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PRIMARY PRODUCTION IN THE SAVANNA

Augustine O. Isichei

Department of Botany,
University of Ife

SUMMARY

1. It is emphasized that there is a dearth of information on primary production in the savanna in spite of savanna occupying nearly 80% of the West African land surface.
2. Known values from the literature of annual primary production are presented. Values range from 150 to 1800g m^{-2}.

   This range is not totally encompassing as primary production is strongly influenced by local conditions.
3. The methods in use for measuring primary production are reviewed and their applicability to the savanna examined.
4. The factors that affect primary production in the savanna are enumerated and discussed.

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1. Introduction

1.1 General results of studies in West Africa

In spite of nearly 80% of the West African land surface being covered by savanna and Sahelian vegetation, information on primary production is remarkably meagre and scattered. A UNESCO-UNEP-FAO (1979) report has recently reviewed world-wide savanna production and has been able to include but little data from West Africa. Detailed production and standing crop figures are given for Derived Savanna at Lamto, Ivory Coast by Menaut and Cesar (1979). Hopkins (1968), twelve years ago, published data from the Derived Savanna of south-western Nigeria. Earlier, Rains (1963) published results from the Northern Guinea zone. Egunjobi (1974) worked in a managed range of almost pure *Andropogon gayanus* at Fashola, also in south-western Nigeria, Derived Savanna. Afolayan (1977 and 1978), working in the Northern Guinea zone, reported maximum grass yields in different vegetation formations in the Kainji Lake National Park which were related to grass species and burning regime. Isichei (1979) reported maximum grass standing-crop figures over two and three

year periods from sites in the Derived, Southern Guinea and Northern Guinea Savanna in Nigeria. The Man and Biosphere programme (MAB) has reported results of maximum grass standing-crop in nine one-hectare plots ranging from Southern Guinea-type vegetation to sub-Sudan Savanna in the Kainji region (Usman 1981). Most of the above-mentioned reports, as indicated, have been concerned with herbaceous vegetation and almost exclusively, grass production.

The only below-ground herbaceous biomass figures available for West Africa are those of Menaut and Cesar (1979) and Cesar and Menaut (1973) for Derived Savanna in Ivory Coast, and Isichei (1979) for Nigeria.

Menaut and Cesar (1979) reported woody biomass production at Lamto. No other published figures are available for West African natural savanna except the crude estimates by photographs of Isichei (1979). There is also a similar dearth of information on woody root production.

1.2 A review of methods

Generally, net primary production is estimated as annual maximum standing-crop, usually at the end of the growing season in October/November/December, depending on the location. Wiegert and Evans (1964) (see also Sims and Singh 1978) have criticised this method on at least four grounds.(1) That it ignores the possible growth stimulating effects of moderate grazing with a resultant increase in total production. Afolayan (1977) assessed the effects of grazing on maximum standing crop in natural grass-land production within Borgu Game Reserve, Kainji Lake National Park, and his results showed no statistically significant difference between grazed and non-grazed plots. Usman (1981), working in open savanna outside the Reserve, has, however, noted considerable difference in maximum standing grass attributable to livestock grazing and trampling. (2) The method does not account for the mortality of green plants before the standing-crop peak period. This can be overcome by litter collection, but if species selection is intended, it is extremely difficult to sort dry parts of plants into their various species. (3) Growth may occur during the decline in standing-crop after peak crop has been attained. For example, I have observed flushing by inflorescence branches of *Andropogon tectorum* and *A. gayanus*. (4) Finally, the method does not take into account the differences in time at which different species attain their peak standing-crop. This could be an especial problem in a situation where there is a mixture of perennials and annuals. The perennials start growth first, immediately after burning, but most often reach maturity later than the annuals. In Borgu Game Reserve, the maximum standing-crop in October/November at some sites is dominated (in terms of biomass) by *Hyparrhenia involucrata* (regarded as an annual), while perennials are dominant in standing-crop estimations at the

same sites earlier in the season. I have also noticed among perennials at Olokemeji that *Schizachyrium sanguineum* matures before any other perennial and starts going brown in November.

An often suggested alternative method is the sampling of individual species at the various times of their peak attainment with summing up for maximum biomass. In the savanna, only a few species may sometimes be dominant, but there are usually many species, thus this method would be tedious and time consuming, but enhanced accuracy achieved might well compensate for this. Even this method would not, however, account for material which had died and fallen as litter. Menaut and Cesar used a modification of the Weigart and Evans method (Lomnicki et al. 1968) in their study of seven savanna formations in Ivory Coast.

The UNESCO report (1979) mentions attempts to develop techniques through which particular aspects of plant physiology or structure can be used to indicate all elements contributing towards production. For example, Broughman (1960) has shown the relationship between leaf area index, the amount of chlorophyll within a community and its net primary production. Leaf area index is particularly difficult to measure in tropical vegetations because of the multi-layered complexity of most formations.

Standing crop measurements, with the outlined problems in mind, will continue to be used for rough estimation of herbaceous production, at least for some time.

What needs urgently to be done is to find a way of measuring woody biomass production with a minimum of destructive sampling. There is need to re-appraise the role of trees in the savanna as a whole and in rangeland development in particular. Isichei's (1979) method of estimating woody biomass by photography needs to be rigorously tested to see if it will be widely applicable. Menaut (1977) has outlined the problems associated with girth measurements as a means of estimating production.

Root (woody and herbaceous) biomass production estimation is also problematical because it is difficult to distinguish between small dead and living roots. Root yearly turnover could reach 100% in Andropogoneae savanna and 70% in wooded savannas (Menaut and Cesar 1979). It is also worth noting that different grasses have different rooting systems (Pratt and Gwynne 1977, p. 86) so adjustments would have to be made for this when determining herbaceous biomass. It is, however, generally agreed that herbaceous root biomass is maximum at the beginning of the dry season.

2. Review of results

2.1 Above-ground herbaceous biomass

Milligan and Sule (this volume) observed that, depending on local site conditions, the yields of the herbaceous material of natural savanna rangelands are reported to vary between 1.5 and 18.0t ha^{-1}, though yields between 2.0 and 6.0t ha^{-1} would be more typical. Most of the results obtained so far are within the 1.5 to 18.0t ha^{-1} range

except in the southern Derived Savanna where this maximum may be exceeded (for example, Egunjobi 1973: 19t ha^{-1}).

2.1.1 Factors affecting herbaceous yield

(a) Moisture regime

Milligan and Sule (this volume) further stated that in addition to the effect of total annual rainfall, which in Nigeria is highly correlated with latitude, herbage yields are also closely related to catenary sequences of soil. Lowest yields tend to occur on shallow, gravelly soils which have a low, sparse grass cover usually consisting of annual species. Rainfall is, however, generally thought to be the major determinant of production, hence De Leeuw (1978) suggested a predictive relationship between total annual rainfall and maximum annual herbage standing crop where:

Grassland primary production (kg ha^{-1}) = 2.36X (rainfall mm) + 34.7

It is true that water is primarily a limiting factor in savanna production; but, as Hopkins (1968) pointed out, what matters is not necessarily the amount of rainfall but the length of the rainy season. This, in turn, is related to annual mean maximum temperature and potential evapotranspiration. For example, Ibadan (446'N), Ilorin (489'N) and Bida (546'N) have almost the same amount of rainfall - 1230, 1290 and 1240 mm, respectively, while Kaduna (636'N) has more - 1300mm - but there are great differences in length of rainy season or/and evapotranspiration. Ibadan has an average rainy season length of 245 days, Ilorin 230 and Kaduna 175. The ratio of rainfall to potential evapotranspiration is 1.0 at Ibadan, 0.78 at Ilorin, 0.66 at Bida and 0.68 at Kaduna. Both length of rainy season and the rainfall: evapotranspiration ratios appear more closely related to vegetation type and production than does annual rainfall.

(b) Shade

The proportion of shade and woody vegetation cover are reported to be inversely related to grass yield (De Leeuw 1978). The influence of the woody vegetation on species composition of the herb layer may, however, produce the opposite result (Milligan 1979). For example, Pratt and Gwynne (1977) in East Africa noted that *Beckeropsis uniseta*, a highly nutritious grass, occurs more often in the shade. This can be said of *Andropogun tectorum* when it occurs in Guinea Savanna and of *A. gayanus* when it is found in the Northern Guinea zone.

The end of the first year results of the MAB project in the Kainji region (Usman 1981) show that density of woody material greater than or equal to 1cm in girth at breast height is negatively correlated ($P < 0.10$; $r = -0.62$) with herbaceous production. However, when trees 30cm and above in girth are considered, the correlation is insignificant.

In an attempt to assess the effect of canopy on grass production, Usman used 3 arbitrary measures of canopy - no canopy at all, light canopy, more than half the area covered - and found positive, although slight and statistically insignificant, correlation between production and canopy

cover. When, however, analysis allowed comparison of grass yields and canopy cover to be made independently of plot-to-plot variation (by using the grass weight of each metre sampled and assessed for canopy, divided by the total yield of the plot), comparison of no canopy and light canopy showed significantly higher yield (at $P < 0.05$) from the light canopy samples ($n = 161$). Overall, the data of Usman (1981) tend to substantiate the view of Milligan.

(c) Vegetation type

The results obtained by Usman are typical of savanna vegetation in that, even over a relatively small area, he obtained peak season standing-crop figures that ranged from 80g m^{-2} to 600g m^{-2} in nine one-hectare plots. This variation in results, often related to soil differences, is especially apparent in situations where workers have obtained results from different vegetation formations in a vegetation zone. Thus Afolayan (1978), working in *Terminalia macroptera* tree savanna, *Isoberlinia* woodland and *Burkea/Detarium* open savanna obtained values that ranged from 150g m^{-2} to over 700g m^{-2} in a two year (1974 and 1975) study. The same amount of variability is also seen in the results of De Leeuw (1976) in a study of the rangelands of north-eastern Nigeria. He obtained values that ranged from 201 to 450g m^{-2}, with the higher values coming from floodplains and lacustrine and lithomorphic clays.

Yearly and cyclic climatic variations (see Milligan 1979) are common. For example, Hopkins (1968) obtained a herbaceous production figure of 570g m^{-2} at Olokemeji in one year and 680g m^{-2} in another; Isichei (1979) at another site in the same Olokemeji Reserve obtained 400-500g m^{-2}. Braun (1973) in *Andropogon greenwayi* savanna in Tanzania obtained values between 150 and 400g m^{-2} the first year and between 600 and 1,150g m^{-2} the second.

(d) Burning

Often production studies are related to burning with the usual assertion that 'late' burning results in higher grass yield than 'early' burning. Sanford (this volume) has discussed this and other results usually associated with burning.

2.1.2 Summary of the author's results

Having noted the various factors that affect savanna production, one can conclude that rainfall, which is the prinicpal basis on which climatic/vegetational delineations are made, is not the sole determinant of grassland production. Soil - its nutrient levels, mainly in terms of nitrogen, phosphorus and carbon content, with the latter in turn related to water-holding capacity and cation exchange capacity, are perhaps most important. Isichei (1979) attempted regressions of annual maximum standing crop on several environmental factors. There was no clear relationship with annual rainfall in the humid savanna (Derived, Southern Guinea and Northern Guinea) zone where he worked, but there was a highly positive

relationship with length of rainy season, indicating that there is ample moisture for grass growth throughout the rainy season: it is the length of the rainy season that limits production. A high negative correlation was found between maximum grass standing crop and mean daily maximum temperature. While this may be a 'pseudo-correlation' in that high temperature is in turn correlated with a longer dry season, I have observed that savanna grasses are often rolled or wilted after mid-day, particularly in the early rainy season before they have grown enough to shade themselves. This would clearly decrease photosynthesis. Furthermore, partial correlation analysis showed that the high negative correlation between maximum temperature and grass yield remained unchanged when the effect of the number of rain days was removed.

Other factors that seem to influence production are soil carbon and nitrogen content. While the amounts of these two elements are highly positively correlated and the amount of carbon is, in turn, correlated with mean annual rainfall (Jones 1973), the relationship shown by my limited data appears independent of the rainfall effect to a considerable degree: maximum standing crop is positively correlated with soil carbon with an r^2 of 0.99 and with nitrogen with an r^2 of 0.97 (n, however, is only 5). Partial correlation shows the carbon effect to be related to maximum temperature rather than to rainfall, suggesting mineralization rate as a strong determinant of soil carbon levels. One cannot, however, draw rigid conclusions from these results - Isichei worked in only six sites in the three savanna zones.

2.2 Below-ground production

The known estimation of below-ground production is that of Menaut and Cesar (1979) which showed that, depending on savanna type, net below-ground herbaceous production ranged from 100g m^{-2} to 200g m^{-2} per year. They stated that root systems often constitute about 30% of total biomass but that there are great variations from site to site: total root biomass is remarkably constant in wooded savanna but increases in grass savannas according to edaphic conditions.

Isichei (1979) obtained ratios between herbaceous below-ground and above-ground biomass at the time of above ground maximum standing-crop that ranged from 0.44 to 0.55 for six sites in the Derived, Southern Guinea and Northern Guinea zones. The ratios showed a trend of increasing below-ground biomass with increasing climatic/burning severity from early burnt Derived Savanna at Olokemeji to the Northern Guinea sites at Borgu. Other comparable figures from the literature are 0.59 from a study in India (Singh and Yadava 1974), and a range of 0.38 to 1.04 with a mean of 0.64 for 7 savanna formations in Ivory Coast (Cesar and Menaut 1974).

2.3 Woody biomass production

2.3.1 Above-ground and total biomass

Menaut (1977) published leaf, bole and root biomass values of 170, 3,260 and 1,430g m^{-2}, respectively in savanna woodland at Lamto, Ivory Coast. Isichei (1979) obtained overall woody biomass values of

4,700, 14,900 and 11,700g m^{-2} in three plots at Olokemeji (late burnt, early burnt, fire protected, respectively) and 1,030 and 5,490g m^{-2} in *Burkea/Detarium* savanna and *Isoberlinia* woodland, respectively, at Borgu. Menaut found average annual increments in girth from 0.5cm for *Piliostigma thonningii* to 2.4cm for *Cussonia barteri*. The annual height increase ranged from 0.5cm for *Bridelia* to 14cm for *Cussonia*. On the whole, he obtained an average overall annual increase of 1.5% and a net production figure of 300g m^{-2} for his research sites. This differs from an annual average of 2.5% obtained for all the trees in the three fire plots at Olokemeji (Derived Savanna) whose girths were measured in 1969 and then in 1976 Menaut even observed wide differences between the two years (1970 and 1973) during which he took his measurements.

There is definitely a dearth of information on woody production in the savanna. Menaut discussed the difficulty of measuring woody production. He noted particularly that litter production measurement was difficult because of termite activity and the fact that dead branches remain and start decaying on the tree for a long time and suddenly fall off during a storm.

Menaut (1977) estimated that leaf biomass constituted 5% of total biomass for a woody plant and 3.5% of above-ground biomass, but it is likely that this will vary with the age of the site.

He also obtained, for every species, correlations between weight data (weight of leaves, annual shoots, wood, roots) and simple external measurements (height, girth). It is thus possible to calculate the different components of the biomass and, from growth data, to give an estimation of the net production of shrubs and trees.

2.3.2 Below-ground woody biomass

Measurements of below-ground woody net production are rare. Menaut and Cesar (1979) reported results from 4 savanna formations in Ivory Coast that ranged from 5 to 40g m^{-2}, with ratios of 0.37 for open savanna, 0.39 dense savanna and 0.45 for woodland savanna. Lamotte (1975, p. 191) obtained a mean ratio of 0.33 for open shrub, dense shrub and tree savanna.

3. Discussion

Below-ground production is extremely difficult to measure. First, there is the difficulty of separating dead and living small roots, and Menaut and Cesar (1979) observed that root turnover could reach 100% in some savanna formations and be much less in others. Also, below-ground biomass is highly variable depending on vegetation formation and edaphic conditions. It is almost impossible to separate roots on a species basis Until a reliable method is devised, below-ground biomass will continue to be expressed as only crude approximations.

The major problem with estimating woody production is that often destructive sampling may not be possible or desirable. Ways have to be evolved to determine woody production without destruction. Here indirect

measures will be useful. These again do not often result in accurate measurements.

Major problems of herbaceous biomass estimation are also considerable, but not as intractable as those of woody biomass estimations.

All-in-all, however, the major gap in production knowledge is methodological, and more attention should be turned to feasible yet accurate methods of measurement in the field

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