*, and in southern Africa, various grass formations are called *'bushveld'*, *'karoo'*, or *'grassveld'*. Subtropical and temperate formations range from the prairies of drier regions which are open grasslands to the shrub lands of the Mediterranean, variously called *'maquis'*, *'macchia'*, *'garrigue'*, *'chaparral'*, *'matorral'*. The term 'tropical grasslands' is used here.

Unity of functioning and environment

Despite the welter of names and subdivisions there exists considerable unity of structure, physiognomy and functioning of tropical and subtropical vegetation having a ground layer of grass. There is also considerable uniformity in the general type of environment where such grasslands occur. The climate is sharply seasonal, with a period of at least four months of water deficit. The annual rainfall generally is from 600 to 1,200 mm, but the amount is much less closely related to the occurrence of grasslands than is its seasonal distribution and yearly variability.

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Thus in the Brazilian *cerrado* annual rainfall is from 1,100 to 1,900 mm, but there are always from four to seven months of drought stress. In most tropical American grassland regions, 80 to 90 per cent of the rain falls within five to eight months. Along the Atlantic coast, however, in the regions of the 'white sand savannahs' of Belize and parts of Honduras, Nicaragua, Trinidad and northern Brazil, rainfall may be as high as 2,000 to 3,000 mm with only three months with less than 100 mm, but the soil of these regions has such a low water-holding capacity that plants growing there are frequently under drought stress in spite of the heavy annual rainfall. Furthermore, nutrients are rapidly leached from such loose sandy soil. On many such areas grass is replaced to a great extent by sclerophyllous shrubs and 'heathland' results. In East and West Africa, savannah occurs in regions receiving from 600 to 1,200 mm of rainfall and having a dry season varying from five to seven months. On the other hand, some of the *Burkea* high elevation savannahs of South Africa have an annual rainfall of from only 400 to 600 mm.

In general, as the amount of rainfall decreases and/or the length of the dry season increases, grass becomes shorter and has narrow leaves, sometimes cylindrical or rolled to conserve water. The plants are more sparsely scattered so that areas of bare earth exist between them. Such vegetation is found in arid and semi-arid regions or in small patches in humid savannah where the drainage is poor or the soil very shallow. It is sometimes called 'steppe' or 'thorn scrub', though steppe is more often restricted to physiognomically similar temperate-zone vegetation. Roughly speaking, such formations occur in the tropics and subtropics in regions receiving from 200 to 600 mm of rainfall with from seven to eleven months of drought stress.

Besides highly seasonal rainfall, often coupled with great variation from year to year, the soils of grasslands are usually very low in available nutrients, especially phosphorus and nitrogen. The two unfavourable conditions—lack of available nutrients and of adequate moisture—often go together. Sometimes, however, one set of factors may be so extreme that it compensates for the other factors. In Brazil, for instance, the *cerrado* regions have extremely poor soils which together with the length of the dry season lead to grassland in spite of the high annual rainfall; the *caatingas* have much more fertile soils but the rainfall is low and the dry season long so that dry woodland or scrub develops.

Sometimes micro-nutrients occur in the soil to toxic levels. Aluminium is the most frequent offender. Many sedges and some grasses are resistant to this soil poison, giving them a competitive advantage over other plants. Furthermore, aluminium toxicity is most frequent at lower soil depths and thus affects deeply rooted trees more than grasses and may contribute to the replacement of forest by savannah.

Disturbance by man is becoming an increasingly important factor in the development of grasslands—and in their destruction. For example, clearing of trees may convert woodland to open grassland, or forest to secondary grassland, or overgrazing or large-scale mechanical tillage may convert dry grassland to thorn scrub or steppe—or desert. Annual burning, common to most humid and semi-humid grasslands of the world, does not normally alter grassland formation but is, rather, an integral part of the grassland environment. If, however, a woodland is cut, annual burning will usually prevent its regeneration.

Fire in the grassland environment

An early explorer named Hannon reported seeing fire along the west coast of Africa in about 300 B.C., and this has contributed to the belief that grasslands are caused by fire destruction of forest. Actually, grasslands are brought about by the interaction of soil and climate over long periods of time, even if fire has extended such climatic-edaphic formations and is important in maintaining them. More important than fire is tree clearing, as neither forest nor woodland can regenerate after cutting unless protection from both fire and animal browsing are given for at least six years. Thus many grasslands are secondary and relatively recent.

Once a grassland has developed, fire becomes almost an inevitable yearly occurrence. A few fires are caused by accident and some are caused by lightning, but these are usually not widespre Most fires are purposefully started l cause it is only by frequent burning tl grasslands can be utilized by man. Lit and standing dead grass is relatively sl to decompose and prevents the growth grass flush. Furthermore, this early flu appearing in the late dry season, not o provides animal fodder at a time of gr scarcity of food but is also very rich crude protein. Herdsmen have, therefo since the very beginning of animal h bandry, burned the old grass in orde stimulate this flush and make it accessi to the livestock. Burning is also associa with hunting. It has long been a us practice for the men and boys of a vill to get together and burn an area in or to drive out the animals for easy killi With the development of farming, bu ing has been the only practical wa clearing the land, preparatory to cult tion and planting.

In sum, fire may be said to affect structure and species composition of vegetation, and primary production. sides being usually poor in phospho and nitrogen, grassland soils also ha low concentration of organic matte humus. In fact, the major problen savannah soils from the standpoint nutrients, cation exchange capa water-holding capacity and texture is of sufficient humus. Unlike tempc regions and some tropical forests, sa nah humus does not come primarily l litter but from the underground bion Thus fire, by removing surface litte herbaceous standing dead, has little e on soil humus except to a depth of Rather, the effect of fire on soil or matter will be determined by its effe the underground or root biomass, thus by its effect on the species com tion and structure of the vegetation a as on total primary production. In g al, annual burning increases grass pr tion, removes a high proportion of sl and small saplings but does not affc larger trees. Woodland, once establi remains stable with annual burnin enough small saplings escape burni that regeneration and replaceme dead trees occurs. Whether or not fi increase soil humus, depends not o the species of plants and their tota duction but also on the soil and clim

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Many grassland areas have been planted with crops like maize. Although initial yields may be high, planting on slopes can also lead to erosion and reduced fertility.

the location. The most important aspect of humus resulting from burned vegetation is the relative underground biomass turnover of grass as compared with that of trees.

Grass-root turnover rates vary from about 97 per cent per annum in the semi-arid grasslands of India to from 250 to 460 per cent in swards of the perennial grass *Panicum maximum* in Africa and tropical America. Well developed grass swards may then contribute more underground organic matter than scattered trees. Another aspect must, however, be considered: soil temperature and rate of mineralization. An increase of 9 or 10 °C in the soil temperature doubles the rate of decomposition and subsequent mineralization. Trees not only add humus from their roots but by surface litter and canopy shading keep soil temperatures lower so that humus is mineralized and lost more slowly. Thus the most stable and favourable situation for providing adequate soil humus is light woodland with a dense ground cover of grass.

Grass production is significantly higher with, and usually higher after, late burning in the dry season than after early burning, with underground biomass following the same trend. This is apparently because the flush stimulated by early burning can seldom survive the period before the rains come, whereas that stimulated by late burning does survive and so gives a head start to annual production. In very hot and dry regions, however, higher grass production is sometimes obtained with early burning or even with fire protection. Controlled burning experiments in north-eastern Ghana gave such results partly through control of species composition and partly through amelioration of the high temperatures of unshaded areas which bring about high respiration and translocation rates. Also, tall perennial grasses were better able to compete with the shrubs and small trees more prevalent with fire protection and early burning, and this led to greater grass standing crop. Such a situation, however, is not favourable to animals grazing as such grass species are both less palatable and less nutritious than the less competitive shorter grasses.

It becomes clear that any burning regime must be adapted to the climate and soil, to the vegetation formation and to the utilization to be made of the area; but throughout the world, fairly late and intense burning appears most suitable for maintaining good grazing lands. Failure to burn or burning too early leads to an increase of shrubs and saplings, a decrease in palatable grasses—effects similar in every way to those resulting from over-

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grazing. The maintenance of woodland is also usually dependent on burning. In Australian eucalyptus woodlands, fire is necessary to promote seed germination and to clear away competing shrubs. Furthermore, with fire protection there is such a build-up of small trees and shrubs and herbaceous material that accidental fires are intense enough to destroy mature trees. It has also been reported in several parts of the world that germination of legume seeds is promoted by fire. Legumes are especially important because of their ability to fix atmospheric nitrogen in association with bacteria in their roots.

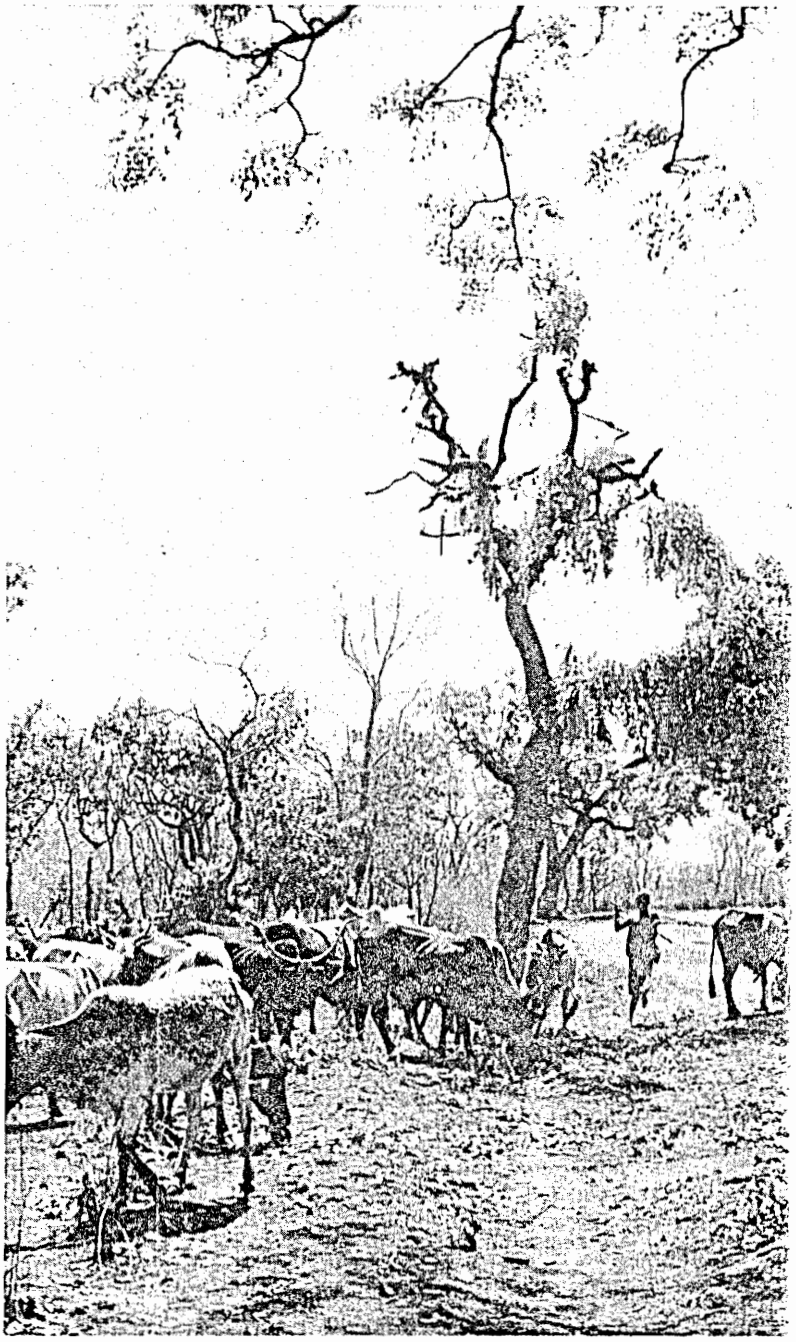
The importance of grasslands to man

Grasslands were probably of especial importance to early man, where he could hunt animals and gather a variety of fruits, seeds and leaves for food. In his later development, when he became an agriculturist, it was in the grasslands that he practised the new arts of domesticating animals and growing grain. Those men who ventured into the forests were forced by their less malleable and variable environment to remain hunter-gatherers for a much longer time.

Grasslands have continued to be of major importance in the tropics because of their vital role in food production. One reason is the nature of tropical light. Though the rays of the sun are more direct at the Equator than elsewhere, the amount of light actually available to plants for photosynthesis throughout the tropics increases with distance north and south of the Equator. For example, the mean annual radiation per square centimetre in the equatorial belt of South-East Asia ranges from 586 to 670 kj, in the Congo Basin of Zaire from 502 to 544 kj, in the Amazon Basin of Brazil from 419 to 502 kj; whereas the average in lowland rain-forest areas is about 670 kj and in dry grasslands (savannah) 837 kj. The reason for this seeming anomaly is that the skies of equatorial regions are more often banked with heavy cloud.

Besides the obvious advantages to primary food production of higher light intensity, the grasslands are more easily cleared for cultivation than forest lands, and their soils are somewhat less subject to water erosion and leaching. Furthermore, the incidence of fungal and bacterial diseases of both plants and animals is less in grassland, the long dry season and generally lower atmospheric humidity being unfavourable for the reproduction of most micro-organisms.

If man has been adapted to life in grasslands for thousands of years, and if such lands are today widely recognized as vital for the production of food, why is it that tropical grasslands throughout the world tend to be improperly or under-utilized? And why is there the ever present danger of vast grassed areas degenerating into desert or the soil becoming so impoverished that they will be useless to future generations?



Cattle are a familiar feature of ma grass- and woodlands. However, ity of herbage during parts of the some areas, the effects of the tsets major problems.

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The evolution of grasslands

Some grasslands are very old systems and are more or less stable, the result of very many years of interaction and adaptation between plant and animal organisms, soil and climate. And even those secondary grasslands which have been brought about by human activities are inhabited by plants and animals which evolved over thousands of years in other 'natural' grasslands. Perhaps the least disturbed systems are found in tropical America, while the most disturbed ones are found in Asia, with Africa having a foundation of very old grass systems on which are superimposed a variety of younger, highly disturbed systems.

Grassland formations and species of herbs and woody plants adapted to periodic drought began development in Gondwanaland some 120 million years ago, before this great land mass split up into the present drifting continents of America, Africa, Asia, Australia, and Antarctica. In tropical America there is much evidence that extensive grasslands existed long before the arrival of Europeans and before the development of any indigenous cattle. African grasslands, especially those of eastern Africa, are very ancient, and some workers believe that they pre-date the development of rain forests. Certainly savannahs existed during most of the Quaternary, a million years ago, and savannah species are of very ancient evolution, many being present already in the middle Eocene.

Special adaptations of grassland organisms

The plants and animals of grasslands are thus the products of very long evolutionary development and environmental selection fitting them for the special conditions of grassland regions: severe drought stress during part of the year, low soil fertility, frequent high air and soil temperature, and intense competition among the organisms for moisture, nutrients, light and space itself. Perhaps most basic to the survival of any tropical grassland organism and its competitive ability in relation to other organisms is its adaptation to drought stress. Two different types of solution are possible: drought endurance and avoidance. Avoidance is the most common adaptive mechanism of animals—they simply move from a region where there is no water to a region where there is water—a splendid solution so long as a place with water can be found. This search for water and the vegetation accompanying it imposes nomadism or transhumance on the pastoralists and herds of livestock, as well as on wild animals, in many tropical and subtropical regions, most especially in Africa. Ethnic groups such as the Masai of East Africa and the Fulani of West and Central Africa have led a migratory existence for many generations. Distances travelled by men and herds are often great. For example, in Central Mali, annual movements of at least 1,000 km are common. In recent years, however, these traditional ways of life are increasingly threatened. With the development of farming has come increased friction between migratory herdsmen and the settled farmers.

Plants, in a strategy somewhat analagous to that of animals, often survive dry periods by 'migrating': many weeds have such efficient seed-dispersal mechanisms that when one habitat becomes unfavourable they are able to spring up in another. One particularly notorious traveller is a perennial member of the daisy family. This tropical American weed has small, parachute-carrying seeds: it invaded Asia probably along with grain and spread rapidly. Much of its spread is said to have been by way of soldiers' boots during the Second World War. From Sri Lanka, this time with the seeds of a tree being imported to establish pulp-wood plantations, it migrated to eastern Nigeria in about 1949. Since then it has quickly covered cleared areas throughout the humid regions of West and East Africa. It is only held in check by cultivation or by tree shading or by severe dry seasons which allow more adaptable grasses to take over.

Rather than migrating, many animals, especially insects, and many plants synchronize their life-cycles with moisture availability, surviving the dry periods as pupae or seeds or underground storage organs. Some annual plants, termed ephemerals, spring up from seed with the first rain, grow, flower and produce seed within only a few weeks.

Drought endurance is also an adaptive mechanism of many grassland organisms. Plants have developed a fantastic variety of swollen roots, stems, leaves, buds for the storage of water, as well as such complicated mechanisms as controlling the osmotic pressure of their cells to allow water withdrawal from almost dry soil. In tropical and subtropical America, the most obvious drought endurers are cacti.

But water storage presents a great problem to tropical plants: fleshy organs tend to overheat. Much more radiant energy is absorbed by fleshy leaves than is used in photosynthesis and this is transformed to heat. With little surface in relation to their volume for convectional cooling, the leaves are slow to cool and so are about 15°C warmer than the surrounding air. This may lead to protoplasm death or, more insidiously, to such an increase in respiration that the organ's food store is exhausted and the leaf or the whole plant withers and dies.

Various means of enduring drought through dormancy or quiescence are common among plants. The most spectacular drought endurers are the 'resurrection plants', which in the dry season cease most metabolic activity, lose most of their tissue water and become withered and dry, seemingly dead. Then with the first rain they suddenly, often within twenty-four hours, become 'alive' and green again.

Grass is more adaptable to dry periods than most trees. Trees, even without leaves, possess a very considerable mass of tissue which respires and requires water, whereas grass can exist completely underground during the dry season as small, nearly inert rhizomes. Many tropical grasses also have the metabolic trick of raising cell osmotic pressure by accumulating solutes and thus being able to continue taking up water metabolic activity and growth under severe water deficits.

Furthermore, grasses have the advantage of speed: plants establish from seed within only a matter of weeks, while tree seedlings remain fragile and vulnerable for years. It is during this regeneration phase of the tree that grass becomes a serious competitor for light, moisture, nutrients and space. The infant tree is often crowded out.

Besides such dramatic adaptation for drought endurance as quiescence and dor-

mancy, 'death' and 'resurrection', there are a host of less obvious, more ordinary plant adaptations. Perhaps the most important of these is the waterproofing of leaves and stems by a secreted waxy coat, the cuticle, which varies in thickness and impermeability with the plant species and the environment. Also important is the regulation of the opening and closing of the stomata of the leaves.

Some plants have evolved a very clever dodge by which they keep their stomata closed all day, so conserving water, and open them at night for carbon dioxide absorption. Naturally, this carbon dioxide cannot be used to synthesize carbohydrates without light energy, so it is fixed without energy gain onto acid molecules and released for photosynthesis during the day.

As in the case of storing water in fleshy leaves, conserving moisture by reducing transpiration endangers the leaf to overheating, since evaporative cooling, which may account for up to 20 per cent of the leaf's heat loss, is curtailed. Plants growing in periodically hot and dry habitats must strike a precise and precarious balance between conserving water and preventing overheating.

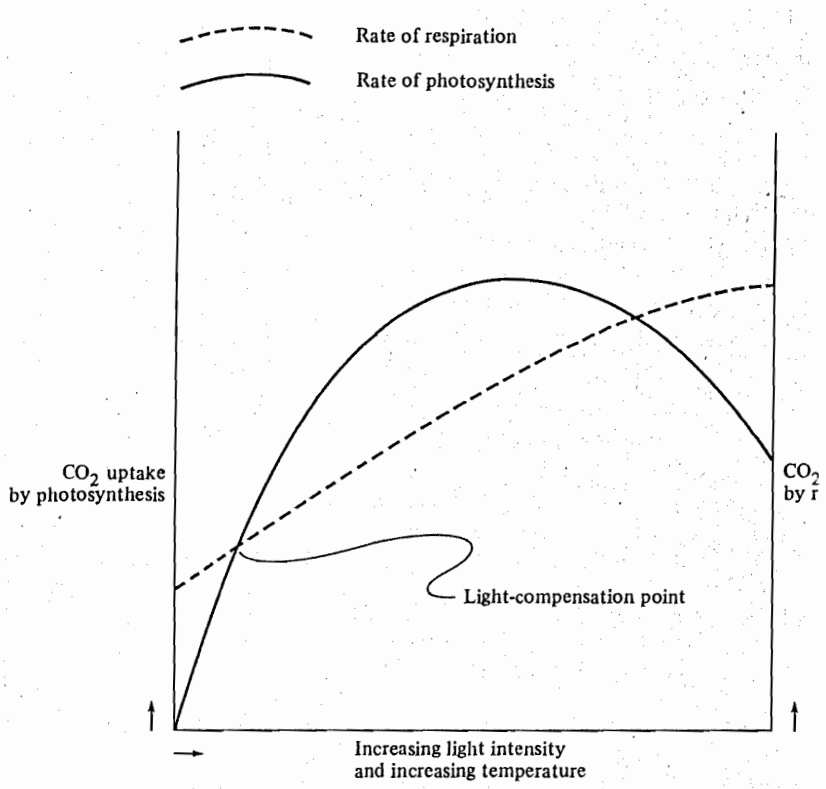

FIG. 1. Relationship between photosyn respiration, and light and temperatur

Special physiological features of grass

More usual than protoplasmic death from overheating is tissue starvation through increase in respiration brought about by elevated temperatures. Respiration increases almost linearly with increasing temperature and this depletes stored carbohydrates. Most animals become inactive and seek the shade as the day progresses; some plants are able to live in shady areas, possessing photosynthetic mechanisms able to manufacture sufficient food at low light intensities; these are said to have low light-compensation points, as illustrated in Figure 1.

However, many plants require high light intensity and many habitats are fully exposed. Unfortunately, photosynthesis is inhibited in most plants by temperatures above about 25 °C, thus as the temperature rises, the rate of food-making decreases, while the rate of using it up by respiration increases (Fig. 1). An elegant solution to this dilemma is the C_4 metabolism of most tropical grasses. The usual metabolic pathway of photosynthesis common to all green plants is called the C_3, or Calvin, pathway, because in the reduction of carbon dioxide the first stable molecule formed is a 3-carbon compound. Most tropical grasses, many sedges and desert-growing Chenopodiaceae, and some Amaranthaceae, have in addition to this pathway another route of carbon-dioxide absorption and fixation of which the first stable molecule is a 4-carbon compound. Plants possessing this added metabolic luxury are more efficient in absorbing carbon dioxide, especially at very low concentrations so that they can snap up the carbon dioxide given off by their own respiration as well as taking atmospheric carbon dioxide. Moreover, photosynthesis continues efficiently at high leaf temperatures; in some plants optimum temperature is as high as 50 °C. And there is still another advantage: C_4 plants do not respire as much as do C_3 plants. The normal plant respires in both darkness and light, the rate of respiration being dependent upon temperature; in addition, photorespiration occurs, that is, respiration induced by light. C_4 plants do not have this additional photorespiration and

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so are able to conserve more hard-earned carbohydrate for growth and storage.

Where C_3 and C_4 grass production has been compared in climatically and edaphically similar locations, as in northern Australia, the maximum daily yield of the C_3 grass was only 50 per cent of that of the C_4 grass which was, at maximum, able to produce 3 g of dry matter per square metre per day. The presence of C_4 metabolism is therefore of great importance to the plant and helps to explain the apparent competitive advantage of grasses over other plants in the hot, bright areas where grass formations are found.

Adaptation to tropical soil conditions

The infertile and fragile soils so often associated with tropical and subtropical grasslands impose additional adaptations on long survivors. In this case, the burden of adaptation falls on the whole system rather than on the individual species. The plant assemblage must be such that the ground is continually covered with several layers of vegetation to minimize rain impact and runoff, water and wind erosion; and a dense network of roots must exist underground at several levels for the absorption of all available nutrients before they are leached away. Also the formation must ensure that the nutrients taken up from the soil are eventually returned for re-use with minimum 'leakage' from the system. Animals as well as plants are important parts of such a system. Some of the nutrients are immobilized by plants or transferred to animals (earthworms, termites, insects, vertebrates). These, together with micro-organisms, are important in breaking down the plant material into smaller particles for return to the soil. The eventual chemical breakdown or decomposition is accomplished by bacteria and fungi. It has been estimated that in rangeland the biomass of micro-organisms in the soil is about ten times that of animals above the soil.

The nutrients most often in short supply in the world's tropical grasslands are nitrogen and phosphorus. This is to say that these nutrients are present in the soil in an available form at such low concentrations that the amount present determines the amount of primary production, and thus also of secondary production. Nitrogen occurs in the soil mainly in organic form, as does phosphorus, in humus. About 5 per cent of humus consists of nitrogen, but little of this is available to most plants until it is nitrified or mineralized, that is until the nitrogen of the complicated organic molecules in which it was immobilized in the plants and animals is oxidized into nitrate or nitrite. Similarly, organic phosphorus is mineralized to phosphate.

Unless the negatively charged nitrite, nitrate and phosphate ions are taken up at once by plants they may be leached or washed away, as they cannot be held for ion exchange by the negatively charged particles of humus and clay colloids. Thus a considerable bank of humus is needed to provide sufficient nitrogen and phosphorus together with a nice balance between their mineralization in the soil and their uptake by plants. The major difficulty is that there simply is not enough humus to provide the necessary nitrogen (as well as phosphorus and sulphur). In some circumstances it may appear that the rate of nitrification, which varies with environmental and soil conditions from about 1 per cent to 4 per cent per year of the organic store, is the limiting factor, but should this rate be increased, the ultimate supply would obviously still depend on the humus store. In addition, humus is extremely important in preventing the leaching of positively charged nutrient ions, such as the essential plant nutrients calcium, magnesium and potassium—by holding them with its negatively charged colloidal particles. Humus is also important for its water-holding capacity and for the structure it gives to soil' making it more permeable to both water and air.

Some grasses bypass part of this complex cycle by using, at suitable soil pHs, ammonium (reduced) nitrogen directly instead of waiting for the oxidized forms. This ability not only allows such plants to obtain nitrogen before humus mineralization is complete but it also saves them the metabolic work of reducing nitrites and nitrates back to ammonium ions, the first step in amino-acid and protein synthesis. There is considerable evidence that many perennial grasses not only utilize ammonium nitrogen but also secrete chemicals (phenolic compounds) from their roots, which inhibit nitrification and so reduce leaching losses of nitrogen as well as discourage other plants able to use only oxidized nitrogen, so gaining still another competitive advantage. Plants have also been shown to be able to absorb gaseous ammonia from the atmosphere. Thus, if the vegetation is dense enough with several layers, the ammonia produced by bacterial ammonification is not lost from the system.

Many tropical grasses are endowed with still another advantage over most other plants: they are adapted to low soil fertility either by more efficient uptake or utilization of nutrients, or by lower requirements. This is especially true of perennial African grasses, which have successfully adapted to poor soils in both the Old and New Worlds.

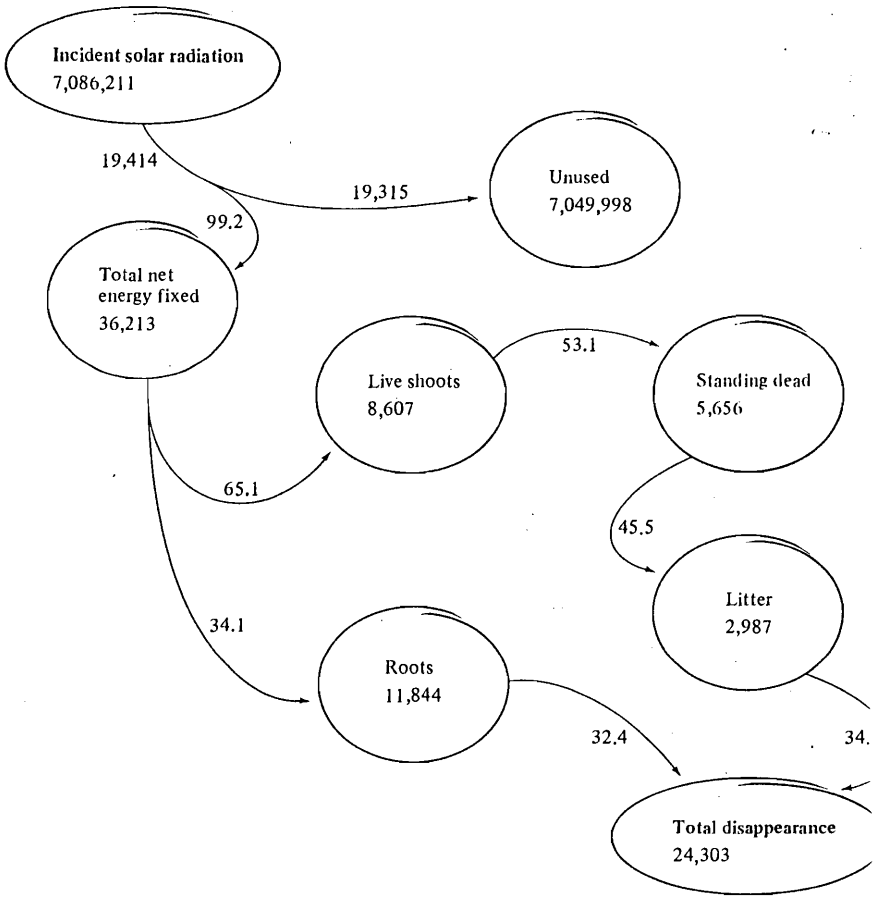
The ability of so many tropical grasses to survive with less nitrogen and/or phosphorus is a mixed blessing to range managers: such grasses can manage on poor soils but, accumulating only low amounts of protein-building nutrients, they provide poor livestock fodder. In fact most of the tall perennial African grasses are nutritionally so poor—except at the very stage of flushing—that cattle cannot get sufficient food even by eating large quantities.

One reason that savannah plants are so efficient in the use of the limited nutrients of the soil is that 95 per cent of them form associations with mycorrhiza: that is, their root tissues and soil fungi form complex associations which enhance the ability of the plant to take up nutrients and water. It has also been shown that mycorrhizal formation enhances nodule development in legumes and thus increases the fixation of atmospheric N_2. A puzzling complication, however, occurs in relation to soil phosphorus: while phosphorus often limits nitrogen fixation—that is, low phosphorus reduces fixation—high phosphorus inhibits mycorrhiza formation. Clearly, more research is needed in this area.

Besides the problems of insufficient moisture, low soil fertility and frequent high temperatures, light is often a constraint to primary production, even in the savannah regions. During the growing season, the sky is often heavily clouded, reducing the efficiency of solar radiation use.

Most natural savannah has about 138

FIG. 2. Annual energy flow (kj/m²) in dry si humid Indian grassland. (After J. S. Singh. P. Singh and P. S. Yadava, 'Ecosystem Syn thesis', in R. T. Coupland (ed.), Grassland Ecosystems of the World: Analysis of Gra lands and their Use (IBP Programme 18), *Cambridge University Press, 1979.) Boxes show energy stored in mean standing crop and lines indicate net mean daily flux.*



per cent of the mean efficiency of agricultural systems. Overall efficiency of tropical grasslands varies from 0.005 to 0.028 per cent of the solar constant, while that of rain-forest ranges from 0.015 to 0.075 per cent. In a recent MAB study in north-western Nigeria, the efficiency of open, low tree and shrub savannah was estimated at 0.03 per cent, while an adjacent savannah woodland had an efficiency of 0.05 per cent. An example of the way light energy may be partitioned in a grassland ecosystem is shown in Figure 2.

Present concern with grassland management

Recent grasslands conferences have underlined that many problems of management and mismanagement are shared by tropical, subtropical and temperate grasslands all over the world. It is generally agreed that crucial areas of concern are:

- Understanding and predicting the stability and resilience of grassland ecosystems.
- Controlling herd size and grazing patterns in arid and semi-arid regions and increasing the utilization of humid and semi-humid savannahs.
- Understanding the relationship between grass and trees and nutritious herbage production.
- Increasing the productivity of grasslands, both the production of fodder plants by range improvement and the production of crops by suitable methods of farming.
- Preventing soil and vegetation deterioration.

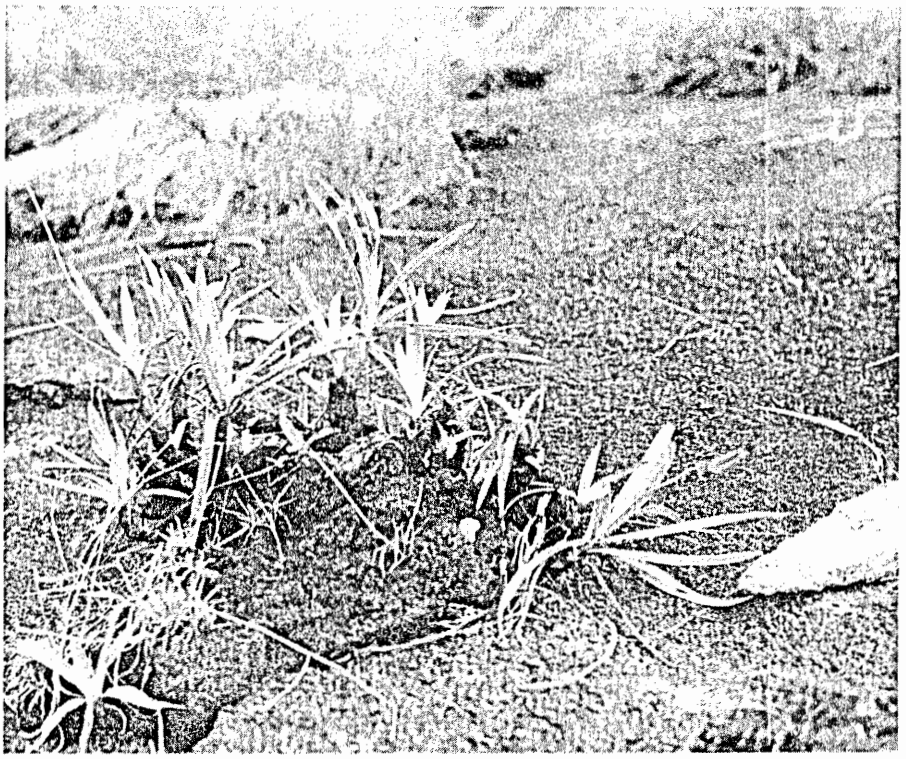
It is also very clear that different interest groups are in sharp conflict with each other: herdsmen and rangers are eager to do away with woodlands but are not anxious for widespread farming; foresters are sometimes blindly concerned with the preservation of trees at all costs; politicians are sometimes anxious for immediate results regardless of future consequences.

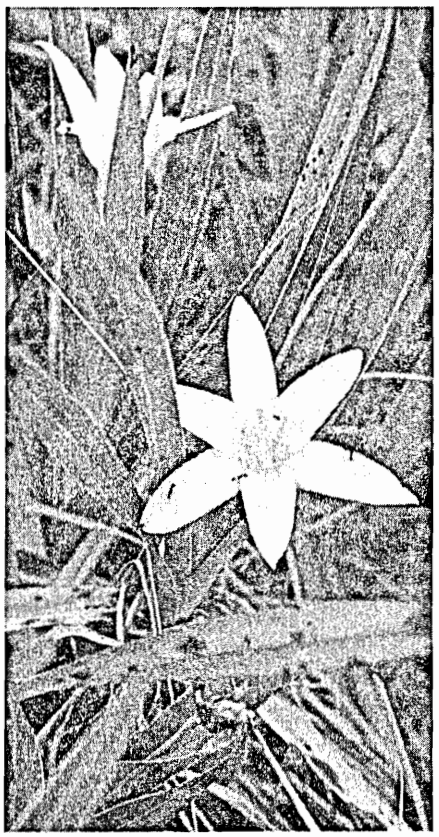
Stability and resilience

There are two kinds of ecosystem stability (not always parallel): compositional stability and functional stability. A system which is compositionally stable will remain about the same in its species composition; a functionally stable system will remain more or less constant in the amount of biomass it produces. In both cases, stability is quantified by the robustness of the system, that is, how much disturbance it can absorb without changing. An important example of the temporary divergence of compositional and functional stability is often encountered in range management. The practical ranger is concerned with meat or milk production, and if he monitors only this secondary production, his management may eventually lead to disaster: the vegetation may be so overgrazed that considerable plant death and changes of species composition occur, exposing the soil to erosion and leaching. But this deterioration may be initiated, even well advanced, before animal production ceases to be profitable. Alternatively, overgrazing may lead to a shift in the composition of the vegetation from palatable and nutritious to unpalatable and non-nutritious plants. animal production alone is being monit ed, these profound changes in vegetati and soil may initiate destabilization of t whole system before an economically a preciable decrease in animal producti occurs. And in fact it has been shown th overgrazing is actually profitable in t short term and thus inevitable in m situations.

Similarly, on cultivated land, crops m continue to be profitable for a period time after soil deterioration has starte For instance, overuse or misuse of t Kimberley regions in north-western A stralia led to the degradation of grassla to bare semi-arid conditions and to an i vasion of poorer grasses and shrubs in once profitable pastures. As a result, t region now supports an average of on one head of cattle per 40 hectares.

The first overgrazing danger signal usually a change in the composition of t





The 'resurrection' plant is an example of adaptation to the seasonal and annual extremes occurring in many tropical grasslands. During the dry season the plant loses its chlorophyll, shrivels up, and appears dead. But within twenty-four hours of rainfall the plant comes back to life.

herbaceous component of the system—that is, compositional destabilization—followed by the encroachment of shrubs in more humid regions and the increase of bare ground in drier regions. Similar effects follow the cultivation of land not suited to cultivation, or cultivated by inappropriate methods.

To understand stability it is important to be able to determine how much use the grassland system can bear and the best method of utilization before it becomes unstable. To do this it is clearly necessary to have an understanding of both functional and compositional stability and the relationship between them—not an easy task.

Considerable variation in the variety and number of plants and animals in a system may occur without affecting functional stability; however, a seemingly small compositional shift such as an increase in shrub density or a shift in the ratio of annual to perennial grasses may disrupt functional stability. Particularly destabilizing in semi-arid and subhumid regions are seed-eating insects, birds and rodents, and an increase of only 10 per cent in the insect population may bring about irreversible destruction of vegetation.

Resilience is the ability of a system to change and to return to its former state—it bounces back. It was once generally believed that if, for example, a woodland were cut down, it could form again if the area were left alone; that if a range were overgrazed to the point of becoming eroded shrubland, it could return to usable rangeland if further grazing were prevented.

There are no grounds for such optimism. There is no evidence that grasslands are stable climaxes, and no evidence that disturbed grasslands will return to grasslands. Experiments in the Ivory Coast have shown that woodland cut down can only be regenerated if there is considerable intervention by man. This means that every effort must be made to maintain the stability of useful ecosystems and to increase their resilience.

Unfortunately, the ecosystems preferred by man because of their high productivity are inherently unstable. As indicated in Table 2, rangeland is less fragile than cultivated land. In fact a major cause

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of land degradation is the attempt to cultivate land unsuitable for cultivation or the use of unsuitable methods of cultivation. However, it is obvious that much grassland, especially in the more humid regions, must be brought under cultivation, and therefore suitable methods for doing so are needed.

Some idea of the energy inputs made to livestock systems is given by Table 3. Cultivation for crops such as a grain, cotton and vegetables requires even greater inputs not only of fossil-fuel energy but also of fertilizers, and this leads to even less stable and resilient systems. Unless these inputs are sufficient and continuous, the system—and its land—will degenerate rapidly. Ranching leads to somewhat less instability, but as we have seen, the necessary monitoring of the system for both plant and animal production is difficult and often ignored in practice.

The greatest improvements in animal production in much of Africa and perhaps in some of tropical America, coupled with the least danger to the land, could be achieved through improving transhumance pastoralism. In Australia, Asia and most of tropical America this would entail seeding grasslands with suitable legumes, controlling livestock density and establishing many scattered water points. While both open or natural rangeland and managed ranches or improved rangeland are more stable and resilient than cultivated land, it is obviously necessary to increase by a good amount the savannah land under cultivation and to improve production. Humid and sub-humid grassland regions are particularly suitable for carefully managed agriculture. The best hope is offered by the development of farming systems which achieve the most favourable ratio between production and input and are therefore the least unstable. The International Institute for Tropical Agriculture (IITA) at Ibadan, Nigeria, is especially concerned with such development. For most tropical regions, considerable modification of American and European temperate zone agriculture is required, but this is slow in coming about. Most Third World agriculturists at present teaching at universities and working with government agencies were either trained abroad or trained by foreigners from temperate regions. Foreign aid in tropical regions has generally had a bias towards foreign methodology. Thus, far too many attempts are still being made to crop grasslands by using inappropriate models, and there is resistance to innovation. Particularly promising developments are no-tillage and minimum tillage whereby the soil is not mechanically cultivated by ploughing. Rather, the preparation of the seed bed is achieved by use of herbicides, and seeds are drilled or scratched into the surface soil, and both dead weeds and the previous season's crop residue remain as mulch. Such a practice reduces weeds, conserves soil moisture and increases humus content of the soil and, most importantly, prevents erosion and leaching; but safe and efficient herbicides must be economically available and farmers must be taught how to use them, and the proper machinery for both large- and small-scale farming must be developed for seeding, weed-cutting, harvesting.

Very promising work has also been done in encouraging and improving inte cropping methods whereby several cro of different heights are grown at the sam time—this is really the mixed farming traditional agriculture. Development crops with varied canopy heights and de sities and light compensation and satur tion points is an important, but great neglected, area of research necessary f further development of effective inte cropping. Such a practice not only resul in more economical use of space but pr tects soil from rain impact and cons quently decreases surface runoff and er sion, and, by shading, leads to lowe more favourable soil temperatures. Agr forestry and alley cropping are other in portant developments—as old as trad tional agriculture—whereby crops a grown under woodland or tree plantatio or in alleys between tree or shrub plan ings. When trees are nitrogen-fixing l gumes, the soil is improved as well as pr tected from leaching and erosion.

TABLE 2. Relative stability and resilience of natural and managed ecosystems in tropical savan

System	Stability	Resilience
Open grassland and sparse tree savannah	High	High
Woodland	Very high	Moderate
Forest and game reserves	High	Moderate to low
Managed range	Moderate to low	Moderate to low
Small-scale and shifting farming	Moderate to low	Moderate
Ranching	Low	Very low
Large-scale agriculture	Very low	Very low

TABLE 3. Protein production and energy input in pastoral systems of several regions of the wo

Region	Animal protein production (kg per year)		Fossil energy input (10^3 kcal per man-hou
	$ha^{(-1)}$	per man-hour	
USA	0.3-0.5	0.9-1.4	25 to 35
Australia	0.4	1.9	150
African Sahel			
Nomadism	0.4	0.01	0
Transhumance	0.6-3.2	0.01 to 0.07	0
Sedentary	0.3	0.04	0

Source: H. Breman and C. T. de Wit, 'Rangeland Productivity and Exploitation in the Sahel', *Science*, Vol. No. 4618, 1983, pp. 1341-3.

Factors of soil stability

The most important factors of soil stability are the prevention of particle removal (erosion), prevention of loss of water and soluble nutrients (runoff, leaching), and maintenance of an adequate sink of humus. Humus, which is largely concentrated in the upper levels of the soil, is therefore easily lost by erosion. Its loss cannot be compensated for even by continual fertilizer inputs, which can only make up for the nutrients lost, or for the loss of water-holding capacity, cation exchange capacity and soil texture. Figure 3 illustrates the importance of no-tillage in maintaining soil humus and pH. Loss of organic carbon from the soil during seven years of no-tillage cropping is seen from Figure 3 to be less than half the loss with conventionally tilled cropping.

Effects on soil carbon and pH of various fallow or rotation systems are summarized in Table 4. It is obvious that natural fallow —the natural regrowth which occurs when a field is left uncultivated—may often be most effective, though this will depend upon the soil, climate, plant materials available to enter the fallow, in other words, on its resilience. But it is clear that cultivable land is often too scarce in relation to expanding human populations to allow this luxury, and a second-best system must be chosen. Shorter-term rotation with legumes is almost as good, and if cropping must be continuous, mulching and no-tillage with fertilizing is a viable alternative. Alley-cropping systems or agroforestry with such leguminous shrubs and small trees as *Gliricidia* and *Leucaena* not only control erosion but, by the fixation of atmospheric nitrogen, add this element to the soil. Further nitrogen enrichment is achieved by pruning the woody legumes and using this material as mulch.

Such agricultural schemes are mainly suitable for the humid and semi-humid grasslands that are at present often underutilized. It is thus of great importance to find safe means of using these regions for increased food production. In more arid regions, cropping is not usually viable without irrigation.

In such marginal regions, crop failure is frequent and as yet unpredictable. The main problem is usually the absence of an adequate water supply for irrigation and the danger of salination with irrigation.

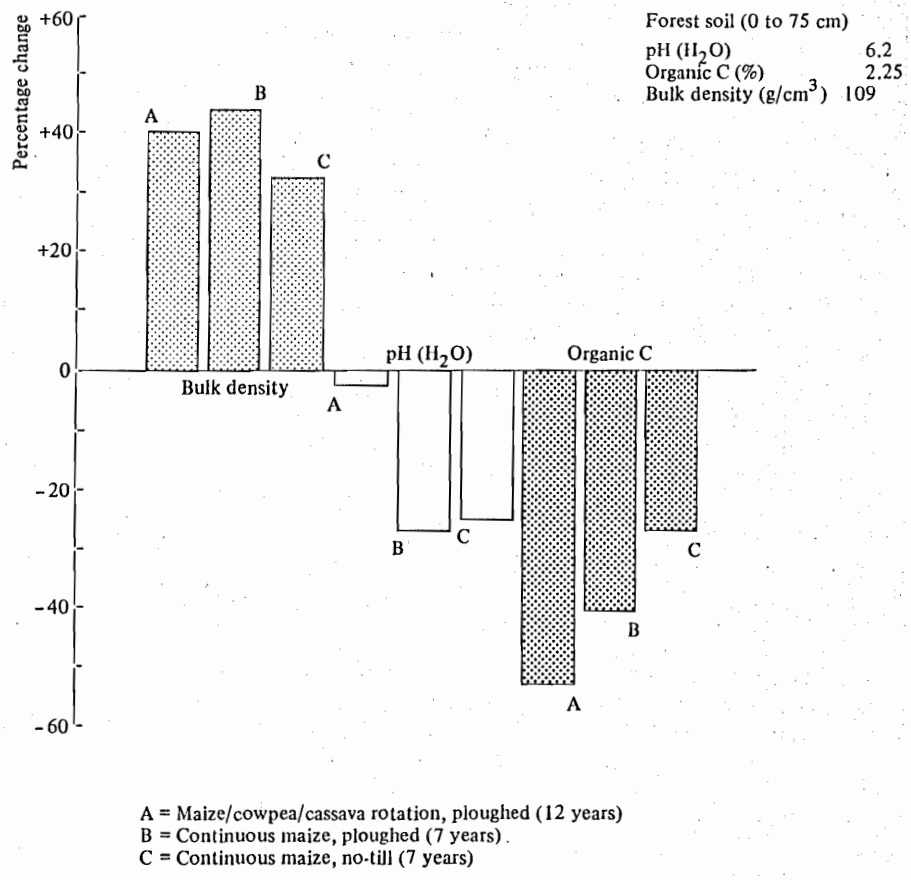

FIG. 3. Changes brought about by continuous cropping in the surface layer of Alfisols. (After International Institute of Tropical Agriculture, Ibadan, Nigeria, Annual Report, 1982.)

TABLE 4. Effects of continuous cropping compared with those of natural and planted fallow, 1972-82

Treatment	Organic C (%)		pH (H_2O)	
	0-7.5 cm	7.5-15 cm	0-7.5 cm	7.5-15 cm
Fallow (no fertilizer)				
Bush regrowth	2.81	1.05	6.3	6.0
Guinea grass (ratooned twice a year)	2.56	1.26	6.6	6.5
Leucaena (ratooned once a year)	2.68	1.12	6.1	5.9
Pigeon peas (ratooned or replanted once a year)	1.79	0.84	5.1	5.0
Cropping (fertilizer, no-tillage)				
Maize/cassava mixed, residue mulched	1.28	0.80	5.4	5.5
Maize, residue mulched	1.58	1.01	4.6	4.8
Maize, residue removed	0.80	0.65	4.3	4.2
Soybeans, residue mulched	0.81	0.45	4.7	4.4

Source: International Institute of Tropical Agriculture, Ibadan, Nigeria.

Improvement by controlled transhumance

Many uninformed people believe that all the arid and semi-arid grasslands of the world can be managed as livestock ranches, while all the humid and semi-humid savannahs can be ploughed for farming. In both regions there are vast expanses unsuitable for either range management or cultivation by large-scale mechanical methods. It is certainly true that the extent of cultivation in humid regions can and must be increased by perfecting cropping methods, but there will remain large areas unsuitable for cultivation because of topography, soil or climate. These should not be neglected but utilized in order to reduce dangerous pressure of over-utilization on drier regions.

The simplest solution would seem to be for migratory livestock to remain longer in the humid regions to consume the herbage which now, in most places, goes up in flame during the dry season. In many parts of Africa, tsetse-flies become a serious constraint in the humid areas as the rainy season advances, but these can usually be controlled by burning regimes which reduce the shrub and small-tree layer where the flies breed and/or by spraying. The real constraint in these moister regions is that the tall perennial grasses that are dominant there very soon cease to become nutritious and palatable because their bulk is stem and supportive tissue rather than leaf tissue. The protein concentration of these grasses decreases linearly with the reduction reaching at least 80 per cent by the time the grasses are mature. Livestock cannot consume enough of such herbage to compensate for its low food value. Also, as the stem tissue develops, the grass becomes coarse, hard and often abrasive from silica depositions within the cell walls. Several possible solutions to this problem are currently being tested. One possibility might be to keep a high enough stocking rate in the humid areas to prevent the formation of stem tissue by keeping the grasses grazed down to a low level. But with this method there is a danger of overgrazing with consequent death of the best grasses, because they are prevented from developing enough photosynthetic tissue to manufacture the food necessary to carry them through the dry season. A similar approach would be to harvest grass as hay while it was still at the foliar stage. In north-western Nigeria, MAB tests have shown that at least four harvests per growing season are possible. But this is actually a form of overgrazing with the same danger as overstocking. Tests in Zimbabwe have so far shown that such harvesting soon leads to the elimination of one of the most nutritious and palatable grasses, *Andropogon gayanus*. Certainly, however, one or two harvests should be possible without leading to the deterioration of the sward.

Another approach, already highly successful in many parts of Australia, is to replace at least part of these tall perennial grasses by legumes. Species of *Stylosanthes* (of the pea family) have proved especially useful. In Brazil, however, such exotic legumes cannot compete with the native grasses and so are soon lost. Similar results have been obtained in northern Nigeria. In both countries there is now extensive research on indigenous legumes which can compete with the tall grasses and not only provide richer grazing but also enrich the soil through nitrogen fixation. Even more promising for other arid regions is the possibility of seeding in leguminous shrubs and trees which will provide browsing during the dry season.

Improvement of open rangelands

In regions where transhumance is not or cannot be practised or controlled, sedentary management is of course necessa and this demands improvement of rang lands. The problem throughout the wo is generally to increase nutritious w season production and provide for the d season. An interesting possibility is t wider use of both herbaceous and woo legumes which continue growth duri the dry season. An African example *Indigofera pulchra* which is in luxuria growth in the middle of the season and relished by livestock. Its protein content high and it can fix nitrogen. But like *St losanthes* spp. it cannot compete with ta perennial grasses, and therefore is prac cal only in regions that do not have exte sive tall grass swards, such as the mo arid regions, or regions of very poor an shallow soil.

A controversial subject is the effect tree removal on grass production. Som workers consider that grass production in creases almost linearly with increasing re moval of trees, while others insist that thi is true only up to a certain point, afte which continued tree removal leads to de creased grass production and decrease nutritional value of the sward.

Removal of trees may, even when re placed by grass, lead to soil erosion. Fo instance, tests in Costa Rica showed tha when forest was replaced by the Africa grass, *Hyparrhenia rufa*, there was a los of 11 cm of topsoil during a twenty-two year period. Another important contribution of trees is leaf litter which mainly falls after grassland burning and so may cove the soil during the late dry season and early rains. Tests in Zimbabwe showed that rain penetrated soil covered by such litter nine times more readily than bare earth. Clearly, the relationship between trees and grass production and nutritional value may vary widely with locality. Also, in any evaluation of the effect of trees, the time element is crucial.

It is necessary that the optimal ratio of grass and trees be determined for each region, always bearing in mind that the tree–grass system is more stable than either the grass or forest system alone. Selection of legume tree species which provide both browse and soil nitrogen through atmospheric fixation is an obvious approach to increased sustained production in both humid and semi-arid regions.

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Photographs courtesy of W. Sanford.

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Large, spectacular herds of wild ungulates still roam free in many tropical savannah areas. These zebra were photographed in Serengeti National Park, Tanzania.

Safe farming and increased food production

Most of the problems of erosion and leaching throughout the world have been brought about by clearing the earth of its protective vegetation. In the grasslands this comes about in three ways: most immediately disastrous is mechanical large-scale tillage in regions where this fundamentally temperate-zone technique has been inappropriately applied, secondly by grazing and thirdly by wood-cutting.

Perhaps the biggest problem is to utilize the humid and semi-humid grasslands more extensively for food production without ruining the soil. Most fundamental to this problem is adequate land-use planning on a scale such that each management unit is appropriately situated. The parameters of special importance for land-use planning vary with the type of use envisaged but generally include: estimation of soil fertility; fragility in regard to leaching and erosion and water-holding capacity through estimation of the concentrations of humus, clay, sand and silt; topography; moisture regime—annual rainfall, number of rain days or length of the rainy season, precipitation/evapotranspiration ratio, reliability of rainfall; estimation of ecosystem stability; structure and physiognomy of the vegetation.

Even with a more or less physically stable soil system, large-scale agriculture usually requires special management: (a) minimum or no tillage; (b) mulching with crop residues; and (c) rotation and multi-storey plantings or alley cropping. Besides these innovative, though traditional, techniques, farming in the tropics requires the development of special machinery both for large-scale agriculture and small subsistance farming. All over the world people continue to desert the land in increasing numbers in favour of the cities where they add to congestion, unemployment and often crime, unless subsistance farming can be made more profitable than bare subsistance and unless special machines can reduce the back-breaking labour of using the hoe and the machete.

It is clear that experts of all kinds need to get together to work out a way of making the grasslands of the tropics and subtropics productive without destroying them. Much of the required knowledge is already available but requires implementation; for example, relevant land-use surveys, legume seeding of rangelands, the farming systems and techniques which were mentioned above. On the other hand, in many areas, considerable research is necessary. For example, the relationship between tree species and density and grass production must be determined for each soil/climate region; new herbaceous legumes able to compete with indigenous vegetation must be found or bred; schemes for the utilization of humid grasslands where the grasses soon become unpalatable and non-nutritious must be worked out; fodder for the dry season and for arid regions must be developed; machines especially suited to the problems of tropical grassland farming must be perfected. Thus it is necessary that many types of specialists be involved: ecologists, range managers, soil scientists, botanists, plant breeders, agronomists, engineers—to mention just a few.

The diversity and complexity of grassland ecosystems necessitates great flexibility in their management. It has taken grasslands at least several million years to evolve; man can afford but a few years to evolve suitable systems for their management or else his descendants may starve in deserts and near-deserts throughout the tropical and subtropical world. The first step towards prevention of this is awareness on the part of citizens, as well as politicians and decision-makers.

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