BIOMASS PRODUCTION AND NUTRIENT STATUS OF THREE TROPICAL RANGE GRASS SPECIES

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ABSTRACT: Three range grass species namely, Chrysopogon plumulosus Hochst, Bothriochloa radicans (Lehm.) A. Camus and Ischaemum afrum (J.F. Gemel.) Dandy were studied at Illala-sala grassland plain in Awash National Park, Ethiopia to asses their nutrient status and productivity. Annual and seasonal biomass production of these grasses, seasonal effects on grass moisture content and on accumulation of N, P, K and Na were studied. Seasonal and annual biomass production was estimated from four 6 x 6 m fenced quadrates. The grass stand was mowed, at the beginning of the study, to a height of two cm. The biomass production showed marked seasonal variation following rainfall. Peak biomass was obtained during the wet periods. April-June and July-September. It ranged from 116 g m⁻² for *B. radicans* to 409 g m⁻² for *I. afrum* stands. There was very little growth in the dry period (October-December). The annual biomass production ranged from 397 to 792 g m⁻² for B. radicans and mixed species stands, respectively. The biomass production of B. radicans stands were significantly lower than I. afrum and the mixed species stands. Significant seasonal changes in the amount of moisture and nutrient (N, P, and K) content were observed in relation to the amount of rainfall. The moisture and N, P and K content of all the three species decreased with the dry season. The crude protein content of the grasses fell below the maintenance level required for ruminants during dry periods, indicating that herbivore populations may be limited by shortage of nutritionally adequate food during the dry season. The relative importance of each species as pasture is discussed.

Key words/phrases: Awash National park, biomass production, Bothriochloa radicans, Chrysopogon plumulosus, Ischaemum afrum

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INTRODUCTION

Awash National Park (ANP), which is one of several national parks in Ethiopia, was known for its high population of grazers. However, the populations of grazers, such as oryx [Oryx gazella (Linn. 1758)], soemmering's gazelle [Gazelle soemmerringi (Cretzschmar 1882)] and swavne's hartebeest [Alcelaphus buselaphus swayni (Pallas 1766)] have been declining (Schloeder and Jacobs, 1993). Several factors such as poaching, predation, interference by pastoralists and town people, competition with livestock for grazing land and changes in quality and quantity of forage may have contributed to the decline or disappearance of these grazers. The contribution of some of these factors to the decline of the grazer populations has been considered in the management plans of the Park (Schloeder and Jacobs, 1993) and in numerous reports of park wardens. However, the ecology of forage species of the Park vis-a-vis the requirements of the grazers has never been studied. Nor has there been a quantitative assessment of the overall potential of the area to support wildlife. There is little quantitative information concerning the seasonal and spatial variation in plant biomass and nutritive quality of east African grasslands (Boutton et al., 1988a). In tropical African grasslands in general, there have been few studies of primary production and there is a lack of quantitative information on the contribution of individual species to the primary production (Kinyamario and Imbamba, 1992). Likewise, for grasslands of ANP in particular, the quality and quantity of forage, the nutrient status and productivity of the major range grasses are among the least known ecological aspects.

The value of a pasture is largely determined by three factors: the quantity (biomass production), the energy and the protein content of forage that are eaten by herbivores (Soneji and Musangi, 1972; Boudet, 1975; Field, 1976). However, the most critical limiting factor for herbivores is the nitrogen (crude protein) content of the forages available in the area (Boudet, 1975; Field, 1976; Prins and Beekman, 1989). Nitrogen is the best indicator for explaining the palatability of forage (Eadie, 1970). There are reports that grazers show preference for those plants which have the highest crude protein value (Von Richter and Osterberg, 1977). The crude protein value can be estimated from the percent nitrogen content. Other good indicators of the nutritional quality of

forages include phosphorus, low crude fibre content and high moisture content (Heady and Child, 1994; Ben-Shahar, 1994).

Proper management of an area that is primarily maintained for its populations of large herbivores, presupposes knowledge on the availability of resources for grazing (Ridder et al., 1982). Thus, biomass production is considered as an important ecological characteristic as it reflects the significance of grass species in a plant community. Determination of biomass production of different species is a pre-requisite to identify the ecologically important grass species of the area (Theunissen, 1995). Therefore, a study on total biomass production of an area will give information on the carrying capacity of the area since grazing animals adjust their densities in relation to grassland productivity (McNaughton, 1985). In general, both chemical composition and quantitative yield of forages are important determinants of grassland production (Soneji and Musangi, 1972). Since diet selection by large herbivores is aimed at obtaining maximum quality and adequate quantity (Senft et al., 1987), it is important to understand the potential of an area to support grazers. Ben-Shahar (1994) suggested that differences in nutrient levels among the available species in different seasons can be used to indicate nutritious forage species particularly at the peak of the dry season. Thus, acquiring quantitative data on the nutrient status of the dominant grass species of a wildlife concentration area, its variation in different seasons as well as on overall productivity of the area is an essential requirement for a proper assessment of the suitability and capacity of an area to support grazers (Tolsma et al., 1987). The present study stems from this understanding. The study aims to characterize the biomass production and nutrient levels of the three major grass species of ANP (Schloeder and Jacobs, 1993) namely Bothriochloa radicans (Lehm) A. Camus, Chrysopogon plumulosus Hochst, and Ischaemum afrum (J.F.Gmel.) Dandy under field condition during the wet and dry seasons.

DESCRIPTION OF THE STUDY AREA

Location

The study was conducted at Awash National Park (ANP) which is located within the Ethiopian Rift Valley between latitudes 8° 45' N and 9° 15' N and longitudes 39° 45' E and 40° 5' E. ANP covers approximately 756 km² and its altitude ranges between 970 and 2000 m. The study was conducted at Illala-sala grassland plain which is north of the Addis Ababa-Assab road, approximately 13 km from the Headquarters and 3 km from the main entrance gate of the Park.

Climate

The climate of ANP may be characterized as semi-arid. The annual rainfall ranges between 400 and 700 mm (Daniel Gamachu, 1977). Rainfall is bimodal with two distinct seasons: the small rains which usually begins in February and extends to the end of April and the big rains which extends from July to September. Since the area is located within the Inter-Tropical Convergence Zone, there is both temporal and spatial variability in rainfall, humidity and temperatures (Daniel Gamachu, 1977). Data collected at Park Headquarters between 1966 and 1993 show that the mean annual rainfall is 555 mm. The least rainfall occurs during October, November and December and the maximum rain falls during the months of July and August. There is only one distinct dry season in which there is usually no or low rainfall recordings. This extends from late October to January. The lowest monthly day time and night time temperatures occur during October - January and the highest of either of these temperatures occur during May and June. The mean maximum temperatures vary from 36.6° C in June to 29.1° C in November and the mean minimum temperature from 21.1° C to 13.3° C in November.

MATERIALS AND METHODS

Description of the study grasses

The study was conducted on three tropical grasses: Chrysopogon plumulosus, Bothriochloa radicans and Ischaemum afrum during the period from January 1996 to January 1997.

Chrysopogon plumulosus is a loosely tufted perennial grass that grows from a short stout rootstock. Culms are numerous, thin but hard, branching and bushy above the base and form loose clumps. The plants do not form dense stands but

rather grow scattered by leaving a considerable space between the tufts. C. *plumulosus* is an important drought resistant perennial grass which is readily grazed by all kinds of stock (Bogdan, 1977). It grows on stony or black clay soils in semi-desert grassland areas and open Acacia bushlands at an altitude ranging from 400 to 1600 m.

Bothriochloa radicans is a perennial grass which forms loose tussocks of 25 to 100 cm high which are much branched with dense leafy above ground parts. The plant grows on various soils but mainly on dark volcanic or black soils in grasslands or in thin bush. *B. radicans* is distributed in various regions of Ethiopia and other African countries at an altitude ranging from 600 to 1900 m. It is liked by cattle and has according to Bogdan (1977) high nutritive value.

Ischaemum afrum is a tufted perennial with rhizomes, branched stem up to 1.5 m high. The grass is found distributed in dry Acacia bushland or savanna region of Ethiopia and other African countries on clay soils at an altitude ranging from 600 to 1500 m. This grass is grazed when it is young and its crude fibre content is also high even in young leaves (Bogdan, 1977).

Experimental design to estimate seasonal and annual biomass production

Above ground seasonal and annual biomass production of the grass species was estimated according to Singh and Yadava (1974). At the beginning of the study, four 6 m x 6 m quadrates were established and fenced at Illala-sala grassland to exclude large grazers. Each of the three quadrates were established systematically in such away that only pure stands of the individual grass species were included whereas the fourth quadrat was established in such a way that it included mixed stands of the three grass species. Each quadrat was divided into 36 sub-quadrates (plots) of 50 cm x 50 cm which were numbered.

At the beginning of the study all the grass in the quadrates was mowed up to 2 cm level above the ground. Portions of the sub-quadrates were mowed at three months interval to estimate the seasonal and annual biomass production of the grass species. On each sampling occasion, nine subquadrates were randomly selected from each quadrat and mowed at 2 cm level from the ground.

Sampling was done such that it allowed a three, six, nine and twelve months of growth for each species. Mowing was performed manually with the help of sharp sickles. The harvested grass from each plot was packed in plastic bags and brought to the laboratory separately. The samples were then dried in an oven at 80° C for 48 hours and the dry weight was determined.

Determination of seasonal variation in moisture content and nutrient levels of grass species

The seasonal variation in moisture content was determined from samples collected for estimation of biomass production. Nutrient levels of the three grass species were investigated by taking about 500 g above ground parts for each of the three species from good grass stands outside the quadrates at Illala-sala plain. Samples were collected in six replicates per species at three months interval starting from April 1996 to January 1997. Samples were wrapped tightly in a plastic bag to avoid moisture loss. The samples were weighed in the laboratory before opening the bags and the fresh weight was recorded after subtracting the weight of the plastic bag. The samples were dried in an oven at 80° C for 48 hours and weighed again. Percent plant moisture content was then calculated as the difference between the fresh and dry weights.

The levels of the important minerals in the plant samples such as N, P, K, and Na were determined following Yerima (1992).

Physical and chemical characteristics of soil samples

The soil found at the Illala-sala plain at depth of 0-300 cm has been identified as *Eutric Histosol* – based on an FAO survey (FAO, 1965 cited in Schloeder and Jacobs, 1993). Soil samples were collected from the study area to determine physical characteristics and content of important nutrients. The texture of the soil samples and pH were determined following Juo (1978). Bulk density and soil porosity were determined following Wilde *et al.* (1979). Total nitrogen was determined following the microkjeldahal method. Available phosphorus was determined following Bray No. 2 method (Olsen and Sommers, 1982; Tamirie Hawando *et al.*, 1986). Soil exchangeable potassium and sodium were determined using flame-photometry following Juo (1978). Organic carbon of the soil was determined following the Walkley and Black wet oxidation method (Chopra and Kanwar, 1976). CEC was determined by measuring the total equilibrating the charge of the exchanger by neutral sodium acetate following Juo (1978).

Statistical analysis

Data were analyzed using the MINITAB statistical package version 10. Variance analysis (one way ANOVA) using Tukey's Family Error Rate was used to test for significant differences among the biomass and nutrient data sets.

RESULTS

Annual and seasonal biomass production

The annual biomass production of the three species and the mixed stands, estimated after removing the biomass produced before January 1996 and allowing all the stands to grow for 12 months, is shown in Fig. 1a. It ranged from 396.7 ± 108.6 g m⁻² for *B. radicans* stands to 791.8 ± 189.8 g m⁻² for mixed species stands. The annual biomass production of *B. radicans* stands was significantly lower than that of *I. afrum* and the mixed species stand.

The seasonal variation in above ground biomass production of the grasses is shown in Fig. 1b. Maximum values of biomass (within a growth period of three months) were obtained during the period from April to June and July to September. In the period from April to June, it ranged from 180 ± 35.4 g m⁻² for *C. plumuloses* to 408.7 ± 92.2 g m⁻² for *I. afrum* stands. A second but much smaller peak biomass was accumulated during the period from January to March which corresponds to the small amount of rainfall during the period. However, the biomass produced during the period from October to December, the typical dry period of the year, was very little.



Period of the year

Fig. 1. Annual (a) and seasonal (b) biomass production of the three grass species. (Cp, C. plumulosus; Ia, I. afrum; Br, B. radicans and Mx, Mixed).

× 11

The increase in biomass production of the grasses from all the four types of stands at different growth intervals (*i.e.*, after 3, 6, 9 and 12 months of growth) is shown in Fig. 2. The biomass produced with three, six and nine months growth intervals were significantly different (p < 0.05) from each other but the biomass produced after 12 months growth was not significantly different from the biomass produced after nine months growth for all the stands. Biomass value after 12 months growth was slightly lower than the biomass obtained after 9 months growth for all the stands due to defoliation.



Fig. 2. Biomass production of the three grass species and the mixed stands in different growing intervals. The values were obtained after allowing the stands to grow for three (January-March), six (January-June), nine (January-September) and 12 (January-December) months.

Moisture and nutrient content of the three grass species

The percent moisture content of the grasses decreased from April, 1996 to January, 1997 (Table 1). The highest moisture content was obtained in April after the small rains and the lowest in October and January during the beginning and the peak of the dry period, respectively (see Fig. 3). The moisture content ranged from 29.9 ± 2.2 percent in October for the mixed species stands to 79.9 ± 6.1 percent for *I. afrum* stands in April. The percent moisture content of the grasses in the three consecutive sampling periods (April, July and October) were significantly different from each other at p < 0.05. However, the moisture content of the grasses in October was not significantly different from that of January for all the stands.



Fig. 3. Monthly rainfall data for the year 1996 at ANP headquarters.

When we compare the moisture content of the different stands in the same sampling period, *I. afrum* stands had significantly higher moisture content than the other three groups of stands in April. In July *I. afrum* and *B. radicans* stands had significantly higher moisture content than that of *C. plumulosus* and the mixed stands. The mixed species stands too had significantly higher moisture content than *C. plumulosus* stands. The latter had the least moisture content in July. However, there were no significant differences in moisture content among the four stands during the dry season in October and January.

Table 1. Mean moisture (%) content of the grasses in different periods of the year $(n=9, mean \pm sd)$.

Period	C. plumolosus	B. radicans	I. afrum	Mixed
April, 1996	69.5 ± 4.1 ^{nA}	69.6 ± 3.0ªA	79.9 ± 6.1^{bA}	70.5 ± 1.6^{aA}
July, 1996	47.1 ± 4.8^{aB}	61.7 ± 3.0 ^{bB}	60.6 ± 2.1^{bB}	54.4 ± 2.8 ^{cB}
Oct., 1996	33.7 ± 5.8^{aC}	30.6 ± 5.9^{aC}	$35.3 \pm 3.8^{\text{sC}}$	29.9 ± 2.2^{aC}
Jan., 1997	$30.3 \pm 12.5^{\text{aC}}$	32.7 ± 8.9^{aC}	33.8 ± 10.0 ^{aC}	39.0 ± 15.9^{aC}

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

Significant seasonal differences in concentration of nitrogen and phosphorus occurred in all the grass species (Tables 2 and 4). Content of both nutrients in the grasses decreased with the dry season. Values ranged from 0.397 ± 0.06 to 1.106 ± 0.211 % for nitrogen and from 257.2 ± 73.0 to 1140.3 ± 327.0 ppm for phosphorus. Maximum values were recorded in April during the small rains for *B. radicans* and the minimum values in January during the peak of the dry period for *I. afrum*. When we compare the nitrogen values of the three species, which is also presented as percent crude protein content in Table 3, there was no significant difference among the species in April and October. However, *I. afrum* had significantly lower nitrogen values than that of *C.*

plumulosus (in July) and B. radicans (in January). From the mean values, I. afrum had lower % N in all the periods as compared to the other two species.

Period	C. plumulosus	B. radicans	I. afrum
April, 1996	0.964 ± 0.043 ^{aA}	1.106 ± 0.211**	0.820 ± 0.288*A
July, 1996	0.961 ± 0.250 ^{AA}	$0.912 \pm 0.122^{\text{abA}}$	$0.671 \pm 0.056^{\text{bAB}}$
Oct., 1996	0.683 ± 0.232 ^{aAB}	0.528 ± 0.052^{B}	0.497 ± 0.143 ^{•AB}
Jan., 1997	0.534 ± 0.123^{abB}	0.609 ± 0.140^{aB}	0.397 ± 0.060 ^{bB}

Table 2. Mean nitrogen content (%) of the three grass species in different periods of the year (n=6, mean \pm sd).

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

The potassium concentration of the grasses also showed significant seasonal variation (Table 5). It ranged from 2224 ± 389 ppm in January (dry period) for *I. afrum* to 9366 \pm 2929 ppm in July (wet period) for *B. radicans*, similar to the variation in nitrogen and phosphorus values. In January, the values of potassium in *C. plumulosus* and in *B. radicans* were significantly lower than in the other three periods. However, *I. afrum* had significantly higher potassium concentration in July and October than in April and January (Table 5). There were no significant differences in potassium content among the grasses in April, July and October. In January *I. afrum* had significantly lower potassium concentration than *B. radicans*.

Period	C. plumulosus	B. radicans	I. afrum
April, 1996	6.025 ± 0.269*A	6.913 ± 1.319**	5.125 ± 1.800**
July, 1996	6.006 ± 1.563 ^{AA}	5.700 ± 0.763^{abA}	$4.194 \pm 0.350^{\text{bAB}}$
Oct., 1996	4.269 ± 1.450 AB	3.300 ± 0.325 ^{aB}	3.106 ± 0.894 ^{aAB}
Jan., 1997	3.338 ± 0.769 ^{abB}	3.806 ± 0.875 ^{aB}	2.481 ± 0.375 ^{bB}

Table 3. Percent crude protein content of the three grass species in different periods of the year $(n=6, mean \pm sd)$.

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

Table 4. Phosphorus content (ppm) of the three grass species in different periods of the year (n=6, mean \pm sd).

Period	C. plumulosus	B. radicans	I. afrum
April, 1996	1069.7 ± 247.2 ^{*A}	1140.3 ± 327.0 ^{•A}	810.9 ± 278.8 ^{aA}
July, 1996	1064.0 ± 305.3 ^{AA}	619.0 ± 248.2^{bB}	624.1 ± 280.6 ^{bA}
Oct., 1996	772.7 ± 251.3 ^{*A}	892.7 ± 253.3 ^{aB}	624.4 ± 192.7 ^{*A}
Jan., 1997	363.3 ± 51.3 ^{ebB}	440.9 ± 140.23 ^{aB}	257.2 ± 73.0 ^{bB}

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

Unlike for the other mineral elements, there was very little seasonal variation in sodium content among the grass species. *C. plumulosus* and *I. afrum* had almost the same sodium content in all the four periods. But *B. radicans* had significantly higher sodium concentration in October than in April. The concentration of sodium ranged from 1091.3 ± 112.4 ppm in April for *I. afrum* to 1612.9 ± 75.7 ppm in October for *B. radicans*. However, there were no significant differences among the species in their sodium content in all the four periods of the year (Table 6).

Period	C. plumulosus	B. radicans	I. afrum
April, 1996	6732 ± 1338 ^{eA}	6169 ± 2798**	2721 ± 2559**
July, 1996	6385 ± 1653**	9366 ± 2929**	6989 ± 1670 ^{*B}
Oct., 1996	6534 ± 2094 ^{aA}	7317 ± 1141 ^{aA}	7121 ± 1811 ^{*B}
Jan., 1997	2596 ± 556 ^{6B}	$3106 \pm 304^{\text{aB}}$	2224 ± 389 ^{bA}

Table 5. Potassium content (ppm) of the three grass species in different periods of the year (n=6, mean \pm sd).

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

Table 6. Sodium content (ppm) of the three grass species in different periods of the year (n=6, mean \pm sd).

Period	C. plumulosus	B. radicans	I. afrum
April, 1996	1288.7 ± 216.7 ^{aA}	1175.9 ± 124.5 ^a	1091.3 ± 112.4^{aA}
July, 1996	1175.9 ± 422.6 ^{aA}	1316.9 ± 306.1 ^{*AB}	1175.9 ± 376.1 ^{aA}
Oct., 1996	1471.9 ± 115.6 ^{aA}	1612.9 ± 75.7 ^{aB}	1443.7 ± 278.0 [‡]
Jan., 1997	1429.6 ± 98.6^{aA}	1463.5 ± 158.8^{aAB}	1373.3 ± 124.5 ^{aA}

Means followed by the same lower case letter in rows and means followed by the same upper case letter in columns are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

For the purposes of comparison, the physical and chemical characteristics of the soil of the study area and the seasonal soil moisture content are shown in Table 7 and 8, respectively.

Table 7.	Physic	al and	l chemica	ıl charac	teristics	of soil	of Illal	a-sala	grassla	ind plai	n (n=1	2, meau	n±sd	
	Te	xture (%) Po	re space	Density	;				:			;	;
Depth	Sand	Clay	Silt	(%)	(g cm ⁻)	Нq	B	CEC	c (%)	N (%)	C/N	(mqq)	(ppm)	(ppm)
0–3cm	33.1° ±4.6	31.8° ±6.6	• 36.2 [•] i ±3.3	54.8 ±2.0	1.20 ±0.05	7.97 [•] ±0.25	0.78ª ±0.03	58.8" ±3.74	1.86ª ±0.45	0.188" ±0.061	10.33⁴ ±2.49	87.3ª ±61.52	60.2* ±6.76	4.96ª ±2.00
25-30cm	18.7 ⁵ ±4.1	56.3 ⁵ ±5.6	° 25.6⁵ i ±3.5	1 1	1 1	8.45 ^b ±0.22	1.35 ^b ±0.59	57.9* ±6.62	1.10 ^b ±0.15	0.121 ^b ±0.024	9.45⁼ ±2.56	32.26 ^b ±17.88	37.52⁵ ±3.27	80.03⁵ ±50.41
Means fol	lowed by	y the s	ame letter	in column	is are not	significa	ntly diff	ferent at	t p<0.0	J5.				
Table 8.	Season	al mo	isture con	ntent of	the soil a	at Illals	t-sala g	rasslar	nd plai	, u				
								Mois	sture (5	(%				{
				April	, 1996	Ju	ly, 199	6	Octobe	sr, 1996		January	, 1997	
Surface	(0–3 cr	(1		18.	27ªA	~	24.03ªA		11.	STEA		7.6	٧q	

Means followed by the same lower case letters in rows and means followed by the same upper case letters in columns for the two depths under each species are not significantly different at p < 0.05 as determined by Tukey's, Family Error Rate.

13.36^{bB}

16.2^{bB}

17.26^{bB}

23.73*^A

Depth (25-30 cm)

DISCUSSION

The annual grass biomass production at Illala-sala plain ranged from 404 ± 175 g m⁻² (B. radicans) to 838 \pm 228 g m⁻² (mixed stands). This range is within those reported by Strugnell and Pigott (1978), 500-700 g m⁻² from grasslands of Rwenzori National Park in the western Rift Valley of Uganda and higher than the value obtained by Boutton et al. (1988b) which ranged from 368-466 g m⁻² from Masai Mara Game Reserve in Kenya. In this study, significant seasonal variation in biomass production was recorded. All the stands showed high production peak during the rainy seasons and the lowest during the dry season (Fig. 1b). Many investigators have attempted to relate range production to rainfall, either on a seasonal or on annual basis (Boutton et al., 1988b; Le Houerou et al., 1988; Prins and Beekman, 1989; Kinyamario and Imbamba, 1992). In grasslands of Uganda, which are dominated by Hyparrhenia filipendula and Themeda triandra, Strugnell and Pigott (1978) reported that monthly biomass production and protein content of grasses were significantly correlated with rainfall. Boutton et al. (1988b) and Kinyamario and Imbamba (1992) also found peak values for live biomass at Nairobi National Park at the end of the long rains. They obtained strong correlation between biomass and rainfall and between biomass and soil moisture.

The quantity of forage is determined not only by climatic factors but also by edaphic factors such as texture, pH and fertility (Clayton and Renvoize, 1986; Agboola, 1987). Thus, the chemical and physical characteristics of the soil of a study area play an important role. As shown in Table 7, the bulk density of the soil of the study area is low $(1.20 \pm 0.05 \text{ g cm}^{-3})$. This indicates the suitability of the soil for good root growth and water penetration. Root growth and water penetration is slowed significantly by soils having bulk density of 1.5 – 1.6 g cm⁻³ and root growth is generally stopped by soil layers having bulk densities of $1.7 - 1.9 \text{ g cm}^{-3}$ (Thompson and Troeh, 1978; Wilde, 1993). According to Wilde (1993), such low bulk density could be due to higher pore space between the granules. Also, low bulk density may indicate low grazing intensity on the area (Zerihun Woldu, 1985; Heady and Child, 1994), as compaction increases the bulk density of soil thereby decreasing production (Agboola, 1987).

The textural classes of the soils at the surface at Illala-sala belonged to loam and clayloam, while the clay content increased at depth. Such type of soils have sufficient water-holding capacity and a high supply of nutrients for the growth of plants (Wilde *et al.*, 1979), since clay fraction has the capacity to store water and plant nutrients (Thompson and Troeh, 1978).

The pH of the soil is one of the most indicative measurements of the chemical properties of a soil as it indicates the relative availability of plant nutrients (McLean, 1982; Moore and Chapman, 1986). The soil pH of Illala-sala grassland $(7.9\pm0.3 - 8.4\pm0.2)$ is within the maximum availability range for most nutrients (N, P, Ca and Mg) except for K which is not readily available at pH ranging between 7.6 and 8.4 (Thompson and Troeh, 1978). Total nitrogen in all soils falls within the required range for most plant growth (Murphy, 1959). Likewise, the available phosphorus content both at surface and at depth was above the required concentration for plant growth (above 20 ppm) and plants grown on such soils do not usually show phosphorus deficiency (Murphy, 1959; Olsen and Sommers, 1982; Tamirie Hawando et al., 1986). Exchangeable potassium both in soil samples at surface and at depth was in the range described as low concentration for plant growth (Thompson and Troch, 1978). However, the values were not below the critical limit for potassium (0.13 meq/100 g soil) (Singh, 1987). From the foregoing observation, it may be concluded that, the productivity of Illala-sala grassland is limited neither by low concentration of soil nutrients nor by the physical properties of the soil but rather by the low amount of rainfall.

Grazers generally show preferences for the plants with the highest crude protein value (Von Richter and Osterberg, 1977). Thus, it is important to compare the nutrient (crude protein) and moisture content of these three grass species in different periods of the year to rate their qualitative importance for grazers. The present study showed significant seasonal fluctuations in the concentrations of most nutrients, except for sodium, among all the grass species (Tables 2–6). These changes appeared to be directly related to the seasonal moisture content of the grasses and thereby to the seasonal variation of rainfall of the area. Moisture contents, crude protein, phosphorus and potassium contents of the grasses decreased from April to January.

The highest levels of nitrogen, phosphorus and potassium in the grasses were obtained in April after the short rain period because the grass sampled during April had recently been produced and did not have large proportion of stems to leaves. However, the percentage concentration of these nutrients dropped in October and January when the grass became fully mature and accumulated the highest biomass. This shows that the three grass species are best suited for the game animals at the beginning of the growing season (wet periods) while the grass is still wet and has high nutritive value. The animals utilize very little of these grasses during the dry periods when the grasses are tall, coarse and low in moisture and nutrient content (Afolayan and Fafunsho, 1978).

The crude protein content of the two grass species: C. plumulosus and B. radicans in wet periods of the year (April and July) (Table 3) was above the maintenance levels of crude protein content of forages required by ruminants, i.e., 5% crude protein (Von Richter and Osterberg, 1977; Boutton et al., 1988a). However, that of I. afrum was below the level except in April. The crude protein content of the grass species was below the maintenance levels in samples collected in the dry periods (October and January). Likewise, McNaughton (1979) and Prins and Beekman (1989) reported that during the post rainy season, the quality of the grasses they studied fell below the maintenance level for the grazers. Our results indicate that grazers in ANP experience seasonal shortage of nutritionally adequate fodder (Hesla et al., 1985; Boutton et al., 1988a). They may overcome the problem of low levels of nutrients in the grasses during dry periods partly by diversifying their food intake. Otherwise, they will be obliged to feed upon these lower quality foods in quantity in order to supplement their diet with specific essential nutrients (Ben-Shahar, 1994). There are reports that during dry periods large generalist herbivores adapt to using foods which are abundantly available but low in nutritional value (Westoby, 1974). However, Illala-sala grassland plain is dominated by perennial grasses and part of the vegetative biomass of these perennials is always alive. Thus, the grassland can still provide forage of limited quality even at the peak of the dry season for herbivores though their activity could be limited (Ridder et al., 1982).

Afolayan and Fafunsho (1978) reported that the highest percentage of the grass species were grazed in periods when their crude protein content were highest

whereas little grazing took place in periods when the percentage crude protein contents of the grasses dropped. Thus, during these dry periods they recommended that any management practice that totally remove trees, shrubs and herbs in favour of grass should be avoided. This management practice is important since during dry periods, when the grass is completely dry and low in nutritive values, herbivores need to supplement their grazing with browse plants until the beginning of the next growing season.

From anecdotal observation on the area, it can be said that Illala-sala has good grass cover all year round (except when there is fire), due to also low intensity of grazing. The latter is indicated by the low bulk density of the soil (Heady and Child, 1994). In some areas of the grassland large quantities of dead grass are accumulated due to lower herbivore pressure. Also it is observed that oryx and sommering's gazelle ignore areas with large accumulation of standing dead grass. Instead they concentrate on areas which have been burnt recently and with young sprouts. Because burning removes the nutritionally poor forages and stimulates growth of fresh palatable forage it benefits herbivores (Edroma, 1981). Thus, areas with large accumulation of dead tissue are poor quality habitat for grazing animals (Boutton *et al.*, 1988a) and carefully managed burning need to be considered.

CONCLUSION

The study showed that the productivity of Illala-sala grassland plain falls on the higher range of productivity for similar ecosystems. Productivity was mainly limited by the amount of rainfall during the dry seasons. It was also found that there were significant seasonal variations in moisture and nutrient (N, P and K) contents of the three grass species. The highest values for biomass, moisture and nutrient content were obtained during the rainy seasons and these values declined during the dry periods of the year. The contribution of *B. radicans* for annual biomass production of the Illala-sala grassland plain was comparable to that of *C. plumulosus* but was lower than *I. afrum* and the stands which contained mixed species. However, although its biomass production was relatively high, the crude protein content of *I. afrum* was generally below the maintenance level required for grazers except in April after the short rains. *C.*

plumulosus and B. radicans had crude protein contents above the maintenance level during the wet periods. However, the preference of grazers for B. radicans may be reduced due to its smell as shown to be the case for some wildlife. During the dry periods these two species had crude protein values which were all below the required maintenance level. Thus, it may be concluded that grazers in Awash National Park face shortage of nutritionally adequate forage during the dry periods.

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