VEGETATION ECOLOGY IN AFRICAN SAVANNA

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INTRODUCTION

African savannas, sensu latu, cover almost half the continent. They occupy the areas between the equatorial forests and the tropics as well as the East African plateau. They occur in arid to subhumid, seasonal climates with one or, close to the equator, two dry seasons and the (main) rainy season in the summer.

The northern and southern savannas in Africa have, during much of the evolutionary time, been connected by the dry corridor through East Africa. Thus, there are considerable phytogeographic simularities between the savannas of northern, eastern and southern Africa. In the phytogeographical map by LEBRUN (1947, ex WERGER 1978) all savannas constitute the Sudano-Zambezian Region, divided into several domains. Later maps, (MONOD 1957, WHITE 1965, 1971) largely agree in the over all classification, but differ in the subdivisions. WHITE (1976) recognizes 8 regional centres of endemism in Africa, of which the Sudanian south of the Sahel, and the Zambezian covering much of southern Africa north of the tropic of Capricorn, have influence on the northern and southern savannas respectively. The East African savannas are largely classified as regional mosaics, and the savannas south of the tropic of Capricorn mainly belong to the Kalahari highveld regional transition zone.

Functionally, savannas have often been divided according to physiognomy, e. g., shrub savanna and woodland, or moisture availability, e. g., moist, semi-arid and arid savannas. HUNTLEY (1982) described for southern Africa the general agreement between relative nutrient availability and aridity, and the ecological differences between arid/eutrophic and moist/dystrophic savannas. SCHOLES & WALKER (1993) extended this classification to all African savannas.

The present paper aims to give an introduction or a background to savanna vegetation ecology, based on old and new understanding of the structure and function of these ecosystems.

PLANT AVAILABLE MOISTURE

Many savanna models have water as the principal limiting factor (WALTER 1954, 1971, NOY-MEIR 1982, WALKER & NOY-MEIR 1982, EAGLESON & SEGARRA 1985). WALTER (1971) showed that above ground net primary production (NPP) of the herbaceous layer in these savannas was linearily related to the annual rainfall up to ca 900 mm y^{-1}.

The lines from different savannas in Walters graph showed, however, to have different slopes and X-axis intercepts. The relation between rainfall and plant available moisture in the soil depends, apart from rainfall, on infiltration rate and water holding conditions, which varies with soil texture and structure and with the vegetation, and influences particularily the X-axis intercept of the lines. While soil moisture determines the time available for plant growth in dry savannas, the rate of production, when water is available, i. e., the slope in Walters graph, largely depends on nutrient availability. Thus, the water based savanna model is widened to include both water and nutrients as driving forces.

The increase in NPP and biomass along the rainfall gradient, also implies an increase in the ratio of trees and shrubs to herbaceous vegetation, and in the allocation to supportive tissue, e. g., stem wood. Thus the turnover rate of above ground biomass, that for the driest savannas is little more than one year, increases. At the same time the proportion of NPP to gross primary production decreases.

NUTRIENTS

The large scale nutrient gradient in the African savannas is given by the geology of the continent. The old central African plateau is characterized by deeply leached, acid soils, often with coarse texture, while more base rich, fine textured soils dominate to the north and east. To the south extensive dry areas are covered by nutrient poor aeolian Kalahari sands.

Generally the poor soils are occupied by broad-leafed savannas with trees/shrubs dominated by the families Combretaceae and Caesalpiniaceae and with coarse caespitose grasses. On the more base rich soils, or where shortage of water is more limiting to plant growth than shortage of nutrients, are fine-leaved savannas, with the woody layer dominated by the family Mimosaceae, mainly Acacias, and typically with stoloniferous grasses.

HUNTLEY (1982) described the fundamental ecological differences in soil conditions, climate, physiognomy, flora and fauna between the two types of savannas. He showed that the gradient between fine-leaved and broad-leaved savannas at the same time generally reflects the rainfall gradient, with fine-leaved, savannas dominating in areas with rainfall below ca 400–600 mm, and broad-leafed savannas in areas with higher rainfall. The distinction between arid/eutrophic and moist/dystrophic savannas seems to hold as a large scale generalisation, but there are a number of areas and vegetations which do not fit comfortable within the system. The Kalahari savannas are in many respects intermediate between the two categories.

On landscape scale, nutrient and water content varies along the topographic catenas, with coarse, nutrient poor soils and broad-leaved trees on the upper slopes and increasing moisture and nutrient content, and dominance of fine-leaved trees, e. g., Acacias, down slope.

FIRE

While in a regional scale, savanna ecology may be said to be a function of climate and nutrient availability, vegetation structure and function in any particular situation may be more influenced by fires, herbivory, short term fluctuations in rainfall or by direct human impact, for example in the form of cutting of trees (KLÖTZLI 1980, FROST ET AL. 1986, MEDINA 1987, SARMIENTO 1983, 1992).

Fire is an important, perhaps defining, factor in savanna ecosystems. Fire intensity, frequency and area burnt per fire event varies with the environmental conditions. The driest savannas burn only after exceptionally wet seasons, when enough grass fuel has been produced. The wet savannas may have the highest fire frequency and intensity, but there may also be situations where the dry season is too short and/or wet to allow the fuel to dry up enough.

Natural savanna fires are mainly lit by lightening, and are probably most common with the first thunderstorms at the beginning of the rainy season, while there is still dry grass available as fuel. Fires at that time damage the woody vegetation, of which many species are already flushing new leaves and shoots, while the dormant grasses are less affected. The new growth, that in perennial grasses is often triggered by the fire, can continue as normal, as the rains soon follow, and the plants can rebuild their nutrient stores.

Most savanna fires are lit by humans during the dry season, to promote fresh grazing for livestock, attract game for hunting etc. At that time most woody species as well as the grasses are dormant. The fire-initiated sprouting of the grasses will either wilt due to lack of water, or be grazed away by herbivores attracted to the fresh growth. Thus, the grasses have no possibility to replace the nutrient reserves consumed in sprouting. In this way perennial grasses may eventually be exhausted and replaced by ephemerals and, under certain conditions, woody vegetation (FROST & ROBERTSON 1987).

Generally, woody species are more affected by fires than grasses, and frequent burning over long time leads to reduction or elimination of the tree layer. The mature savanna trees are fairly resistant to fire, but saplings and shrubs with the canopy within the flame zone are often killed above ground. They can resprout from the bases repeatedly, but are finally exhausted. Fire effect is reduced under the canopies of shrubs and trees, facilitating survival of young individuals growing close together or close to an older individual. This promotes a clumped distribution pattern of fire sensitive species and size classes. (MENAUT et al. 1990, SKARPE 1991). When either fire is excluded, e. g. by intensive grazing, or the trees have grown with their canopies above the flame zone, the aggregated pattern may break up and change towards random or regular (SKARPE 1991).

HERBIVORY

A fourth important factor in savanna ecology is herbivory. Insect herbivores, e. g., termites, grasshoppers and caterpillars play major roles in many savanna systems. The significance of small rodents in African savannas is not well known, but bark gnawing by porcupines have some influence on tree populations.

The African savannas are famous for their large mammalian herbivore fauna of mainly ungulates. The wild herbivores are now in most areas outside game reserves and national parks largely replaced by domestic stock. Both indigenous and domestic fauna include species that differ widely in size, digestive system and feeding strategy (HOFMANN & STEWART 1972, OWEN-SMITH 1982). A basic distinction can be made between browsers or concentrate selectors, eating woody species and dicotyledonous herbs; mixed feeders preferring browse; mixed feeders preferring grass; and grazers or bulk-roughage feeders (HOFMANN & STEWART 1982). While browsing is the most common strategy (BODMER 1990), savannas are by metabolic biomass dominated by grazers, often wildebeest, zebra, buffalo or elephant (OWEN-SMITH 1982). While the grass-grazer system is comparatively well known, the browse-browser interactions in the tropics have been less studied (BERGSTRÖM 1992), and the subdominance of the browsers is not well understood.

All herbivores are selective in their feeding on different scales from landscape to patch to the single bite. Generally, selection is for tissue with high content of nutrients and/or energy, for structure that allows a high feeding rate, and against damaging structures or chemicals.

Savanna herbivores experience a period of food shortage during the later part of the dry season. OWEN-SMITH (1982) and OWEN-SMITH & COOPER (1989) suggested that the shortage for grazers was in quality, particularily protein, whereas for the browsers it was a lack of energy, i. e. quantity of acceptable browse. Thus, the grazers would during all year concentrate in the nutrient rich fine-leaved savannas, whereas the browsers during the later part of the dry period would prefer the denser wooded broad-leaved savannas. In the relatively nutrient rich fine-leaved savannas frequently 20-50% (SCHOLES & WALKER 1993) and in some areas 90 % (MCNAUGHTON 1992) of the available biomass is eaten by large herbivores. In the nutrient poor broad-leaved savannas typically less than 10 % is eaten.

Grasses generally have few defensive traits, but their meristems are protected by their situation close to the ground, and they rapidly compensate for biomass eaten. Grazing increases nutrient turn over, and repeated grazing on preferred spots may maintain (or create) nutrient rich patches, »grazing lawns«, »hot spots« with highly productive and palatable grazing (MCNAUGHTON 1979, 1985). The question whether graminoids under these conditions overcompensate for grazing has been intensely discussed (MCNAUGHTON 1979, 1984, BELSKY 1986, BELSKY et al. 1993).

More common, particularily with heavy livestock grazing, is that palatable grasses successively are replaced by unpalatable grasses, unpalatable forbs or by woody thickets (WALTER 1954, KLÖTZLI 1980, 1995, VAN VEGTEN 1983, SKARPE 1990).

Woody plants respond in different ways to herbivory. In some cases browsing increases the resistance to further browsing by inducing higher concentrations of repelling substances (BRYANT 1981). In other cases plants respond by producing shoots which are more palatable for browsers (PELLEW 1983, DANELL et al. 1985, DU TOIT et al. 1990). Generally, fast growing species on resource rich sites are palatable, and have good capacity to compensate for browsing. Slow growing species on resource poor sites typically have developed strong defences against herbivory (BRYANT et al. 1983). They also have less ability to compensate, and higher mortality rates following heavy browsing (DANELL et al. 1991).

Excessive browsing, often by domestic stock as goats and camels, as well as the combination of browsing and frequent fires (PELLEW 1983), may in all environment damage or kill browse plants.

INTERACTIONS

The first water based savanna models have developed into an understanding of savanna ecology based on four main variables: Plant available moisture, plant available nutrients, fire and herbivory (PENNING DE VRIES & DJITÉYE 1982, FROST et al. 1986, WALKER 1987). The four factors are often referred to as »determinants«, although they in most scales of observation are strongly interactive between themselves and with other parts of the ecosystem.

There are strong interactions between herbivory and fire. The fresh shoots after a fire, both of grasses and woody species, are highly palatable. They are dominated by young, nutrient rich tissue, supported by an overdimensioned root system. It may also be influenced by the effect of fire on nutrient cycling. From temperate grasslands a short term increase in nitrogen and phosphorus have been recorded after fires, and has been attributed to increased mineralization rates (DAUBENMIRE 1968, HULBERT 1988). Fires in savanna systems, lead to the loss of particularily nitrogen through volatilization and to a reduction in soil organic matter.

Intensive grazing in savannas remove the potential fuel, and leads to a reduction in fires (GOLDSTEIN & SARMIENTO 1987, MCNAUGHTON 1992). In the moist/dystrophic savanna herbivores remove little biomass, and fires appear every year to every third year, while the heavier grazed arid/eutrophic savannas have a fire interval of five years or more (JUSTICE et al. 1994). In the wet nutrient poor west African savannas most biomass is consumed by fires (SARMIENTO 1992)

WOODY SPECIES AND GRASSES

The importance of trees and shrubs in savannas is influenced by all four determinants: available soil moisture (WALTER 1954, WALKER & NOY-MEIR 1982, GOLDSTEIN & SARMIENTO 1987, SKARPE 1991), available soil nutrients (MEDINA 1987, TOLSMA et al. 1987), fire (BROOKMANN-AMISSAH et al. 1980, GILLON 1983) and herbivory (ARCHER 1989, SKARPE 1990). There is a trend in dry rangelands throughout the world for increase in the ratio of woody to herbaceous vegetation (ARCHER, SCIFRES & BASSHAM 1988).

One reason may be a suppression of fires due to heavy grazing or a non-burning management policy (ADAMOLI et al. 1990, MENAUT et al. 1990). Also the degradation of grasses from heavy grazing, and thus a reduction in their competition with the woody vegetation for soil resources, may result in an increase in woody vegetation (VAN VEGTEN 1983, SKARPE 1990). Other contributing factors may include changes in the timing of fires, subtle differences in climate or changes in atmospheric composition (ARCHER, SCIFRES & BASSHAM 1988).

The classical explanation for the bush enchroachment is based on the two-soil-layer model first presented by WALTER (1954) and further developed, to accomodate more of the dynamic behavour, by WALKER & NOY-MEIR (1982). The model presumes two soil layers with independent water budget, except for recharge of water in the deeper layer through the upper. Grass roots have access only to the upper soil layer. Woody species have access to both, but are competitive inferior to the grasses in the upper layer. There are field observations largely supporting these model (SALA et al. 1989, SKARPE 1990). Other studies have revealed more complicated interactions between the two vegetation components (KNOOP & WALKER 1985, STUART-HILL & TAINTON 1989).

The model by WALKER & NOY-MEIR (1982) has one point of equilibrium between woody and herbaceous vegetation. Including large herbivores in the model, NOY-MEIR (1982), gives, for high grazing pressure, two alternative stable states, one with a »typical savanna« mixture of grasses and woody elements, the other with dominating woody vegetation and no grasses. Two or more stable states have also been hypothesized from field data by FORD (1966), CAUGHLEY (1976), NORTON-GRIFFITHS (1979), PELLEW (1983) and DUBLIN et al. (1990), suggesting that fires, elephants, other browsers and grazers, tsetse fly and humans may cause savannas to switch from one state to another. MCNAUGHTON (1992) describes similar physiognomic changes in the propagation of disturbance through savanna ecosystems, but considers the systems to be sufficiently damped against all but exceptional disturbances. ARCHER (1989) describes the changes between woodland or forest, »typical savanna« and open grassland as positive feedback mechanisms. Both PELLEW (1983) and ARCHER (1989) find that only the woody and the grassy extremes represent equilibrium states, whereas the »typical savanna« is a transition stage. EAGLESON & SEGARRA (1985) assume that grassland and woodland are unstable, whereas the typical, mixed savanna is stable.

CHANGING SAVANNAS

The above models understand savannas as dynamic ecosystems, but still with one or more points of equilibrium to attract them. However, there is much evidence that savannas in most scales are event driven, non-equilibrium systems. The relations between woody and grassy vegetation can be described as non-equilibrium systems, where competitive dominance may change between the two components depending on environmental conditions. It is usually assumed that the woody component increases untill checked by, e. g., fire (JUSTICE et al. 1994).

Many savannas are rapidly changing as a result of changes in intensity and/or kind of human land use. Livestock grazing is expanding and occupying more marginal areas. Stocking rates are in many cases high enough to cause changes in species composition and production of the range, to the disadvantage of the grazers. As the soil is trampled and/or denuded of vegetation, the surface may become compacted, covered by a crust or changed in other ways, usually reducing water infiltration and increasing runoff. Soil organic matter generally decreases, implying poorer retention of water and nutrients. In many cases the soil itself is eroded away by wind and/or water. Such degradation of soil and vegetation is often misleadingly referred to as »desertification«.

With increasing human population density and better access to technology, there is a general trend from nomadic or transhuman pastoralism to settled livestock husbandry, thus reducing the flexibility of the system. For the same reasons, there is an increase in arable agriculture at the expense of grazing even in traditionally cattle based cultures like the massai.

The increase in atmospheric CO_2 may cause increased plant photosynthesis, water use efficiency and nitrogen use efficiency (SMITH et al. 1987, SALA et al. 1988, BAZZAZ & MCCONNAUGHAY 1992). There is some evidence that the carbon fertilization may be less pronounced in species with the C_4 photosynthesis pathway (i. e. tropical savanna grasses) than in species with C_3 photosynthesis (e. g. savanna trees and shrubs) (OWENSBY et al. 1993, POLLEY et al. 1994). The carbon fertilization might result in increased C/N ratio in plant biomass, with subsequent negative effects on herbivores and decomposers (FAJER et al. 1991, NORBY et al. 1986).

Of the large scale environmental changes affecting the African savannas, the changes in landuse have, and will, for the foreseeable future have the strongest impact on vegetation structure, production and diversity (VITOUSEK 1994).

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