

Influence of tree shade on plant water status, gas exchange, and water use efficiency of *Panicum maximum* Jacq. and *Themeda triandra* Forsk. in a Kenya savanna

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Summary

A study of net CO₂ assimilation rate and water vapour exchange of *Panicum maximum* that grows predominantly beneath savanna tree canopies, and *Themeda triandra* that grows primarily in adjacent open grassland sites, was carried out on both sites in Nairobi National Park. *Panicum maximum* exhibited less water stress, had lower stomatal conductance and transpiration, and had higher water use efficiency than *T. triandra* under tree canopies. This indicated that *P. maximum* should accumulate more biomass with less water loss than *T. triandra* under tree canopies, as both grasses had similar rates of net CO₂ assimilation in the shade. More grazing selection pressure for *P. maximum* than *T. triandra* in the open grassland may also help to explain why *P. maximum* is more dominant in shaded habitats; whereas, *T. triandra* dominates open habitats.

Key words: grasses, photosynthesis, net assimilation rate

Résumé

On a mené à deux endroits du Parc National de Nairobi une étude du taux net d'assimilation de CO₂ et de l'échange de vapeur d'eau chez *Panicum maximum* qui pousse surtout sous la canopée des arbres de savane et chez *Themeda triandra* qui pousse d'abord dans les endroits ouverts qui leur sont voisins. *Panicum maximum* présente moins de stress lié à l'eau, une conductance et une transpiration stomatiques moindres et montre une utilisation de l'eau plus efficace que *T. triandra* sous la canopée. Ceci montre que *P. maximum* devait accumuler plus de biomasse, avec une perte d'eau moindre que *T. triandra* sous la canopée puisque les deux herbes présentent des taux comparables d'assimilation nette de CO₂ à l'ombre. La pression exercée par un pâturage sélectif sur *P. maximum* plus que sur *T. triandra* dans les prairies ouvertes peut aussi expliquer pourquoi *P. maximum* est plus dominant dans les zones ombragées tandis que *T. triandra* domine dans les zones ouvertes.

Introduction

African savannas are characterized by the presence of a continuous graminoid stratum and a discontinuous woody stratum that forms the upper canopy of the vegetation (Menault *et al.*, 1984). These savannas usually have alternating wet and dry seasons and often support large populations of grazers.

Interactions among trees and grasses in savannas have been studied previously by several researchers. Sarmiento (1984) noted that trees created horizontal structure above the grasses that influenced the ecological dynamics of savanna ecosystems. Downing and Marshall (1980) observed that *Panicum maximum* Jacq. occurred predominantly under savanna tree canopies, and they postulated that the distribution of *P. maximum* and *Themeda triandra* Forsk. might be controlled by grazing pressure as well as soil fertility. Bernhard-Reversat (1982) viewed trees as an important ecological component that maintained soil fertility as a result of nitrogen fixation and accumulation of organic matter through litter fall. Belsky *et al.* (1989) reported higher mineralizable nitrogen and microbial biomass in soils beneath the tree canopy than in open areas.

Reports on the influence of trees on savanna ecosystems and soil fertility are few. Grassland productivity under tree canopies has been found to be higher than in nearby open grasslands (Bernhard-Reversat, 1982; Maranga, Trlica & Smeins, 1983; Belsky *et al.*, 1989). Other researchers have found the opposite trend and associated it with competition for water, light, and nutrients between trees and grasses (Grossman *et al.*, 1980; Dye and Spear, 1982).

Trees have been observed to create micro-environments that improved water status of plants growing beneath their canopies (Maranga *et al.*, 1983; Belsky *et al.*, 1989). This may have resulted in the occurrence of different grass species in the shade of the tree canopy and in open grassland areas (Ellis, Vogel & Fuls, 1980; Maranga *et al.*, 1983; Belsky *et al.*, 1989). Less precipitation is received beneath tree canopies in semi-arid savannas because of canopy interception losses, but evapotranspiration is modified by the canopy shade (Maranga *et al.*, 1983). This makes the microsites under tree canopies specialized habitats that may support a different mix of species (Ellis *et al.*, 1980). Downing & Marshall (1980), Maranga *et al.* (1983), and Belsky *et al.* (1989) found that *P. maximum* was almost entirely restricted to growing underneath the canopies of woody species in African savannas.

In spite of the above observations, the ecophysiological basis of this phenomenon is not well understood. Maranga *et al.* (1983) found that *P. maximum* growing under tree canopies maintained higher plant water status and, therefore, avoided drought longer than did *Digitaria macroblephara* (Hack.) Stapf., which maintained lower plant water status. Possible differences in carbon assimilation and water use efficiencies of species beneath the tree canopies or in the open may explain changes in species composition in the shade and in open grasslands. The present study was, therefore, carried out to attempt to establish the ecophysiological basis for the distribution of *P. maximum* (dominant beneath the tree canopy zone) and *T. triandra* (dominant in the open grassland zone) in Nairobi National Park.

Study site

The study was carried out in Nairobi National Park situated about 10 km southeast of the city of Nairobi. The park covers an area of about 112 km² and lies close to the Equator (1°20'S, 36°50'E). The elevation of the area is approximately 1800 m above sea level. Soils of the area are red to brown clays derived from volcanic ash showers (Scott, 1963). The soils at the study site were red friable clays.

Table 1. Environmental conditions at the study area in Nairobi National Park during the study period

Day	Grass phenology	Cloudiness	Grazing factor	Soil-plant water status
26/11/87	Both species at 3-4 leaf stage	Partly cloudy	None noted	No water stress noted in plants
11/12/87	<i>P. maximum</i> : 4-5 leaf stage <i>T. triandra</i> : 5-9 leaf stage	Rained previous day Clear skies	None noted	No water stress noted in plants
17/12/87	<i>P. maximum</i> : early anthesis	Partly cloudy	None noted	No water stress noted in plants
22/12/87	<i>P. maximum</i> and <i>T. triandra</i> : anthesis	Clear skies	None noted	No water stress noted in plants
13/01/88	Both species: seeds developing	Partly cloudy	None noted	Soil wet; recent rains
20/01/88	<i>P. maximum</i> : seed shatter <i>T. triandra</i> : hard seed	Cloudy	Grazing noted Moderate use of <i>P. maximum</i> and light use of <i>T. triandra</i>	No water stress noted in plants
01/02/88	Both species at seed shatter	Partly cloudy	Moderate use of both species	Slight water stress: leaf rolling noted in <i>T. triandra</i>
15/02/88	Plants mature Seed maturity in both grass species	Clear skies	Moderate grazing of both species	Plants water stressed with leaf rolling more in <i>T. triandra</i>
02/03/88	All plants mature Leaf necrosis noted	Clear skies	Heavy grazing of <i>P. maximum</i>	All leaves were water stressed Leaf rolling in both grass species

The study site was located in an upland area on the western side of the park, where three large trees of *Acacia gerardii* Benth. var *gerardii* Brenan were selected for the study. The dominant elements of the vegetation consisted of interspersed trees of *A. gerardii* in the upper canopy, while *P. maximum* dominated in shaded areas beneath the trees. *Themeda triandra* dominated in the open grassland zone outside the tree canopy zone. Several other species of grasses and forbs also occurred in the community.

The climate of the area consists of two rainy seasons and two dry seasons each year. Rainfall of the area during the study period is shown in Fig. 1. Rainfall data were obtained from the nearest meteorological station at Wilson Airport, 1 km from the study site. Rainfall is generally received from March-May (long rains), and from October-December (short rains). Average rainfall is about 850 mm per year. Mean annual temperature is around 20°C, with monthly maxima and minima in the ranges of 23-28°C, and 12-14°C, respectively.

Materials and methods

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Company, U.K.) with a hand-held cuvette and an air supply unit. The analyzer was operated in the differential mode during the measurements. The analyzer was regularly calibrated using standard CO₂ gases in aerosol cans (CryoService Limited, Worcester, U.K.). A quantum sensor attached to the leaf cuvette was used to measure incident photon flux density. Sample air was provided to the analyzer from the air supply unit. The sample air was drawn from a mast extending 3 m above the grass canopy to minimize variations in ambient CO₂ concentration.

Net CO₂ assimilation rate, stomatal conductance to water vapour, and transpiration rate were calculated from simultaneous measurements of CO₂ and water vapour exchange in the leaf cuvette, using equations of von Caemmerer & Farquhar (1981), and as described by Long & Hällgren (1985). Leaf temperature was calculated using air temperature and energy balance equations of Parkinson (1985). Water use efficiency was calculated by dividing CO₂ assimilation rate by the rate of transpiration. All rates were expressed on a projected leaf area basis. Four leaves each of *P. maximum* and *T. triandra* were sampled in a horizontal position at each site on each date. Areas around three large trees of *A. gerardii* with well-spread canopies were chosen as study sites. Data were collected underneath the tree canopy (tree canopy zone) and outside the canopy (open grassland zone) for each of the two grasses. Measurements were made on four fully expanded leaves of each species, starting with *P. maximum* and *T. triandra* under the canopy of study location 1, then progressing to plants of both species in the open area at location 1. Similar data were then collected at locations 2 and 3. The distance between study sites ranged from 300 to 500 m. All data were collected between 1100 h and 1400 h on each date of sampling.

After each measurement of leaf CO₂ assimilation and water vapour exchange, the leaf was cut and its water potential determined with a portable pressure chamber (PMS Instruments, Corvallis, Oregon), with a minimum reading of -4.0 MPa. Data were collected on nine days throughout one growing season from November 1987–March 1988. Environmental conditions, grazing effects, and plant phenology were noted on each day of sampling (Table 1).

The study was designed as a randomized complete block experiment with a factorial arrangement of treatments (Steel & Torrie, 1980). The three study sites served as replications. Treatments were microsite (beneath tree canopy or open grassland), species (*P. maximum* and *T. triandra*), and time (nine sample dates). Four leaves of each species sampled at a single location on each date served as sub-samples. Analysis of variance was conducted for parameters of photon flux density, leaf temperature, leaf conductance, net CO₂ assimilation rate, transpiration rate, leaf water potential, and water use efficiency. Significant differences were accepted at $P \leq 0.05$. Separate analyses of variance were done for each parameter and for each date of sampling and for all dates throughout the growing season.

Results

Photon flux density. (PFD). Photon flux density (PFD) varied little among sites, but was significantly different ($P < 0.001$) among sampling days. It varied from about 600–1950 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the open grassland zone, and about

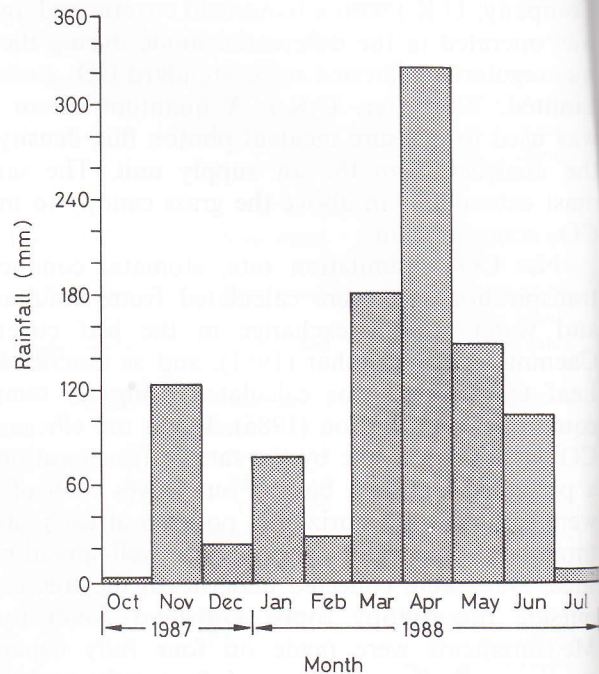


Fig. 1. Monthly precipitation during the study period at Wilson Airport adjacent to the study site.

250–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ beneath the tree canopies (Fig. 2). PFD was significantly reduced ($P < 0.001$) in the tree canopy zone to about 25% of that in the open grassland zone.

Leaf temperature. Leaf temperature for both *P. maximum* and *T. triandra* showed an increase with time in both the tree canopy microsite and in the open grassland zone (Fig. 2). However, leaf temperatures were significantly lower ($P < 0.001$) under tree canopies than in the open grassland for both grass species. Leaf temperatures under tree canopies ranged from 20.8 to 28.3°C for *P. maximum* and from 21.0 to 27.8°C for *T. triandra*. Significantly higher ($P < 0.002$) leaf temperatures were experienced by *T. triandra* than by *P. maximum* in the open grassland zone.

Leaf water potential. Leaf water potential ranged from -0.88 to < -4.00 MPa for *P. maximum*, and -1.38 to < -4.00 MPa for *T. triandra*, underneath the tree canopies (Fig. 2). In the open grassland zone, leaf water potentials ranged from -1.46 to < -4.00 MPa in *P. maximum*, and -1.48 to < -4.00 MPa in *T. triandra*. Leaf water potential declined from 17 December to 22 December in both species under tree canopies and in the open grassland zone because of limited precipitation (Fig. 1). However, there was an increase in leaf water potential between 22 December and 20 January in both species (Fig. 2). Increased rainfall during January (Fig. 1) was responsible for improved leaf water potentials. There was a sharp decrease in leaf water potential after 20 January under tree canopies and in the open grassland zone for both species, as February was a dry month and plants attained maturity.

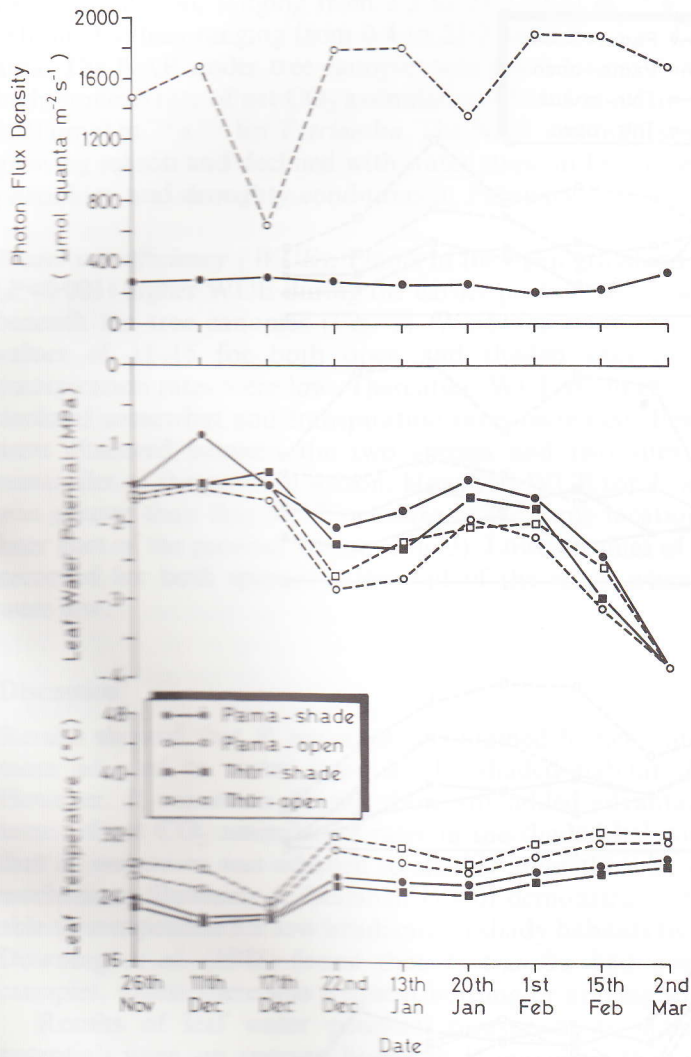


Fig. 2. Photon flux density, leaf temperature, and leaf water potential for *Panicum maximum* (Pama) and *Themeda triandra* (Thtr) in open and shaded habitats.

Stomatal conductance. There was a significant interaction ($P < 0.05$) among species, microsite, and date for leaf stomatal conductance. Conductance was greatest for *P. maximum* in the open during the early part of the growing season, but was greater for *T. triandra* in the open during the latter part of the season (Fig. 3). Conductance was often greater for *T. triandra* beneath the *Acacia* canopy than it was for *P. maximum*.

Transpiration. Transpiration rates for both grasses were greater ($P < 0.001$) in the open grassland zone than under tree canopies (Fig. 3). *Themeda triandra* exhibited the highest rates of transpiration in the open grassland zone ranging from $1.0\text{--}3.9\text{ mmol m}^{-2}\text{ s}^{-1}$, while *P. maximum* exhibited values ranging from $1.0\text{--}2.6\text{ mmol m}^{-2}\text{ s}^{-1}$. Beneath the tree canopies, *T. triandra* transpired more

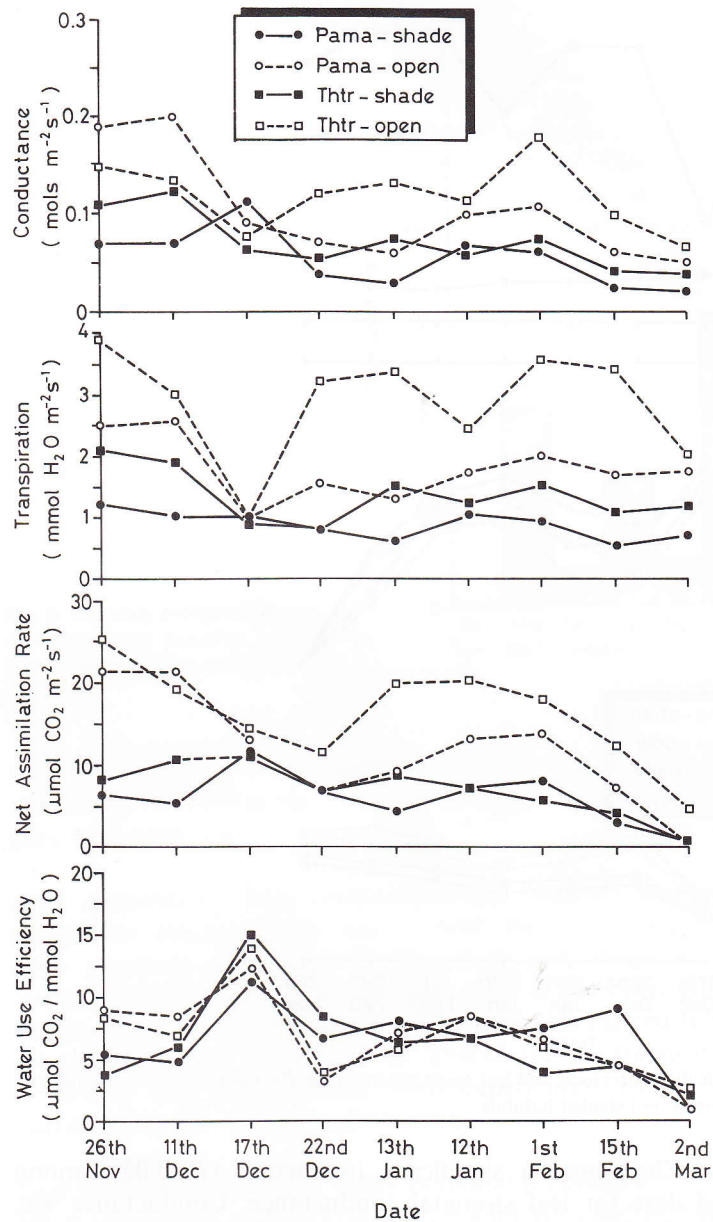


Fig. 3. Leaf conductance, transpiration, net assimilation rate, and water use efficiency for *Panicum maximum* (Pama) and *Themeda triandra* (Thtr) in open and shaded habitats.

than *P. maximum* with values in the range $0.8\text{--}2.1\text{ mmol m}^{-2}\text{ s}^{-1}$, as compared with $0.5\text{--}1.2\text{ mmol m}^{-2}\text{ s}^{-1}$ for *P. maximum*.

Net CO₂ assimilation rate (NAR). Both grasses in the open grassland zone fixed significantly more ($P < 0.001$) CO₂ than they did when growing beneath the canopy of *Acacia* trees (Fig. 3). *Themeda triandra* exhibited the highest rates of

CO₂ assimilation, ranging from 3.3 to 25.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while *P. maximum* exhibited values ranging from 0.4 to 21.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the open grassland area. The NAR under tree canopies was much lower; *P. maximum* attained the highest mean rate of net CO₂ assimilation of 11.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as compared to 10.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *T. triandra*. The NAR was highest at the beginning of the growing season and declined with water stress in December and with advancing phenology and droughty conditions in February.

Water use efficiency (WUE). Plants in the open grassland area had significantly ($P < 0.001$) higher WUE during the earlier part of the growing season than those beneath the tree canopies (Fig. 3). WUE for both species reached maximum values of 11–15 for both open and shaded sites on 17 December when transpiration rates were low. Thereafter, WUE declined as photosynthetic rates declined somewhat and transpiration rates increased. Few differences in WUE were observed between the two species and two sites during much of the remainder of the growing season. However, WUE for *P. maximum* in the shade was greater than that for *T. triandra* at the same location during much of the later part of the growing season (Fig. 3). Lowest values of WUE of 0.6–2.0 were recorded for both species at the end of the study when photosynthetic rates were low.

Discussion

Results showed that *P. maximum* maintained higher water potentials and was more adapted to water stress in the shaded habitat than was *T. triandra*. However, *P. maximum* did not show any added advantage over *T. triandra* in terms of net CO₂ assimilation rates in the shaded habitat. This would suggest that *P. maximum* was adapted to shaded areas through some other ecological mechanism. Downing & Marshall (1980) demonstrated that *P. maximum* was able to compensate for low irradiance in shady habitats by doubling its leaf area. Downing *et al.* (1978) found that *T. triandra* had poor growth under tree canopies, unless there was frequent burning or grazing to reduce shading.

Results of leaf water potential measurements indicated that leaf water potentials were, on average, higher in *P. maximum* than in *T. triandra*, both in the open and under tree canopies. This in addition to the findings that *P. maximum* maintained lower stomatal conductances and transpiration rates than *T. triandra* under tree canopies, indicated that *P. maximum* was less water stressed than *T. triandra* under tree canopies and, hence, had an added advantage over *T. triandra*. Again, lower transpiration rates in *P. maximum* beneath the tree canopies, coupled with similar rates of NAR for the two grasses in the shade, resulted in *P. maximum* having higher water use efficiency than *T. triandra* beneath tree canopies. This was especially apparent during the later part of the growing season when soil moisture became less available, as reflected in decreasing leaf water potentials with time (Fig. 2). This gave *P. maximum* an adaptive advantage over *T. triandra* under tree canopies.

It has already been noted that *P. maximum* remained less water stressed than *T. triandra*, both in the open and under the tree canopies. Therefore, *P. maximum* remained more succulent than *T. triandra* over most of the study

period, which may help explain why *P. maximum* was preferred by grazers over *T. triandra*, both in the open grassland and beneath the tree canopies (Table 1). Downing & Marshall (1980) noted that high succulence in *P. maximum* caused it to be selected by grazers over other grasses. Eventually this may result in the reduction of this grass from some open places, where it may be less adapted, and allow *T. triandra* to dominate in these open grassland areas.

P. maximum maintained slightly higher leaf temperatures under tree canopies than *T. triandra*. This probably resulted from lower stomatal conductances and transpiration rates of *P. maximum* as compared with *T. triandra* in the shade (Fig. 3). Lower transpiration rates and higher WUE found in *P. maximum* in the shade, as compared with *T. triandra*, indicates that *P. maximum* should accumulate more biomass with less water loss under tree canopies than does *T. triandra*, as they both exhibited similar rates of net CO₂ assimilation. This may also help to explain why *P. maximum* predominates under tree canopies.

Although the effects of soil nutrients were not investigated, Belsky *et al.* (1989) noted that mineralizable N, organic matter, P, K, and Ca were higher in soils beneath tree canopies of Kenya savannas than in adjacent grassland zones. Nutrient content of forages under tree canopies was, therefore, greater than forages in the open grassland zone (Belsky, 1992). Because areas beneath tree canopies have higher soil fertility than open grasslands, nutrients are less likely to reduce herbaceous production in the shaded zone (Belsky *et al.*, 1989). With higher soil organic matter under tree canopies, it would be expected that there would be improved soil water relations, which may also favour *P. maximum*.

Acknowledgments

This project was made possible through the operating funds provided by a USIS-Fulbright research grant to M. J. Trlica. We would also like to acknowledge the UNEP Bioproductivity Project for the instruments and apparatus used in this study. Technical assistance was provided by the Range Management Department, University of Nairobi. We express our appreciation to the staff of Nairobi National Park for allowing us to conduct the study there.

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(Manuscript accepted 8 December 1993)