2.2 Vegetation

This section will deal briefly with some of the unique and characteristic features of tropical forms of vegetation. The aim is to provide non-botanists and non-ecologists with basic information which will help them to design sustainable land use systems that are appropriate for local conditions.

2.2.1 Permanently humid tropical lowland rainforest

This formation[8] is typical on well-drained soils in equatorial diurnal climates. Despite variations in species composition, the physiognomy is similar on all continents. As a rule, this formation features a more or less clearly pronounced three or four story structure.

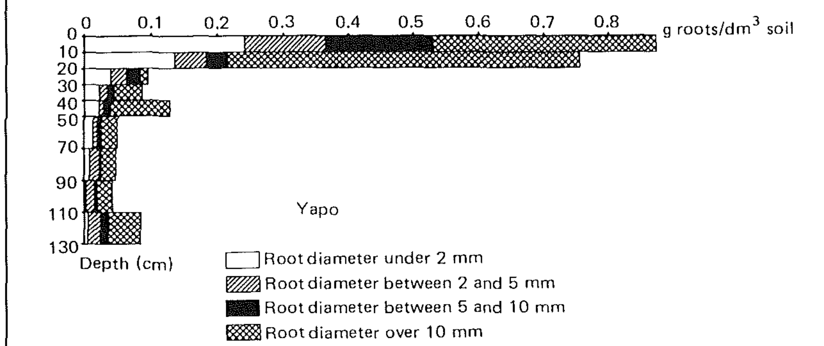
The forest canopy (upper story) is open and extends in height from 35 to 40 m (some individuals reach a maximum of 50 - 60 m). Below this is a relatively closed layer at about 30 m. A third layer is found at 10 to 12 m. As in the second story, many trees in this layer are heavily intertwined with lianas and strangler vines. According to studies in the Amazon region by KLINGE et al. (1975), the upper two stories represent 80% of the above-ground biomass. A bottom story consisting of young growth and shrubs completes the profile. Soil vegetation is absent or very sparse. Most of the trees branch just under the crown. The trunks have thin bark and often develop buttress roots, especially in areas with periodic flooding.

Root systems are strongly concentrated in the upper soil horizon, with only a few taproots found extending below 0.5 - 2 m. The litter layer is only 1 to 5 cm deep. Depending on soil type, about 20 to 50% of the entire root system lies in the upper 10 cm of soil. About 80 to 90% of the roots lie within 30 cm of the surface, and only

[8] "Formation" is used here in the sense used by ELLENBERG (1960) as a plant community with a homogeneous life form spectrum and the same physiognomy (= outward appearance).

10% to 20% below 30 cm (WALTER 1964, NYE and GREENLAND, 1960). There is strong root competition, especially for nutrients. In a study by HUTTEL (1975) on a sandy clay, the proportion of fine roots decreased at an almost exponential rate with increasing root depth (Figure 2.14).

Figure 2.16. Root distribution according to size and soil depth in a rainforest in Côte d'Ivoire



Source: HUTTEL (1975)

With regard to species composition, the permanently humid rainforest is among the most diverse vegetation formations in the world. According to WALTER (1974), 40 to 100 species can be found on a single hectare.

On 23 ha in West Malaysia, POORE (1968) found 374 species (52 families, 139 genera), 37% of which were represented by only one plant (not counting very low-growing ground flora). Including the understory in their survey, KLINGE et al. (1975) reported 500 species on 0.2 ha (more than 30 families). Representatives of the same species are widely distant from one another in space, as well as in time, as their position in the succession is usually taken over by a different species (see also

JANZEN 1973). By way of comparison, in all of New Jersey, USA, HORN (1978) counted a total of only 13 tree species. In other words, in temperate locations individuals of the same species occur in relatively dense stands and the number of different species per unit area is much lower.

According to VARESCHI (1980), vegetation forms whose diversity is unchecked by physical constraints typically consist of a large number of species per unit area represented by a small number of individuals of each species. In contrast, the least favored vegetation forms are characterized by a few species present in large numbers per unit area. This is because, in an unfavorable environment (e.g. with prolonged drought, frost, salinity or waterlogging), only a narrow range of specialists can compete successfully.

Some species-poor vegetation forms occur naturally in the moist tropics, the most notable example being mangrove forests. But most occur outside them, as for example in semi-desert or near-polar regions. There is no doubt that nature's most species-rich vegetation forms occur in the humid tropics. VARESCHI (1980), using his diversity index, reports values from 1100 to over 1500 for tropical rainforest, while forests in temperate climates show diversity indices of 600 to 700.[9]

Woody plants clearly predominate over herbaceous plants in the tropical rainforest. According to WALTER (1964), the ratio of woody to herbaceous species in humid lowland rainforest is about 7:3. SCHNELL (1971) obtained almost identical results from a tract in West Africa, where he counted 975 woody species and 442 herbaceous species. A comparable area in France, on the other hand, produced a 1:10 ratio in favor of herbaceous plants (73:717).

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[9] The diversity index or diversity coefficient ($C_d = a \times f$) is the product of the number of species (a) and the number of leaf-forms or leaf categories (f). The leaf-form categories (e.g. lanceolate or acerose) are also used by VARESCHI as an indicator of diversity, because these are often similar under similar conditions, even though the species may be different. The leaf categories are thus closely related to the number of species, though not equivalent to this, as there are also plants with two or more leaf forms (heterophyllous species) or different species with the same leaf form (e.g. coniferous trees). Hence the number of leaf forms alone does not represent a measure of the vegetation diversity. Example: a species-poor moorland in northern Germany with six species and four leaf forms has a diversity factor of (C_d) 6 x 4 = 24.

Figure 2.17 illustrates the structure of a tropical rainforest. Few statistics are available concerning the animal population. WALTER (1979) refers to a survey of a rainforest in Thailand, where the overall zoomass was reported as 23 kg/ha. Studying the Amazon rainforest, KLINGE et al. (1975) found a total of 45 kg/ha above-ground zoomass (30 kg phytophagous, 15 kg zoophagous) and 165 kg/ha (79%) soil zoomass. Approximately half of the soil fauna was xylophagous (primarily termites and larvae of Coleoptera). These studies, though somewhat impeded by the difficulty of accessing the forest canopy, indicate that the faunal share of the biomass is relatively low.

Figure 2.17. View of a tropical rainforest in Borneo

Source: Drawing based on VARESCHI (1980)

The productivity and character of the tropical evergreen rainforest is unique. This formation exhibits the highest gross primary production. However, respiration losses are also very large, owing to the high night temperatures. As a result, up to 75% of gross productivity is respired (WALTER 1979).

An optimal stand achieves a gross primary production of 120 to 150 t/ha of dry matter per year. The following production data are taken chiefly from WALTER (1979) and NYE and GREENLAND (1960):

* The leaf area index (LAI)[10] is high (around 12).
* The net primary production is about 30 - 35 t/ha of dry matter, 30% of which is litter.
* The stock of an essentially "mature" rainforest represents a biomass volume of 350 - 450 t/ha of dry matter (KLINGE et al. 1975, report occasional values of 500 t DM/ha).

Such a stand, usually composed of more than 90% ligneous growth, represents a sizeable nutrient stockpile. The nutrients themselves circulate dynamically within an essentially closed system (see Table 2.8).

Even in a secondary forest, the nutrients cycled exceed the annual increment many times over after only a few years (after 40 years, the ratio of cycled nutrients to the annual increment in Kade, Ghana, was 190:36 kg/ha for N, 13:2.8 kg/ha for P and 260:58 kg/ha for K). The rain washes considerable amounts of these nutrients directly out of the leaves. This is especially true of potassium; up to 196 kg/ha or 60% of turnover is washed out, compared with 25% of phosphorus. For nitrogen, BERNHARD-REVERSAT (1975) recorded N values ranging between 26 and 88 kg/ha/year.

[10] The leaf area index is the ratio of the total surface area of a plant's leaves to the ground area available to the plant.

Table 2.8.: Nutrients and their annual turnover in a tropical rainforest.

Nutrients	N	P	K	Ca	Mg
Nutrients stored in tropical rainforest vegetation (kg/ha)	1800	125	800	2500	240
Annual turnover (kg/ha)	190	13	260	300	60
As a % of total capital stored in the vegetation	11	11	32	12	18
Annual increment of nutrients (kg/ha):					
a) in a relatively mature forest (+ 40 years)	36	2.8	58	60	12
b) in the first 5 years	112	6	90	83	-

Approximated values in a secondary, 40-year-old tropical rainforest in Ghana.

Source: Adapted from NYE and GREENLAND (1960).

The turnover of forest litter, leaves and humus is rapid. Leaf litter can decompose at a rate of 3.7% per day, part of this being temporarily converted to humus (approximately one tenth of gross primary production, according to NYE and GREENLAND 1960). About 80% of the leaves (2.6% of the standing vegetation) are cycled yearly. This represents some 4 t of leaf litter (dry weight) per ha per year or 88 kg N, 4.8 kg P and 48 kg K (KLINGE et al. 1975; NYE and GREENLAND 1960).

Light, heat and abundant rainfall, operating in what is virtually a closed nutrient cycle, govern evergreen rainforest productivity. The vegetation itself, and its structure in association with soil organisms, is the basis for the maintenance of productivity. NYE and GREENLAND (1960) emphasize the following points with regard to maintaining soil fertility[11]:

* The vegetation catches much of the rain as it falls; through transpiration it reduces percolation and hence the leaching of nutrients from the soil.
* The dense network of surface roots, the development of which is aided by fungi such as ectotrophic mycorrhizae associated with Dipterocarpaceae and Cesalpinaceae takes up nutrients (P, K, Ca, Mg) immediately after their release in the soil (JANOS 1980).
* Nitrogen depletion rarely occurs because of the low activity by nitrifying bacteria (pH around 5). Almost all the nitrogen is present in ammonium, and as such can be sorbed by humus.
* KLINGE et al. (1975) mention the high production of litter as an important condition for a working ecosystem.

These functions are interrupted by repeated shifting cultivation and suspended completely under prolonged annual monocropping, resulting in the destruction of the closed cycle system.

In the forest a biological, tightly closed nutrient cycle prevents nutrients that are washed out of the vegetation or mineralized from the litter from being lost. In addition, the cycle fixes nutrients from the rainfall (BLUM, 1980).

Lichen, mosses and other epiphytes filter some of the nutrients out of the precipitation as it falls. The nutrients that reach or enter the soil are quickly taken up by the dense root network near the surface, sometimes even before they come into contact with the mineral soil. Mycorrhizae play a very important role in this process. These soil fungi exist in symbiotic association with plants. The fungus spins a meshwork over and through the roots, growing into the most remote root cell tissue. From there it sends

[11] The term "site fertility" is a better description in this context, as the rainforest soil itself possesses only a meagre yield potential (see Section 2.3).

out numerous fine filaments (hyphae) into the humus and soil. The original root surface is thus increased several times over. Through its hyphae, the fungus takes up nutrients and delivers these to the plant, which in return provides the fungus with the energy product of photosynthesis necessary for its survival (see also Chapter 8).

Studies of water samples from the Amazon Basin showed that this filter system evolved by the rainforest is highly effective. Water from the soil of an intact rainforest is poorer in nutrients than rainwater, and can be described as "slightly contaminated, distilled water" (KLINGE et al. 1975). This "biological filter" restricts the loss of nutrients through leaching from the weathered rainforest soils, which have such poor sorption that they are barely able to fix nutrients. If the vegetation is removed, the filter is destroyed, and the solar energy-powered circulation of nutrients through the soil-vegetation system is disrupted. Nutrients are then washed away by surface runoff or by water which infiltrates the soil, causing leaching.

The succession on cleared ground is described by RICHARDS (1952, cited in NYE and GREENLAND 1960) for a site in Africa. Following slash-and-burn clearing a) weeds and grasses spring up first; grassland is succeeded by b) shrubs and thicket, followed finally by c) trees, first among which are the typical representatives of secondary forest[12]. Only after about 20 years (if at all) do these again give way to taller, long-lived, less light-demanding trees. According to JANOS (1980), this latter formation almost always develops in close symbiotic association with mycorrhizae, whereas pioneers in the succession are only seldom involved in symbiosis.

As a rule, the removal of vegetation is speedily followed by a decline in site fertility, and productivity drops within 2 to 3 years to below 50% of its initial level. This decline may be regarded as the more or less direct consequence of clearing the original vegetation. Traditional cropping systems in the forest zone seek to offset this effect by allowing some land to revert rapidly to something approaching its original state. (crop-fallow ratio of about 1:10 years).

[12] In Africa, *Musanga cecropioides* (the umbrella tree), which is very fast-growing and light-demanding; in South America, the balsa tree (*Ochroma lagopus*) and *Cecropia* sp.; in Malaysia, *Musanga* and *Cedrela* (height growth 4 - 7 m per year!). Continuous slash-and-burn, followed by grazing or cultivation, leads quickly to derived savannas or even to semi-deserts.

NYE and GREENLAND (1960) emphasize the following reasons for loss of fertility[13]:

* Deterioration of soil physical properties (loss of litter layer, etc)
* Deterioration of the nutrient status (humus, P, etc)
* Increase in disease and pests (decreased diversity)
* Increased weed invasion
* Erosion of topsoil
* Alterations in the density and type of soil organisms (termites, mycorrhizae, etc)

The sustainable use of land for agriculture in the tropical, permanently humid rainforest belt is difficult. Tillage, as well as weed control, is hampered by prolonged soil moisture. Because of the limited nutrient reserves in the soil, cultivating annual crops is usually possible only in the short term, and semi-permanent crops only in the medium term. Systems with permanent crops (bushes and trees) have proved to be the only successful form of long-term land use (ANDREAE 1972). Only land use systems that mimic forest conditions can meet with long-term success in such regions (see also Chapter 3).

2.2.2 The semi-evergreen rainforest

From an ecological viewpoint the semi-evergreen tropical rainforest occupies a position between the evergreen rainforest and the deciduous forests. Its vegetation is a mixture of both types of vegetation.

A typical feature of the semi-evergreen rainforest is its two-story structure, which reflects its transitional nature (WALTER 1964). The upper story (up to about 30 m in height) is the deciduous layer, while the lower story (up to about 20 m) and ground layer are usually evergreen. The upper canopy is fairly dense (crown density increases with decreasing rainfall, from more than 2000 mm/yr to 1300 mm/yr).

[13] For further information on soil fertility, see Section 2.3.

Nevertheless, the incoming sunlight is greater than in the evergreen rainforest, so that tall herbs and weeds as well as shrubs increase in number here. As in the evergreen forest, the root growth is heavily concentrated in the upper soil strata. However, the proportion of roots in the topsoil is some 10 to 15% less, according to NYE and GREENLAND (1960). Buttress roots are uncommon.

The diversity of species is about 20% (to 40%) lower than in the evergreen rainforest. The diversity index used by VARESCHI (1980) attains values of only 960 (compared to 1100-1500 in the evergreen rainforest). Data on the productivity of semi-evergreen rainforest are rare, owing to the lack of research on this formation (VARESCHI 1980). The data shown in Table 2.9 come from a moist (1250 mm rainfall), semi-deciduous forest in the Congo.

Table 2.9. Nutrients in a semi-deciduous rainforest in the Congo

	N	P	K	Ca	Mg
Nutrients stored in the vegetation	1103	110	851	1890	290

Net primary production: 20 - 30 t/yr (estimated); total biomass: 326 t/ha. Succession following land clearance (see moist savanna)

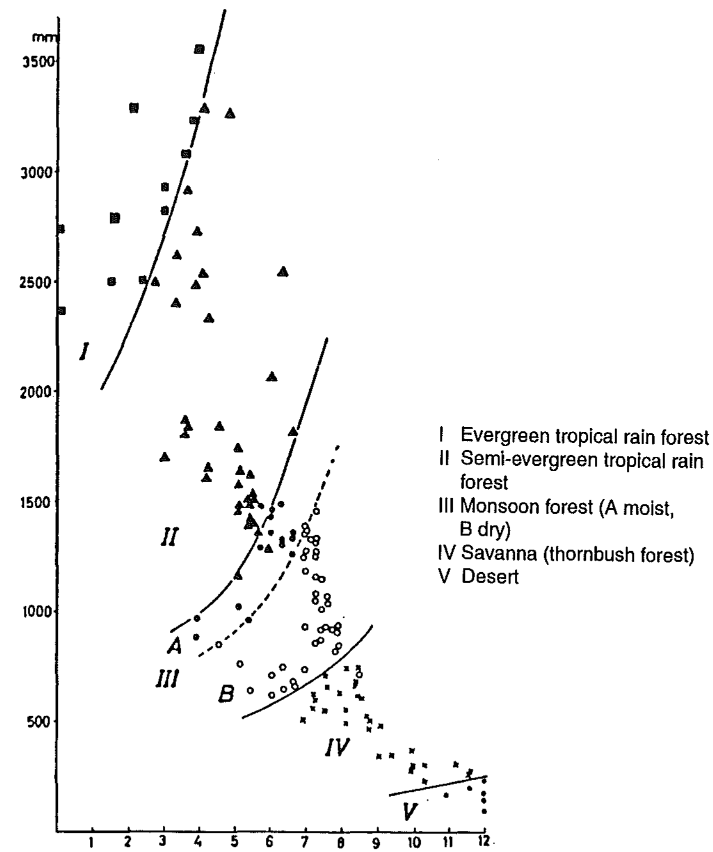
Source: Adapted from NYE and GREENLAND (1960)

A seasonal rhythm of rainfall is discernible in this formation, which has lower absolute rainfall than evergreen forest. This causes a seasonal response in many of the forest species, or an increase in species with a cyclical growth rhythm (WALTER 1964; VARESCHI 1980). This turnover rate of organic matter and nutrients is subject to seasonal variation, exhibiting higher intensity in the rainy season and a decrease in the dry season. Relatively high pH values (5-6) promote turnover, leading to an overall lower C content. This, however, is partially compensated by the better quality of the clay minerals and a closer C/N ratio (around 12). Synchronous leaf-fall and synchronous flowering, at first displayed by only a small proportion of the trees (up to around 10% in seasonal rainforest, according to VARESCHI 1980), become increasingly common. The semi-evergreen rainforest described by WALTER (1964) also includes VARESCHI's moist tradewind forests with a deciduous proportion of 20 to 30%.

Findings by WALTER (1964), shown in Figure 2.18, indicate that the length of the dry season is the main factor governing the formation of the moist forest types, whereas absolute rainfall is the more important determinant of dry forest types. The ecological regions fit well with the findings of VARESCHI (1980).

Clearing land for agriculture by burning is easier here than in the evergreen forest because of the seasonal dry spell, and is often practised. For this reason the semi-evergreen rainforest is now rarely encountered in its natural state, especially in Africa, where it has become a man-made (derived) savanna. Under favorable conditions this is a Panicaceae savanna *(Panicum maximum, Pennisetum purpureum)*, which can be very productive. Under unfavorable conditions, for example when overexploited, andropogon grasses will gradually become established. This marks the final stage of a degraded semi-evergreen or deciduous forest (WALTER 1979; NYE and GREENLAND 1960).

Figure 2.18. Relationship between forest vegetation and rainfall and the length of the dry season in months in India



Source: Adapted from WALTER (1964)

In agricultural use semi-perennial species are increasingly favored. As the forest disappears the cultivation of annual crop plants becomes more frequent, and dry periods for harvesting and tilling facilitate the cultivation of many crop plants.

Rainfed crops are often intensively cultivated in derived savanna, with two crops a year. The most frequently grown crops are maize, cassava, cotton, banana, groundnut, beans and yams).

Farming operations also include animal husbandry and, where animal dung is returned to the soil, the decline in soil fertility is no longer as rapid as in the evergreen rainforest. According to NYE and GREENLAND (1960), it may take 8 to 20 years before yield decreases become acute (depending on initial potential).

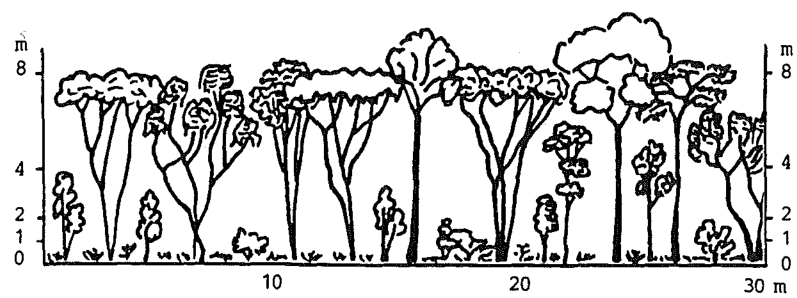
2.2.3 Moist savanna

Pronounced subhumid conditions characterize the vegetation of this zone, which is not as uniform in character as the tropical rainforest. VARESCHI (1980) describes two locations with about 1100 mm annual rainfall, one with a dry tradewind forest (dry period lasting 4 months) and the other with a dry barren forest (with a more clearly defined dry season). The latter is equivalent to WALTER's "dry forest" or the "very dry tropical forest" described by HOLDRIDGE.

This formation colonizes the niche between seasonal rainforest and dry savanna. It has a single-story structure and an evenly closed profile; thus it is very similar to temperate forests. It usually appears as a mosaic and seldom covers wide areas. The "dry tradewind forest" grows to a height of about 8 m, while "dry barren forests" achieve a maximum of 20 m. Figure 2.19 shows a dry tradewind forest in South America.

The understory in its natural state is sparsely developed. There is a true herb layer, however, which benefits from the seasonal leaf-fall from the trees. According to VARESCHI (1980), the proportion of evergreen trees conforms to the definition of moist savanna, accounting for 10% or less of the formation. Grasses first become common on the margins of the savanna. Roots reach deep into the subsoils. Woody plants usually have small leaves (some dentated) and tough bark on the stems. Many leguminous plants are present (20 to 30% and sometimes more) (WALTER 1964; VARESCHI 1980).

Figure 2.19. A dry tradewind forest near Quiriquire in the *llanos* of Venezuela*



* 74 m a.s.l., 1154 mm annual rainfall

Source: Adapted from VARESCHI (1980)

Diversity decreases markedly as water scarcity increases. The dry tradewind forest mentioned above had 62 species. Its diversity index of 682 roughly equals that of a temperate forest. Individual species become dominant for the first time (VARESCHI 1980). Deviating from the rule, the diversity in dry barren forest increases again with increasing dryness and with proximity to the grass savanna. Here the number of species found by VARESCHI was 128, and the diversity index around 1500.

The productivity of this natural formation has still received little study. Gross primary production has been estimated at 10-24 t of DM/ha/year (WALTER, 1979; BASILEVIC, cited in YOUNG 1976). Total biomass was found by NYE and GREENLAND (1960) to be 60 to 100 t DM/ha. Table 2.10 gives estimates of nutrient storage and mobilization in natural vegetation. Derived savanna vegetation does not achieve even 30% of the biomass production that a forest would do on the same site (LAMOTTE, cited in VARESCHI 1980).

As previously mentioned, the floristic character of the moist savanna is less uniform than in permanently moist climates. Thus, bush and grass savannas can evolve naturally though ecologically they belong to the dry (climatic) savannas (WALTER 1979). Special soil conditions are usually responsible for this, as also may be microclimatic differences. These conditions can hinder tree growth, even if rainfall is more than 500 mm a year. WALTER (1964) cites the example of highly impermeable soils with compacted horizons, where flooding alternates with dryness. In such areas, tree growth is limited to such sites as former termite nests or slight rises in the terrain.

Table 2.10. Nutrient storage and mobilization in the natural vegetation in moist savanna forests

	Nutrient quantities (kg/ha)				
	N	P	K	Ca	Mg
Stored nutrients in subhumid forests*	275-300	28-50	200-270	310-430	ca 100
Annual mobilization of nutrients (growth of a bush fallow)**	45	3.3	34	44	10

* Two forests with 900 to 1250 mm annual rainfall
** first to fourth year, with rainfall of 900 mm/year

Source: Estimates based on data from NYE and GREENLAND (1960)

Although exceptional, vegetation forms that are influenced by the soil and atypical for a particular climate can cover very large areas. The *llanos* of northern South America are a striking example.

Favored by their climate, which has a periodic dry season and enough rainfall for rainfed agriculture, the moist savanna regions have supported a high population density since ancient times. Settled or semi-nomadic people have long cleared the land

by fire, planting crops and/or raising livestock. In so doing they have vastly altered the natural vegetation in many areas. Instead of the once productive forests, only relatively unproductive scrub and grasslands remain. LAUER (1956) describes such a development and the stages leading to the formation of derived savannas. His description is summarized in the following example, from El Salvador:

* Utilizable hardwoods are removed, leading to the depletion of the vegetation.

* Clearing and burning destroys the vegetation down to a few stumps and roots. Once the shifting cultivator abandons a patch, after 1 to 3 years, thickets take over. The regeneration of the forest is possible if the land is left fallow for many years, but this seldom occurs nowadays, owing to increased pressure on the land. According to NYE and GREENLAND (1960), land is abandoned primarily because of encroaching grasses and difficulty in weed control, a common problem where soil fertility is declining. Fallow periods need to be longer here than in the rainforest because the biomass production is less.

* Regeneration is hindered if the area is grazed by livestock. Foraging and trampling lead to the domination of thorny plants and grasses; a thornbush-like savanna develops (*Gliricidia sepium, Mimosa tenuiflora, Paspalum* sp., *Melinis* sp., cimbopogon).

* Continued overexploitation through grazing and shifting cultivation totally destroys soil and site fertility and causes erosion and degradation (acacia, mimosa, sometimes *Curatella* sp., *Psidium* sp. and other relatively valueless grasses invade).

NYE and GREENLAND (1960) describe similar processes in Africa and underline the dangers of grass invasion at such sites. *Imperata cylindrica*, *Digitaria scalarum* and other undesirable grasses can easily impede rainfed cropping.

Conditions in this zone are favorable for agricultural use, permitting the cultivation of a wide range of annual and perennial crops. The natural fertility of the soils is higher than in permanently humid regions, and rainfall quantity and distribution permit one or even two harvests. Agricultural systems must be oriented towards maintaining productivity, which is endangered by humus depletion, soil erosion and compaction. If organic substances are conserved, if humus is added regularly and burning and excessive tillage are avoided, then the chances are good for satisfactory medium- to long-term yield performance. NYE and GREENLAND (1960) furnish numerous examples.

Moist savanna conditions favor the integration of animal husbandry into the farming system. Livestock can make an important contribution to building humus and to the self-sustaining potential of a farm. Incorporating trees and shrubs into the farming system also has positive ecological implications and can add considerably to the productivity and stability of the agro-ecosystem. Mixed cropping and irrigation are additional, and climatically compatible, options for intensifying agriculture in the moist savanna zone.

2.2.4 Dry savanna

In discussing grassland nomenclature, it should first be mentioned that the term "steppe" is now used only for grasslands outside the tropics (e.g. the grasslands of Ukraine or North America). Grasslands in the tropical region are known as savannas, regardless of whether they consist of pure grass stands or grasslands with scattered trees (VARESCHI 1980). According to WALTER (1979), dry (climatic) savannas most readily develop in summer-rainfall regions with 200 to 500 mm annual rainfall.

In areas with relatively high rainfall (more than 400-500 mm), trees are still numerous, often dotting the grassland at regular, widely spaced intervals (orchard savannas).[14] The trees are generally low-growing (3-5 m high), with some individuals reaching 10 m or, at most, 15 m. Trees use the rainwater that is not taken up by the shallow roots of the grass layer and percolates through to the subsoil. The water here can be accessed only by trees and shrubs, with their widespread, deep roots.

[14] Forests over a ground cover of grass are described by WALTER (1979) as savanna woodlands.

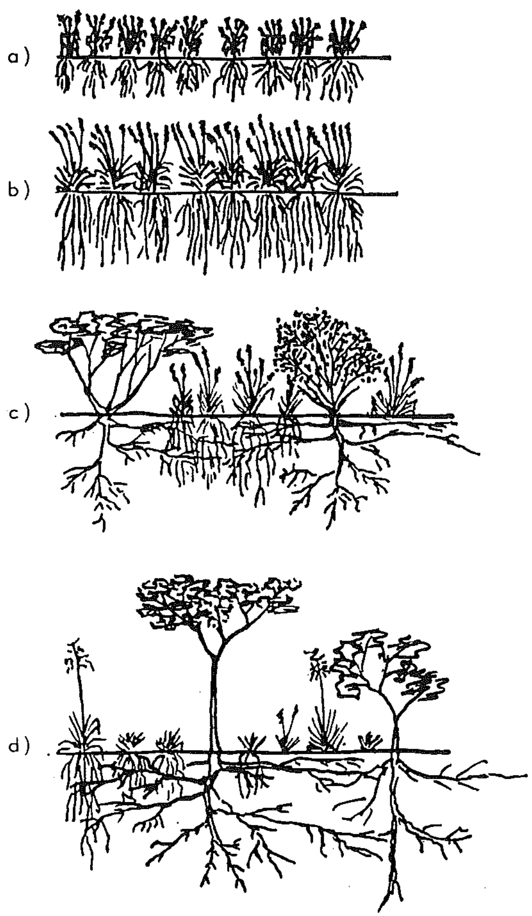
The trees' network of roots usually extends far beyond the radius of their relatively underdeveloped crowns. *Curatella*, for example, with roots over 6 m deep, taps a soil volume of some 3000 m^3, whereas a horst-grass exploits only a fraction of a cubic meter of topsoil (more than 70% of the roots lie less than 15-20 cm deep) (VARESCHI 1980; NYE and GREENLAND 1960). As dryness increases, so also does the competition for water. With declining rainfall, less and less water is able to penetrate deep into the soil, reducing the amount available to the trees. Trees thus begin to decline in size and number, giving way first to bushes and shrubs, then to more or less pure grasslands.

On fine sandy soils in southwest Africa, WALTER (1979) found that this transition to pure grasslands was reached at about 200 to 300 mm of yearly rainfall. Under this quantity, the small horst-grasses utilized all the rainwater entering the soil surface. Grasses transpire heavily and produce considerable biomass in a short period. When water becomes scarce, they continue to transpire virtually without check. As a consequence, the parts of the plant above ground dry out and die back relatively quickly once the water supply has been exhausted. Only a few roots and the protected growth points within the plant survive to put out new shoots after the next rainfall. By closing their stomata, trees and woody plants can generally protect themselves well from water stress, but they cannot tolerate a lack of water over longer periods. They require a certain, albeit small, amount of water to survive the dry season. According to WALTER (1964), shrubs need some 5-7% of their fresh weight in water each day.

Hence the transition from high-grass savannas to horst-grass savannas and finally to short-grass savannas as rainfall decreases. This transition is depicted in Figure 2.20.

The comparatively fertile high-grass savannas (1.5-5 m high) often consist of *Panicum* and *Pennisetum* grasses, while the less fertile, degraded or drier grasslands tend to have andropogons (*Hyparrhenia* spp., *Andropogon* spp.). These latter are typical of the horst-grass savannas, but they can also extend into regions with more than 6 humid months, colonizing man-made savannas that have been regularly cleared by slashing and burning. The short-grass savannas grow to a height of only 30 to 40 cm.

Figure 2.20. Schematic view of the transition, with increasing rainfall, from grassland (a and b) to savanna (c) and to dry forest



Source: Adapted from WALTER (1979)

However, the sequence does not always follow the pattern described above, which is typical for fine sandy clay soils with relatively high water-holding capacity. In these soils the rainfall is adsorbed into the upper soil layer, where it encourages the formation of grass savannas. These are favored by a temporarily available water supply close to the surface. On such soils, grasses are the antagonists of trees, which can only grow when enough rainfall reaches the deeper soil layers.

A different situation arises on stony soils. Here woody plants have an advantage over grasses. The rain penetrates through to the subsoil rapidly, while little soil - and hence little water - remains in the topsoil to support a strong grass layer. With their extensive root systems, trees make good use of moisture reserves that are unevenly distributed through the profile. Thus they maintain their dominance on stony ground. With diminishing rainfall, woody growth gradually becomes shorter in height and more widely spaced (WALTER 1979).

Exceptions in the plant formations of the dry savanna occur when special soil conditions are present or when the two cases described here (sandy clay or stony soils) overlap as they do, for example, in areas with shallow soils over rock.

Species diversity varies considerably in the dry savannas. VARESCHI (1980), studying six locations ranging from a halophyte savanna on extremely poor soil to relatively typical savanna areas, reported species counts of 6, 22 and 144. Following water scarcity, other growth factors decline due to salinity, lack of nutrients, etc. This causes a reduction in the number of species. This is also the case in areas subject to frequent burning (LAMOTTE 1975).

The diversity index developed by VARESCHI (1980) ranges between about 300 and 800 (averaging about 550). This level of diversity seems to be typical for dry savannas worldwide. The variety characterizing forest communities is not found in the savannas, where individuals of a few species occur in greater density. The principle of a high number of species each represented by a small number of individuals, noted in the permanently humid tropical rainforest, is reversed here.

The productivity of climatic savannas is estimated at about 7 t of dry matter per ha/yr by RODIN and BASILEVIC (cited in YOUNG 1976). The values vary, depending on rainfall (200 to 500 mm), nutrient status[15], and vegetation. For semi-arid areas with a maximum of 500 mm annual rainfall, WHYTE (1976) puts the yearly above-ground biomass production at 1 to 6 t DM/ha. Total net primary production, including underground vegetation organs such as rhizomes and tubers, is 2.5 to 10 t/ha. For unburned bush savanna, LAMOTTE (1975) reports maximum values of 13 t DM/ha per year. These are decidedly higher than the productivity values for derived savannas which, in Côte d'Ivoire for example, only achieve a biomass production of 5.5 to 7 t DM/ha despite high rainfall of 1300 mm/yr.

The leaf area index (LAI) of a soil-determined (edaphic) grass savanna in Venezuela was 4 to 5 (SAN JOSE and MEDINA 1975). Interestingly, LAMOTTE (1975) observed that legumes (*Tephrosia elegans*) become profuse and well developed only when the main growth phase of the grasses is over. This may be explained by the greater ability of the grasses to assimilate nutrients (MENGEL 1968).

In the savanna ecosystem, the *zoomass*, consisting of antelope, sheep, camels, rodents, etc, is greater than in the forest ecosystem. However, exact figures on the natural population of herbivorous fauna are difficult to obtain, as the population strongly depends on human influence. With regard to soil organisms, LAMOTTE (1975) reported about 6.8 kg of termites (dry weight) per ha (4.5-5.5 million/ha). These play an important role in decomposition and soil structure. In the same location, earthworms represented a biomass of 40 kg/ha, converting some 500 t of soil per hectare per year. Assuming a soil depth of 1.3 m, this produces a soil layer of 4 cm.

The soil fauna suffers heavily as a result of burning. Not only are termites and earthworms affected but also, according to LAMOTTE, micro-arthropods, of which

[15] WALTER (1964) gives a transpiration coefficient of about 1000 for grass savannas; i.e. 1000 litres of water would be necessary to produce 1 kg of dry weight. However, studies by SAN JOSE and MEDINA (1975) clearly show that these values are substantially higher (less favorable) on impoverished, degraded sites. On a regularly burned over, nutrient-poor site in Venezuela, for example, the transpiration coefficient (TC) was 3000. The better the supply of nutrients to plants, the more effectively they utilize water.

only 30 kg/ha are present on land subject to annual burning, whereas unburned land produces 180 kg DM/ha. In addition, actinomycetales (important decomposing bacteria) are reduced by two-thirds as a result of regular burning. The effect of burning is therefore not merely direct - that is, the loss of humus or carbon. The depletion of soil life must be regarded as an indirect, but no less serious, consequence.

Burning and overgrazing are the most widespread human influences on the savanna ecosystem. The short-term advantages of burning - earlier grass regrowth and, under some conditions, a closer C/N ratio - must be weighed against the serious long-term disadvantages.

The loss of organic matter and the decline in the number of soil organisms mentioned above lead to soil compaction, reduced infiltration by rainwater, diminished water-holding capacity and often, as a secondary consequence, erosion damage. Burning generally results in a decrease in soil and site fertility accompanied by a decline in the number of plant species.

Overgrazing of the savanna usually leads to the presence and often the dominance of plants with a low fodder value. In addition, it causes once densely covered grassland to develop bare patches (burning further aggravates this development). On such land, thorny bushes and shrubs are able to establish themselves in increasing numbers. Because they are usually avoided by grazing animals they gradually displace the grasses, so that in a short time an impenetrable thornbush thicket develops (LAUER 1956; WALTER 1964; VARESCHI 1980).

Preventing burning alone may improve the situation in the short and medium term, but not forever. Bushes will generally continue to invade without check if new grass growth is not simultaneously protected and promoted by reducing stocking levels. (WALTER 1964). According to VARESCHI (1980) allowing grasses to grow for longer periods is possible if pastures are rotated. Contingency forage areas can be set aside for times of need. Thus more productive and ecologically stable pastures can be established for long-term use without burning.

Agricultural use of the dry savannas is limited by the shortage of water. Near the limits of rainfed cultivation only drought-resistant crops such as millet, sorghum, sesame, and groundnut can be grown. Even these may require the use of special methods, such as water harvesting. Although crop cultivation is expanding into the dry areas, it is often unable to compete with livestock production, which is often the principal livelihood of this zone's predominantly pastoral people. If agriculture is to be practised, humus-conserving soil use and erosion protection measures must be strictly observed. The productivity of these areas can be substantially improved through the integration of drought-resistant trees and shrubs (FELKER 1981; MAYDELL 1983).

2.2.5 Semi-deserts and deserts

On the far side of the climatic savannas, usually beyond the 200 mm isohyet, lie semi-deserts and deserts. Here the vegetation is very poor in species. Only a handful of specialists survive, chiefly in basins with run-in (mainly acacia, prosopis, albizzia and cactus varieties). Ephemerals (plants with very short life cycles) are also present, springing up suddenly in response to the irregular rainfall.

According to RODIN and BASILEVIC (cited in YOUNG 1976), the standing biomass of semi-arid vegetation is often about 6 t DM/ha. The growth rate is approximately 10 to 20% (i.e. 0.6-1.2 t/ha) of the standing biomass per year (WHYTE 1976), but this depends greatly on site conditions (rockiness, salinity, etc). In these areas only extensive livestock production is possible under normal conditions. Only with special techniques such as irrigation and water harvesting can the semi-desert be utilized for crops. In some areas, where groundwater is present in the deeper soil strata, growing desert trees (prosopis) may be practicable (FELKER 1981). Establishing trees in these areas is extremely difficult however, because between the groundwater and the briefly moist surface there is usually a layer that always stays dry. According to WALTER (1964), this obstacle may be overcome through irrigation until the roots reach down to the groundwater. Left to nature, trees in these areas are able to establish themselves only under exceptional rainfall conditions occurring once in 100 to 200 years.