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Author(s): I. Deshmukh

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PRIMARY PRODUCTION OF A GRASSLAND IN NAIROBI NATIONAL PARK, KENYA

BY I. DESHMUKH

Department of Zoology, University of Nairobi, Nairobi, Kenya

SUMMARY

(1) Net aerial primary production of a grassland in Nairobi National Park was estimated using the harvest method in conjunction with estimates of mortality in the three most abundant grass species.

(2) As a result of the long rains (March–April) net primary production (dry matter) was 651 g m^{-2} and as a result of the short rains (October–December), 420 g m^{-2} . These estimates were more than twice the peak biomass observed in each season.

(3) The three most abundant grass species differed in their performance. *Themeda triandra* Forsk. had the highest net production relative to its biomass and the highest mortality rate in all seasons. *Pennisetum mezianum* Stapf. was lowest in both these respects and *Setaria phleoides* Leeke intermediate.

(4) Removal by large herbivores was too small to detect by enclosure methods. Calculations based upon population density of these animals suggest that they consumed less than 4% of annual net primary production.

(5) The grassland studied was fairly typical of others with similar rainfall in East and southern Africa with respect to peak herbaceous biomass and average large herbivore population density.

(6) Some implications of these results for management of the park are discussed.

INTRODUCTION

This study is the first published estimate of true net primary production (above ground) in an East African grassland. Previous work has estimated peak biomass of vegetation, with little attention being paid to the dynamics of different species, and equated this with primary production. However, a proper understanding of grazing resources is important for proper management of a conservation area such as Nairobi National Park which is maintained primarily because of its populations of large herbivorous mammals.

Milner & Hughes (1968) defined net primary production (P_n) in grasslands for any period as,

$$P_n = \Delta B + L + G,$$

where ΔB is the change in living plant mass (biomass), L the loss of biomass due to death of plants (or plant parts), and G the loss due to removal by herbivorous animals. For above ground organs, ΔB is usually estimated by successive harvests of the plants. In many African studies G has been accounted for using large-mammal enclosures. Most studies of tropical grasslands have ignored L (review of IBP studies, Singh & Joshi 1979), even though its significance in temperate regions has been apparent since the work of Wiegert & Evans (1964). Among the few estimates of herbaceous production in African savannas which take account of plant mortality are those in the Guinea savanna, Nigeria (Ohiagu & Wood 1979), the Lamto savannas of Ivory Coast (Menaut & Cesar 1979) and Nylsvley, South Africa (Grunow, Groenvelde & Du Toit 1980). A preliminary report of the present

Present address: USAID, Juba Valley Project, c/o Embassy of the USA, Mogadishu, Somalia.

work is the only paper to give estimates of *L* for East Africa (Deshmukh & Baig 1983). In most other African studies peak biomass (live plants) or peak standing crop (live + dead plants) have been used as estimates of net primary production (compiled by Deshmukh 1984). Comparisons between different areas of even such simple measures are difficult because in several cases vegetation was not clipped at ground level, but at some predetermined height 2–20 cm above the soil surface (e.g. Serengeti: Braun 1973; Mweya: Strugnell & Pigott 1978; Nylsvley: Grunow, Groenvelde & Du Toit 1980). These various clipping heights represent estimates of standing crop assumed to be available to large grazing mammals rather than attempts to understand the production ecology of the vegetation.

The present paper has three main objectives. First to estimate total net primary production above ground of a grassland in Nairobi National Park, Kenya. Second to assess the errors involved in the various methods commonly used to estimate net primary production, but which take no account of plant mortality. Third to estimate the importance of grass consumption by large herbivorous mammals.

STUDY AREA

Nairobi National Park covers an area of 115 km² approximately 10 km south of Nairobi city (latitude 1°20'S, longitude 36°50'E, altitude 1600 m). Most of the park is savanna grassland with a dry climate (*sensu* Deshmukh 1986). Mean annual rainfall in the city is 850 mm, falling mainly in two seasons (Fig. 1c), but with large variations from year to year. Mean annual temperature in Nairobi is 19.6 °C with mean monthly maxima and minima in the ranges 23–28 and 12–14 °C respectively. The park is a dry-season concentration area for large herbivorous mammals, most of which disperse into the Athi-Kapiti plains to the south and east for the remainder of the year.

The study site was situated close to the centre of the Park. Perennial tufted grasses comprise most of the vegetation, but there are also scattered *Acacia drepanolobium* Harms bushes. Of the 233 quadrats sampled during the study, the frequency of occurrence of grass species was: *Themeda triandra* Forsk. in 85%, *Setaria phleoides* Stapf. in 71%, *Pennisetum mezianum* Leeke in 21%, *Digitaria macroblephara* Stapf. in 5%, *Panicum coloratum* L. and *Ischaeum afrum* (Gmel.) Dandy in 3% and *Andropogon gayanus* Kunth in 1%. Forbs were found in 43% of quadrats, the major species being the perennials *Indigofera tettenis* Klotz. and *Commelina africana* L. and the annual *Ocimum americanum* L. The soils are black clay vertisols (locally known as 'black cotton soils') which are often waterlogged during the rains and dry and cracked in the dry seasons. Such soils are widespread in the *Acacia-Themeda* savannas typical of the East African highlands (Edwards & Bogdan 1951). The vegetation of the study site was burned accidentally on 26 September 1978 (P. P. N. Keiyoro, personal communication).

METHODS

Samples of herbaceous standing crop were harvested from three treatments at 4–6-week intervals. Ten samples were taken in a stratified random pattern from each of open grassland, from within moveable weldmesh cages (1.2 × 1.2 m) and from within a permanent 20 × 20 m chain-link large-mammal enclosure. The open grassland and small cage samples were taken from within the same 1 ha square adjacent to the permanent enclosure and the cages were moved to new random locations after each sampling. All the

vegetation in a 0.25×0.25 m quadrat was clipped at ground level and placed in a polythene bag. These harvest samples were sorted in the laboratory into live grasses, forbs and combined dead material. Because of their sporadic occurrence, grasses other than *T. triandra*, *S. phleoides* and *P. mezianum* and the various species of forbs are combined in the categories 'other grasses' and 'forbs', respectively, in the remainder of the paper. Each component was dried at 105°C to constant weight.

The method used to estimate grass mortality has been described elsewhere (Deshmukh & Baig 1983). Briefly, clusters of shoots of the three most common species were marked with cotton tags. Ten clusters of each species were so marked in the open grassland and in the permanent enclosure at the time of each harvest sample. Dead tissues were carefully removed. When the next harvest was taken, the marked shoots were removed, sorted in to live and dead portions, oven-dried and weighed.

Removal by large herbivores (ingestion plus other losses due to feeding and trampling) was estimated by comparison of standing crop in the open grassland with that in the moveable cages. The permanent enclosure was erected to determine whether total absence of large grazers affected primary production over the study period. Consumption by smaller herbivores was not estimated. Qualitative observations suggested that rodent and insect populations were low and unlikely to remove significant primary production. Such is the case in many other African savannas (Deshmukh 1986). Litter-feeding termites were absent from the study area and do not, therefore, affect estimates of the mass of dead grass (Deshmukh 1985).

Rainfall data are averages of daily totals for four stations situated around the edge of Nairobi National Park (Warden's Camp to the west, Wilson Aerodrome to the north-west, Kenyatta International Airport to the north-east and Cheetah Gate to the south-east).

RESULTS

Figure 1 shows the seasonal changes in herbaceous standing crop for the three treatments combined, and monthly rainfall totals. Combined data are used because there were no significant differences between treatments (analyses of variance; $P > 0.05$) except in one instance (see below). A notable feature is the predominance of dead material throughout the study (Fig. 1a). The 'long rains' (March–April) produced a much higher and more prolonged biomass peak than the 'short rains' (October–December) even though the total rainfall was only slightly greater (see also Table 1). The different species and types of plants showed similar, but not identical timing of peak biomass (Fig. 1b), although the proportional increases differed. The ratio of peak biomass (June or July) to the March–April trough was 4.5 for *T. triandra*, 3.0 for *S. phleoides*, 3.1 for *P. mezianum*, 3.0 for other grasses and 1.9 for forbs. Statistical errors for the separate plant types were quite large, particularly for those occurring sporadically. Expressed as percentages of their means on each sampling occasion, the standard errors of the various vegetation components through the year were: *T. triandra* 10–17%, *S. phleoides* 16–23%, *P. mezianum* 20–47%, other grasses 26–43% and forbs 16–49%. Thus results for categories other than the two dominant grasses must be viewed with caution.

Figure 2 shows the rate of mortality of three grass species between sampling dates. Whilst variation (particularly of *T. triandra*) was large in some seasons, there is a distinct pattern of highest mortality in *T. triandra*, followed by *S. phleoides* and then *P. mezianum* (average rates over the year were 33, 20 and 14 $\text{mg g}^{-1} \text{day}^{-1}$ respectively). Mortality rate

Grass production in African savanna

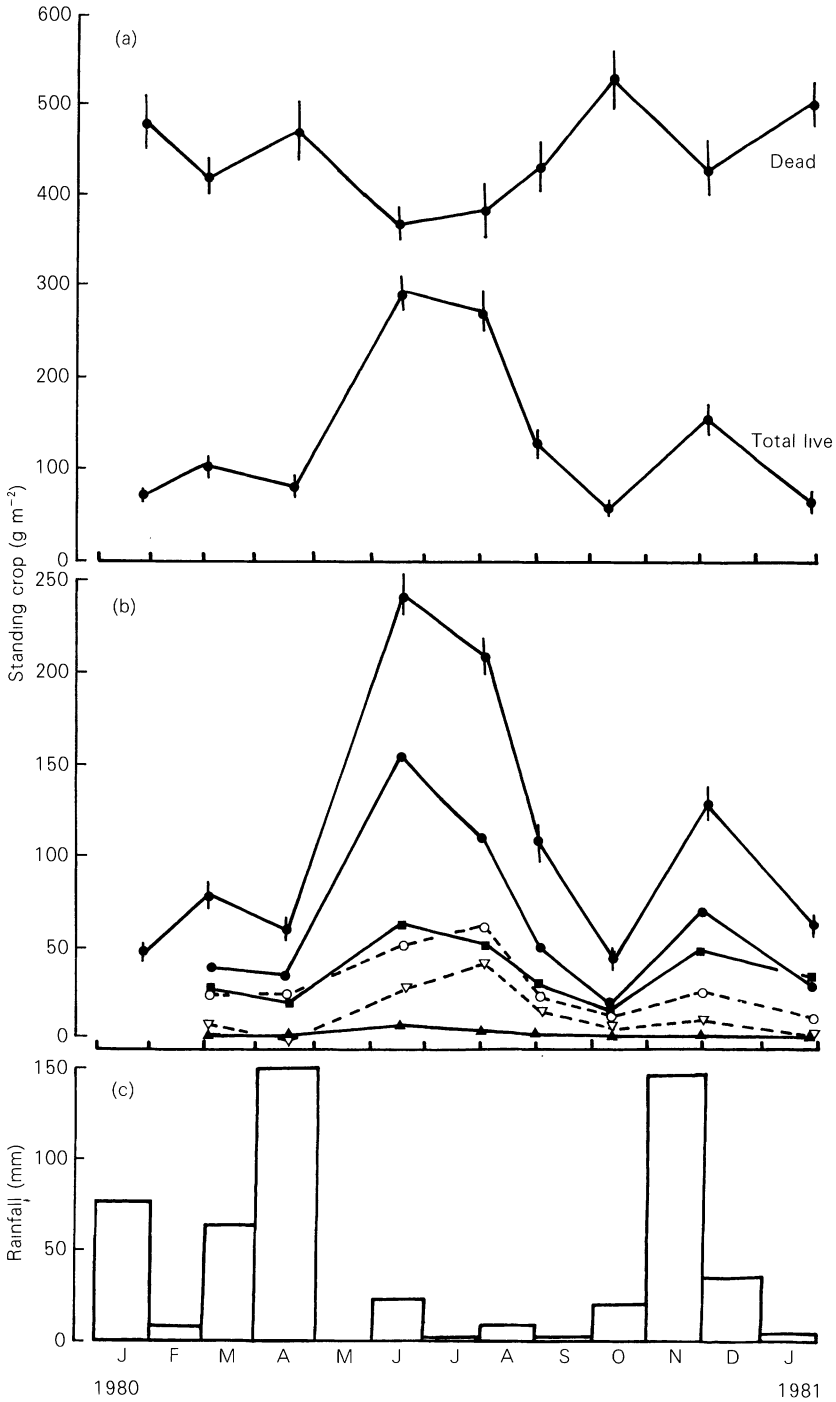


FIG. 1. Seasonal changes in dry weight of herbaceous vegetation and of rainfall in Nairobi National Park. (a) Biomass of living plants and standing crop of dead vegetation; (b) biomass of various components of vegetation; (●), total of grasses; (●), *Themeda triandra*; (■), *Setaria phleoides*; (▲), *Pennisetum mezianum*, (▽), other grasses; (○), total of forbs; (c) monthly rainfall totals, mean of four stations (see text). Where present, vertical bars are standard errors of means.

TABLE 1. Estimates of seasonal and annual dry-matter production (g m^{-2}) in Nairobi National Park, for 1980. (a) Estimates based upon peak mass (aggregate peak biomass is the sum of different plant categories from Fig. 1b). (a) Net primary production as the sum of biomass increment (ΔB) + mortality (L) for three grass species and biomass increment of other grasses and forbs.

	Long rains	Short rains	Whole year
(a) Peak mass			
peak total standing crop (live + dead)	668	597	1265
peak biomass (live only)	294	160	454
aggregate peak biomass (live only)	332	160	492
(b) Net primary production			
$\Delta B + L$ { <i>Themeda triandra</i>	455	250	705
{ <i>Setaria phleoides</i>	103	146	249
{ <i>Pennisetum mezianum</i>	9	4	13
ΔB only { Other grasses	42	7	49
{ Forbs	42	13	55
		Total	1071

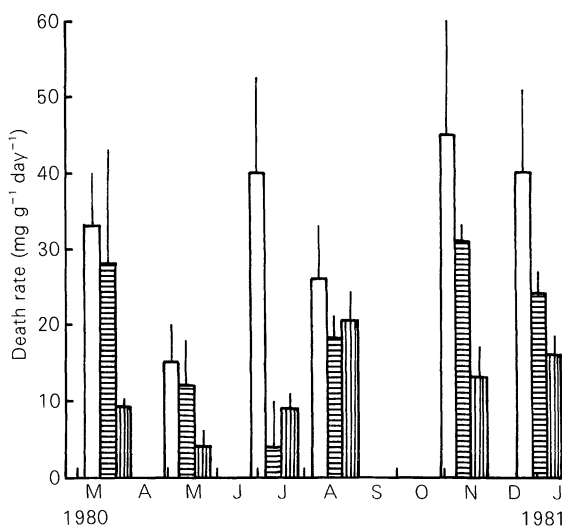


FIG. 2. Average daily rates of mortality in three species of grass from Nairobi National Park (mean \pm SE). (\square), *T. triandra*, (\equiv), *S. phleoides*; (\blacksquare), *P. mezianum*. Dry weight dying (mg) per g dry weight of biomass at the beginning of a period, per day.

was not statistically correlated with rainfall in any of the species. However, the highest rates did occur in the long dry season and the lowest during the long-rains growth period.

Removal by large herbivores was negligible over the study period as a whole. The only occasion upon which there was a significant difference between open grassland and moveable cage harvest samples was in January 1981 when 130 ± 55 (SE) g m^{-2} of dead matter was apparently removed (t -test, $P < 0.05$). During the same period removal of living plant parts was not statistically significant.

Table 1 gives several estimates of 'net primary production' as it is commonly determined in other studies of African savannas. Note that overall peak biomass and aggregate peak biomass for different plant types greatly underestimate true net primary production which

includes losses due to mortality. This last-named estimate ($\Delta B + L$) was calculated in the manner of the following example. The biomass of *T. triandra* increased by 119 g m^{-2} (ΔB) between 7 April and 15 June 1980. During the same period, estimated from mortality samples, 1.009 g had died for every gram of live grass present on 15 June. Since 153 g m^{-2} was harvested on that date, $153 \times 1.009 = 154 \text{ g m}^{-2}$ (L) had died to give a total net production of 273 g m^{-2} during the period. When harvested biomass decreased by more than the losses due to mortality in a period, 'negative production' occurred. These negative values were ignored in summation of seasonal and annual net production given in Table 1.

When mortality is taken into account it becomes apparent that production occurs over some parts of the year in which biomass appears to be declining (cf. Fig. 1b). Thus production occurred in March–April 1980, in December 1980–January 1981 in all three species, in June–July 1980 in *T. triandra* and throughout the year in *P. mezianum*.

Net primary production was closely related to the rainfall received between sample dates. Taking the three grass species together, 2.5 g m^{-2} of production was realized for each 1 mm of rainfall over the whole year. During the growing seasons this value had a narrow range of $1.9\text{--}2.6 \text{ g m}^{-2}$ except in June–July when 5.0 g m^{-2} was produced per millimetre of rainfall.

DISCUSSION

Comparison of true net primary production above-ground in Nairobi National Park with other East African ecosystems is not possible because other studies take no account of plant mortality. In perennial grasslands where dead matter may accumulate over several years, peak standing crop (live + dead) cannot be used to estimate primary production. The grassland studied was burned in September 1978 and dead plant material harvested in 1980 came from several previous growing seasons (see Deshmukh 1985). Peak biomass (living plants) in Nairobi National Park is similar to other grasslands in East and southern Africa. Compared with Table 1, the relationship of Deshmukh (1984) predicts peak biomass of 182 g m^{-2} from the long rains, 135 g m^{-2} from the short rains and 438 g m^{-2} for the whole year, given the rainfall received. However, peak biomass underestimates net primary production by almost 120% (Table 1). This degree of error is fairly typical when compared with other studies. In the Lamto savannas of Ivory Coast, the equivalent underestimation ranges from 50 to 190% (Menaut & Cesar 1979). Substantial mortality was also found at Nylsvley in South Africa with a maximum rate of $3.7 \text{ g m}^{-2} \text{ week}^{-1}$, compared with a biomass increment of 5.2 g m^{-2} in the same week (Grunow, Goenveld & Du Toit 1980). In temperate grasslands, peak biomass underestimates net primary production by between 10% (Deshmukh 1979) and 350% (Wiegert & Evans 1964) with most determinations falling in the range 50–150% (Williamson 1976). Of the methods available to estimate plant mortality, the one used here is simple and appropriate where there is a large accumulation of dead grass. The inherent assumptions, that the marked shoots are representative of the sward, that no dead grass is lost between samples and that removal of dead parts does not affect the shoots are discussed elsewhere (Deshmukh & Baig 1983, Deshmukh 1985).

There were distinct differences in the performance of the grass species studied in detail with respect to biomass accumulation and mortality (Table 2). Besides being the most abundant, *T. triandra* had the highest rate of production relative to its biomass and the highest rate of mortality. *P. mezianum* was lowest and *S. phleoides* intermediate in both

TABLE 2. A comparison of the performance of three grass species in Nairobi National Park in two seasons of 1980. Production:biomass ratio (P/B) compares net primary production (including mortality) with median biomass (mean of pre-growth and seasonal peak biomass) for each growing season. Mortality:biomass ratio (L/B) compares losses due to shoot death with median biomass for each growing season. Data used in calculations are g dry matter m^{-2} .

	P/B	L/B
(a) Long rains		
<i>Themeda triandra</i>	4.9	4.1
<i>Setaria phleoides</i>	2.5	1.6
<i>Pennisetum mezianum</i>	1.9	1.0
(b) Short rains		
<i>Themeda triandra</i>	5.7	5.4
<i>Setaria phleoides</i>	4.4	4.4
<i>Pennisetum mezianum</i>	2.0	1.0

these respects. The dominance and high production of *T. triandra* is suggestive of a favourable environment (despite the high mortality), a conclusion supported by the widespread occurrence of this grass in similar environments (Edwards & Bogdan 1951). The species is important in burned areas (e.g. Trollope 1982) and probably owes its dominance at the study site to fires including the one of September 1978. Little is known of the autecology of these grasses and further work on their growth performance and competitive abilities under different conditions would be rewarding.

Net production was greater and more prolonged and mortality lower during the long-rains growing season than during the short-rains growing season. These differences are probably related to greater water stress following the short rains. January and February are the hottest, least humid and sunniest months on average (mean maximum temperature 27–28 °C, relative humidity less than 70%, almost 10 h day^{-1} of sunshine). In contrast, soon after the long rains, July–August are the coolest, most humid and least sunny months (mean maximum temperature 22–23 °C, relative humidity 80–90%, around 5 h day^{-1} of sunshine). This climatic information may also explain the high rate of production per millimetre of rainfall during June–July (see Results). Presumably evapotranspiration in these months was low enabling the plants to draw on the water remaining from the long rains more effectively.

That more removal by large herbivores was not detected is not surprising when their occurrence of the study area is analysed. According to total counts carried out by the park authorities and other helpers, total biomass (liveweight) of large mammalian herbivores ranged from 1130 to 19 020 kg km^{-2} in the counting blocks which cover the study site, during the study period. Numbers have been converted to biomass using the unit weights of Coe, Cumming & Phillipson (1976). Using a regression prediction relating daily consumption of these animals to the body weight of each species (Deshmukh unpublished data), their total consumption of herbaceous vegetation for the year beginning February 1980 amounts to 40.6 g m^{-2} . This quantity is less than 4% of net primary production and less than 10% of the sum of peak grass biomass for the two growing seasons. At their highest density (January–February 1981) these animals are likely to have consumed only 2% of the total standing crop of vegetation (live + dead) available to them. In such circumstances it is unlikely that exclosure techniques will record significant vegetation removal. This calculated average consumption is lower by an order of magnitude than is often supposed in African savannas (e.g. Wiegert & Owen 1971). However, the mean

annual biomass of large herbivores in the park (8300 kg km^{-2}) is typical of many areas of East and southern Africa in relationship to annual rainfall (see Coe, Cumming & Phillipson 1976). There is no doubt that in some instances much higher vegetation removal occurs locally and/or for short periods (e.g. Strugnell & Pigott 1978; Sinclair, Dublin & Borner 1985). Nevertheless, under conditions of average rainfall and over the whole area used by migratory herbivores, it is unlikely that average consumption rates much exceed those estimated for Nairobi National Park (Deshmukh 1986 and unpublished data).

No account of below ground production was taken in this study. Root production has been largely ignored in African savannas, even though available data indicate that below ground production may be higher than that above ground (Menaut & Cesar 1979; Strugnell & Pigott 1978). Underground organs are likely to be of great significance in areas subject to frequent fires and heavy grazing. An assessment of root production is essential to an understanding of production ecology and of resilience in African savannas and warrants further study.

Nairobi National Park is maintained as a protected area primarily for its populations of large mammals. Clearly, an understanding of production processes of grasses can enhance management capabilities. For example, the continued dominance of *T. triandra* is related to the frequency of fire (see above). Figure 1 and Tables 1 and 2 suggest that *S. pheloides* may be increasing and *T. triandra* decreasing in abundance, in the absence of a fire since 1978. Since *T. triandra* is both more productive and more palatable (Edwards & Bogdan 1951), occasional burning should improve grazing resources. This conclusion is reinforced by the presence of a large accumulation of dead grass of low nutritive value at the grazing intensities observed. Unless this grass is burned, decomposition and nutrient cycling are very slow (see Deshmukh 1985).

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