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# Effect of tillage, clipping and climate on grass phytomass in a Zambian savanna

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**Abstract:** The effect of tillage, clipping, precipitation and temperature on above-ground grass production was investigated in permanent plots at a Zambian savanna site for 5 y (1996–2001) by the harvest method. Mean species richness was 4.6 species $m^{-2}$ with a total of 15 species at the study site. Mean end-of-season grass phytomass was 464 g $m^{-2}$ with no statistically significant differences among years in control quadrats. Grass phytomass recovered within two wet seasons after tillage and a similar trend was observed after cessation of a 2-y monthly harvesting regime. However, in experimental quadrats, plot, treatment and year had significant effects on grass production. Previous- and current-season precipitation had no significant effect on end-of-wet-season grass phytomass but phytomass of the previous season explained 27–53% of the variation in end-of-wet-season phytomass. Grass production peaked in the wet season and declined sharply as the dry season progressed. The interaction between precipitation, temperature, harvesting and duration of the dry season explained 81–91% of the variation in daily grass production but the significance of the interactions varied with season and duration of harvesting. Precipitation-use efficiency (PUE) of grasses declined from 2.25 g $m^{-2}$ $mm^{-1}$ at the start of the wet season in December to 0.25 g $m^{-2}$ $mm^{-1}$ at the end of the season in March. Monthly harvesting for 1 y reduced PUE to less than 25%. The results indicate very complex relationships between above-ground grass production (dependent variable) and climate and land-use (independent) factors that makes the prediction of grass production in central southern African savannas difficult.

**Key Words:** grass production, linear models, permanent plots, precipitation-use efficiency, temperature, Zambia

## INTRODUCTION

Grass production in savanna ecosystems is primarily determined by soil moisture and nutrients (Frost *et al*. 1986, Hopkins 1966, Menaut *et al*. 1985, Rutherford 1980, Strang 1969) but variability in herbage production has been linked to variability in annual rainfall (Dye & Walker 1987, Harrington & Johns 1990, Kelly & Walker 1976, Menaut & Cesar 1979, Prince & Astle 1986). However, the effects of rainfall on herbage production are complex (Rutherford 1978) and production may be significantly related to soil water-holding capacity, the infiltration capacity of the soil and water availability (Barnes *et al*. 1991, de Leeuw & Tothill 1993, Rutherford 1978). Most African savannas are regularly burned and it has been observed that burning increases grass production in such ecosystems (Brookman-Amissah *et al*. 1980, Frost 1985, Oguntala 1980, Strang 1974, Trapnell 1959). Elsewhere studies have shown that a significant correlation exists between previous-season and current-season grass biomass (Jobbagy & Sala 2000, Osterheld *et al*. 2001) and in some cases the interaction between previous-season climate factors account for the largest proportion in the variance in current-season grass biomass (Webb *et al*. 1978). Phenology of savanna vegetation in southern Africa is also influenced by precipitation and temperature (Chidumayo 2001) and at a regional scale, the inclusion of temperature or an index of evapotranspiration has been shown to improve the prediction of grass biomass (Webb *et al*. 1978).

One of the widespread disturbances in sub-humid savannas in Africa is conversion to shifting cultivation that involves shallow tillage and cropping for several years before abandonment. Among the Mambwe people of northern Zambia, the fallow is considered ready for recultivation when the succession stage is dominated by grasses of the genus *Hyparrhenia* (Stromgaard 1990). Apparently *Hyparrhenia*-dominated tufted grassland only develops on fallow after weed grasses, such as *Pogonarthria* and *Rhynchelytrum* have been suppressed (Strang 1974, Stromgaard 1984). However, there are conflicting reports on the speed of grassland recovery after fields have been abandoned. Some workers state that *Hyparrhenia*-dominated grass develops rapidly after abandonment (Araki 1992), while others indicate that grasses, such as *Hyparrhenia* and *Tristachya*, dominate only after more than 10 y (Stromgaard 1984). Burning when the grass is dominant can prevent the development of woody vegetation in wooded savannas and perpetuate the grassland sere (Gambiza *et al*. 2000).

Another widespread disturbance in African savannas is grazing by wildlife and livestock. The impact of grazing on grass biomass varies with the intensity of grazing. In semi-arid areas, sustained grazing may reduce grass production and increase its temporal variability (O'Connor *et al*. 2001). Overgrazing in *Brachystegia–Julbernardia* (miombo) woodland of central southern Africa can eliminate grass biomass completely within 2–3 y (Hood 1972) but the speed of recovery has not been adequately studied. Generally, repeated clipping of grass reduces subsequent production (Rutherford 1978). Improvement of savanna ecosystem management therefore requires a better understanding of grass biomass dynamics following disturbance and the role of interactions between abiotic and biotic factors in the maintenance of grass production.

Three main questions guided the present study: (1) What is the speed of grass phytomass recovery following tillage or repeated clipping? (2) How does grass production respond to precipitation, temperature and repeated clipping? (3) Is there a carry-over effect of the previous year's precipitation and/or phytomass on the current year's grass production?

In order to answer these questions, I monitored grass phytomass in permanent and temporary quadrats subjected to tillage and clipping at a Zambian savanna site that was annually burnt in mid-July. The tillage and frequent clipping treatments were aimed at simulating land preparation under shifting cultivation and grazing, respectively, the two most widespread disturbances in Zambian savannas.

## MATERIALS AND METHODS

### Study site

The study was conducted on a 1.0-ha derived grassland site (15°28′S, 28°11′E) about 15 km south of Lusaka in central Zambia. The site is relatively flat with a slope of < 1° and a relatively uniform sandy clay loam soil derived from limestone rocks. Average texture of 26 topsoil (0–30 cm depth) samples from the site was 47% sand, 34% clay and 19% silt with a pH of 5.4. Mean annual rainfall at Mt Makulu (15°33′S, 28°16′E), 13 km southeast of the study site, is 796 mm and 85% of this falls during the rainy (wet) season from December to March. During the 5-y study period annual rainfall amounted to 851 mm during 1996/97, 557 mm during 1997/98, 880 mm during 1998/99m, 970 mm during 1999/00 and 1010 mm during 2000/01. Mean monthly daily minimum and maximum temperature are 15.7 °C and 24.8 °C, respectively. The lowest and highest temperatures are experienced during May–August and September–November, respectively. The rainy season has moderate temperatures.

The study site was previously a wooded savanna grassland with *Acacia polyacantha* Willd., *A. sieberana* DC. and *Bauhinia* (*Piliostigma*) *thonningi* Schumacher trees forming the dominant component of the tree stratum. Most of the trees were cut for charcoal production between 1990 and 1994, thereby converting the site into a grassland dominated by grasses of the tribes Andropogoneae and Arundinelleae. The area is burned annually in July, the middle of the dry season. The site was fenced off in 1995, prior to the present study, to exclude large herbivores such as cattle and goats.

### Methods

Three permanent plots, each with nine pairs of 1 × 1-m quadrats (Figure 1), were established at the study site in November 1996. Plots were located at least 5 m from shrubs and coppice to avoid the possible effect of shading on grass production (Barnes 1965, Knoop & Walker 1985, Prince & Astle 1986, Strang 1974, Ward & Cleghorn 1970) and each plot was 15–20 m from the other plots. The 1 × 1-m quadrat was used because this is a common quadrat size used in the study of herbaceous vegetation (White 1985). Within each plot there were 8 and 10 permanent and temporary quadrats, respectively. Permanent quadrats A2 and B3 (Figure 1) were tilled with a hoe to a depth of 10–15 cm in November 1996 to simulate tillage under shifting cultivation (Stromgaard 1990) and all the grass tufts and noticeable roots removed and grass regrowth harvested annually in March. In the remaining six

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **B1**<br>**11/97** | **B2**<br>**11/96** | **B3**<br>**11/96** | **B4**<br>**03/98** | **B5**<br>**03/98** | **B6**<br>**11/98** | **B7**<br>**03/99** | **B8**<br>**03/00** | **B9**<br>**03/01** |
| **A1**<br>**11/97** | **A2**<br>**11/96** | **A3**<br>**11/96** | **A4**<br>**03/97** | **A5**<br>**11/98** | **A6**<br>**03/99** | **A7**<br>**03/99** | **A8**<br>**03/00** | **A9**<br>**03/01** |

**Figure 1.** Layout of sample quadrats (A1–A9 and B1–B9) in a 9 × 2-m permanent plot at the study site and time (month/year) when sampling in each quadrat was initiated: permanent quadrats harvested monthly for 1 (A3, A5 and B2) and 2 (A1 and B1) y, tilled permanent quadrats (A2 and B3) and temporary (control) quadrats harvested once in March (A4, A6–A9, B4 and B7–B9).

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permanent quadrats in each plot, the grass was harvested monthly at 4-wk intervals for 1 y in quadrats A3, A5, B2 and B6 and for 2 y in quadrats A1 and B1 (see Figure 1) after which harvesting was done annually in March. The first harvest was made in November 1996 in quadrats A3 and B1, in November 1997 in quadrats A1 and B1 and in November 1998 in quadrats A5 and B6. The monthly harvesting treatment was intended to simulate overgrazing. Although this treatment appears too severe to be realistic, livestock grazing in savannas of central Africa often involves local shifts between continuous grazing on upland areas during the wet season and continuous grazing of wetlands, lower down on the catena (Scoones 1991). Usually cattle are moved from the upland grazing areas during the dry season because of lack of grass regrowth after depletion due to overgrazing (Hood 1972). Furthermore, because of increasing human population pressure, the upland grazing land is declining annually due to extension of cultivation. As a result, it is not uncommon to find livestock restricted to grazing continuously in wetlands throughout the year (Ingram 1991). This has resulted in serious overgrazing and soil erosion in Malawi, Zambia, Zimbabwe and parts of Tanzania (Acres *et al*. 1985). It was therefore decided that monthly harvesting of quadrats for 1–2 y might be the best treatment for approximating continuous grazing as observed in some central southern Africa savannas. All the 10 temporary quadrats in each plot, which were used as controls, were harvested once in March in 1997 (A4), 1998 (B4 and B5), 1999 (A6, A7 and B7), 2000 (A8 and B8) and 2001 (A9 and B9).

In order to determine the pattern of flowering during the wet season, flowering grass stalks were harvested monthly in quadrats A1–A3, A5–A6, B1–B4 and B6 during the 1999/2000 season before the rest of the standing phytomass was harvested in March 2000.

Grass phytomass was harvested by clipping the grass at about 2.5 cm above ground with a cutter. For each species, clipped grass phytomass in each quadrat was separated into live (green) and dead (brown) and any soil removed from the phytomass before weighing to the nearest gram in polythene bags of known mass. The separation by species was not possible for quadrats that were harvested monthly because non-flowering grasses were difficult to identify. If the phytomass weighed > 50 g, a subsample of 50 g was retained for oven drying. If the phytomass was ≤ 50 g, the whole phytomass was retained for oven drying. During the first year of study, the phytomass was weighed after 24, 48 and 72 h of oven drying at 80 °C. Because no further loss in weight was observed after drying for 48 h during this initial period, all samples were subsequently oven dried for 48 h. The mean oven-dry/field weight factor was used for converting the field phytomass measurements to dry weight mass at each harvest.

The major edge effect in perennial tussock grassland, such as the one at the study site, is in-growth into the quadrats of tussocks at the margin. In order to minimize this edge effect, a 40-cm-wide perimeter around each plot was cleared with a hoe in December of each year.

## Data analysis

The significance of variations in end-of-wet-season grass production due to plots and treatment (i.e. tillage and monthly harvesting) was determined by analysis of variance (ANOVA). Annual grass production was estimated as the harvested standing phytomass at the end of the wet season in March (Deshmukh 1984). For quadrats that were harvested monthly, annual grass production was estimated by the sum of all phytomass harvested monthly from April to March. Dry- and wet-season grass production was estimated by summing all monthly harvests from April to November and from December to March, respectively. Mean daily grass production was calculated by dividing monthly harvested phytomass by the inter-harvest interval in days.

To determine correlation of grass production (i.e. end-of-wet-season phytomass and daily production) with independent variables, the data were subjected to regression analysis; initially by the Best Subset Regression technique in order to isolate independent variables that explained a significant proportion of the variance in biomass production and later by linear regression analysis (Analytical Software 2000). For the end-of-wet-season phytomass, the relationship with the following independent variables was analysed: (1) previous-wet-season phytomass (PSB); (2) current-season precipitation (CSP); and (3) previous-wet-season precipitation (PSP). Previous-season phytomass, CSP and PSP have all been shown to affect current-season production in grassland communities (Jobbagy & Sala 2000, O'Connor *et al*. 2001, Osterheld *et al*. 2001, Webb *et al*. 1978). For daily biomass production the relationship with the following independent variables was analysed: (1) mean daily precipitation since last harvest (MDP); (2) mean daily minimum temperature since last harvest ($T_{min}$); (3) mean daily maximum temperature since last harvest ($T_{max}$); (4) number of monthly harvests (H); and (5) harvest month into the dry season (MDS) which ranged from April (MDS = 1) to November (MDS = 8); wet season months were assigned a MDS value of zero. Harvest month into the dry season (MDS) was used as a proxy for changes in soil moisture stress during the dry season. Precipitation and minimum and maximum temperature have all been reported to significantly affect vegetation phenology in southern Africa (Chidumayo 2001) and for this reason, these were included in the analysis. Frequent clipping has also been shown to affect subsequent grass biomass production (Rutherford 1978) and the number of times a quadrat was harvested (H) was therefore included in the analysis to assess the effect of monthly harvesting on grass production. Climate variables were based on data from Mt Makulu weather station, 13 km south-west of the study site. The number of independent variables included in the best subset regression analysis was constrained by sample size and during the analysis independent variables that were highly correlated (collinearity) were automatically dropped from the analysis (Analytical Software 2000).

## RESULTS

### Species richness and flowering pattern

Fifteen species of grass were recorded in sample quadrats at the study site with a mean (± 1 SE) of 4.6 ± 0.10 species $m^{-2}$. The range of species per quadrat was 2–8 with 92% of the quadrats having 3–6 species. Dominant species (with > 10% of total phytomass in at least one quadrat) were *Hyparrhenia* spp. (mainly *H. dissoluta* (Steud.) C. E. Hubbard and occasionally *H. rufa* Stapf and *H. variabilis* Stapf), *Loudetia simplex* (Nees) C. E. Hubbard, *Tristachya superba* Schweinf. & Asch., *Themeda triandra* Forssk. and *Brachiaria brizantha* Stapf. All these species are tufted perennial grasses although *B. brizantha* is also annual (Hood 1967). These dominant grasses flowered from January to March. During the 1999/2000 wet season the phytomass of flowering tillers ranged from 4.5 ± 2.21 g $m^{-2}$ in January to 60.5 ± 11.38 g and 57.2 ± 6.25 g $m^{-2}$ in February and March 2000, respectively. Peak flowering therefore occurred in February and March.

### Annual and seasonal grass phytomass

Yearly variations in end-of-wet-season phytomass were not significant for control quadrats sampled in March of each year ($F_{4,13} = 0.81$, $P = 0.54$); the overall grass phytomass on these quadrats was 464 ± 23.7 g $m^{-2}$. Annual grass phytomass harvested on monthly clipped quadrats during the first year after the initial harvest was 431 ± 29.4 g $m^{-2}$ and consisted of 394 ± 26.7 g $m^{-2}$ for the wet season and 37 ± 5.1 g $m^{-2}$ for the dry season.

### Effects of tillage and monthly harvesting

Repeated-measures analysis of variance revealed that plot, tillage, year and the interaction between tillage and year had significant effects on end-of-wet-season grass phytomass (Table 1). Similar results were obtained for monthly harvested quadrats but whereas the interaction between plot and tillage did not have a significant effect on end-of-wet-season phytomass, the effect of interaction between plot and monthly harvesting had a significant effect (Table 1).

In tilled quadrats, *T. triandra* decreased and *T. superba* increased over the years as though there was a negative interaction between these species (Table 2). The contribution of other species to phytomass composition also varied among wet seasons. Phytomass during the 1997/98 season was shared equally among the species but was dominated by *Hyparrhenia* spp. during the 1998/99 season ($F_{3,20}$ = 5.13, P = 0.009) and *T. superba* during the 1999/2000 season ($F_{3,20}$ = 32.4, P < 0.0001) and 2000/01 season ($F_{3,20}$ = 3.63, P = 0.03) (Table 2). Tillage resulted in significantly lower end-of-wet-season phytomass than in control quadrats for the two consecutive wet seasons of 1996/97 and 1997/98 ($t \geqslant 3.0$, df = 7; P < 0.02), after which there were no significant differences.

End-of-wet-season phytomass in November 1997 quadrats that were subjected to monthly harvesting for 2 y, declined sharply and remained very low while under this treatment (Table 2). However, although the phytomass increased markedly during the 2000/01 wet season following cessation of monthly harvesting, it was still significantly lower than in control quadrats (t = 3.48, df = 4; P = 0.025).

**Table 1.** Results of repeated-measures analysis of variance to assess the effects of plot, treatment (i.e. tillage and monthly harvest) and year on wet season grass production at a savanna site in central Zambia.

| Quadrats/Source of variation | Degrees of freedom | F-ratio | Probability (P)) |
|---|---|---|---|
| Tilled quadrats | | | |
| Plot (A) | 2 | 5.31 | 0.0098 |
| Tillage (B) | 1 | 67.7 | < 0.0001 |
| Year (C) | 4 | 3.60 | 0.0150 |
| A × B | 2 | 0.27 | 0.765 |
| B × C | 4 | 4.77 | 0.0037 |
| Residual | 34 | | |
| Monthly harvested quadrats | | | |
| Plot (A) | 2 | 10.5 | 0.0014 |
| Monthly harvest (B) | 1 | 309 | < 0.0001 |
| Year (C) | 3 | 29.9 | < 0.0001 |
| A × B | 2 | 3.17 | 0.0713 |
| B × C | 3 | 20.3 | < 0.0001 |
| Residual | 15 | | |

### Determinants of grass production

Regression analysis revealed that precipitation, whether for current and/or previous season, explained very little of the variation in end-of-wet-season grass phytomass at the study site ($r^2 < 0.1$). Instead, previous-season phytomass (PSB) was the only single factor among all the independent variables included in the analysis that explained 27–53% of the variation in end-of-wet-season phytomass, except during the 2000/01 wet season. This is presumably because PSB and CSB are not entirely independent of each other, especially in perennial grasses that dominate at the study site.

Grass production peaked during the wet season and declined as the dry season progressed (Figure 2). How-

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**Table 2.** Annual changes in end-of-wet-season phytomass composition in November 1996 tilled quadrats. Phytomass values with different superscripts in each phytomass category among wet seasons were significantly different at $P < 0.05$.

| Treatment/ species | End-of-wet-season phytomass (mean ± 1 SE g $m^{-2}$) in March | | | | |
|---|---|---|---|---|---|
| | 1996/97 | 1997/98 | 1998/99 | 1999/00 | 2000/01 |
| Tilled quadrats | | | | | |
| *Hyparrhenia* spp. | | | | | |
| Live | 0 | 59.1 ± 35.7$^{ab}$ | 121.7 ± 40.1$^{b}$ | 47.1 ± 14.1$^{ab}$ | 88.2 ± 23.9$^{ab}$ |
| Dead | 0 | 8.5 ± 4.5 | 17.1 ± 8.6 | 12.5 ± 4.2 | 20.9 ± 3.9 |
| Total | 0 | 67.7 ± 40.2 | 138.8 ± 47.7$^{a}$ | 59.6 ± 17.5$^{b}$ | 109.1 ± 27.1$^{a}$ |
| *Loudetia simplex* | | | | | |
| Live | 0 | 8.0 ± 6.5 | 17.9 ± 14.8 | 1.7 ± 1.7 | 13.6 ± 9.4 |
| Dead | 0 | 1.7 ± 1.1 | 2.3 ± 1.7 | 0.4 ± 0.4 | 3.3 ± 2.3 |
| Total | 0 | 9.6 ± 7.6 | 20.3 ± 6.5$^{b}$ | 2.1 ± 2.1$^{c}$ | 16.9 ± 11.7$^{b}$ |
| *Themeda triandra* | | | | | |
| Live | 0 | 12.1 ± 11.9 | 3.2 ± 2.8 | 0.8 ± 0.8 | 0 |
| Dead | 0 | 1.5 ± 1.5 | 1.0 ± 1.0 | 0.6 ± 0.6 | 0 |
| Total | 0 | 13.6 ± 13.5 | 4.2 ± 3.8$^{b}$ | 1.4 ± 1.4$^{c}$ | 0$^{c}$ |
| *Tristachya superba* | | | | | |
| Live | 6.1 ± 5.4 | 41.3 ± 16.2 | 53.1 ± 13.5 | 113.6 ± 11.9 | 151.0 ± 71.4 |
| Dead | 0$^{a}$ | 7.3 ± 2.0$^{ab}$ | 13.3 ± 3.4$^{ab}$ | 36.2 ± 6.6$^{b}$ | 39.2 ± 16.5$^{b}$ |
| Total | 6.1 ± 5.4 | 48.6 ± 17.9 | 66.3 ± 16.7$^{ab}$ | 149.7 ± 7.0$^{a}$ | 190.2 ± 87.9$^{a}$ |
| Other species | | | | | |
| Live | 0 | 5.6 ± 4.6 | 32.6 ± 22.2 | 2.1 ± 2.0 | 21.6 ± 12.8 |
| Dead | 0 | 0.9 ± 0.7 | 7.8 ± 4.9 | 0.5 ± 0.5 | 6.7 ± 4.0 |
| Total | 0 | 6.4 ± 5.3 | 40.4 ± 27.1 | 2.7 ± 2.5 | 28.3 ± 16.7 |
| All species | | | | | |
| Live | 6.1 ± 5.4 | 126.1 ± 59.6$^{ab}$ | 228.5 ± 59.3$^{b}$ | 165.3 ± 10.5$^{ab}$ | 274.3 ± 72.3$^{b}$ |
| Dead | 0$^{a}$ | 19.8 ± 6.7$^{ab}$ | 41.4 ± 14.8$^{abc}$ | 50.3 ± 7.9$^{bc}$ | 70.2 ± 16.6$^{c}$ |
| Total | 6.1 ± 5.4$^{a}$ | 145.9 ± 66.2$^{ab}$ | 269.9 ± 73.3$^{b}$ | 215.5 ± 17.9$^{ab}$ | 344.5 ± 88.5$^{b}$ |
| Temporary (control) quadrats | | | | | |
| Live | 333.1 ± 39.5 | 423.4 ± 37.3 | 332.0 ± 38.2 | 436.6 ± 39.8 | 352.7 ± 33.2 |
| Dead | 83.3 ± 9.9 | 105.9 ± 9.3 | 83.0 ± 9.5 | 109.2 ± 10.0 | 88.2 ± 8.3 |
| Total | 416.4 ± 49.4 | 529.3 ± 46.6 | 415.0 ± 47.7 | 545.8 ± 49.8 | 440.9 ± 41.4 |
| Monthly harvested quadrats | | | | | |
| Live | | 377.8 ± 12.0 | 40.9 ± 7.2 | 48.4 ± 14.8 | 151.6 ± 35.1 |
| Dead | | 0 | 0 | 0 | 37.9 ± 8.8 |
| Total | | 377.8 ± 12.0 | 40.9 ± 7.2 | 48.4 ± 14.8 | 189.5 ± 43.8 |

ever, the late-dry-season trough was briefly interrupted by a small rise in production in September that may be associated with the initial rise in temperature after the cool-dry period (May–August). In all the cases analysed, variation in daily grass production was best explained by interactions between a number of independent factors (Table 3). However, in some cases single variables explained a significant proportion of the variation. MDP explained 31–65% of daily grass production on an annual and dry season basis ($P < 0.05$). MDS and H individually explained 25–66% ($P < 0.05$) of the variation in daily grass production on an annual basis. $T_{min}$ explained 66% and 36% ($P < 0.05$) of the variation in daily grass production in the 1997/98 and 1998/99 wet season, respectively, in the November 1996 and 1998 quadrats. For the November 1998 quadrats, $T_{max}$ explained 66% ($P < 0.05$) of the wet-season variation in daily grass production.

The most important factor interaction that explained 81–91% of the variation in daily grass production during the first year of monthly harvesting was between MDP, MDS and H (Table 3). However, in the second year of monthly harvesting MDP did not significantly affect daily production, perhaps because of the greater negative effects on below-ground phytomass of 12 mo of harvesting that probably impaired soil moisture and nutrient uptake with a negative feedback on leaf production. During the wet season, the interaction between MDP, $T_{min}$ and $T_{max}$ explained the largest proportion (80–97%) of the variation in daily grass production, although this interaction explained only 41% of the variation during the 1997/98 wet season that was only significant at $P = 0.10$. During the dry season, the interaction between MDS, H, $T_{max}$ and MDP explained 34–80% of the variation in daily grass production that was significant at $P < 0.0001$ (Table 3).

## Precipitation-use efficiency

Phytomass production per unit precipitation or precipitation-use efficiency (PUE) was used to assess the treatment effects on PUE during the wet season. This was calculated as:

$$\text{PUE (g m}^{-2}\text{ mm}^{-1}) = \text{monthly harvested phytomass/monthly rainfall}$$

Precipitation-use efficiency for the November 1996 quadrats showed a steady decline from 2.3 ± 0.55 g $m^{-2}$ $mm^{-1}$

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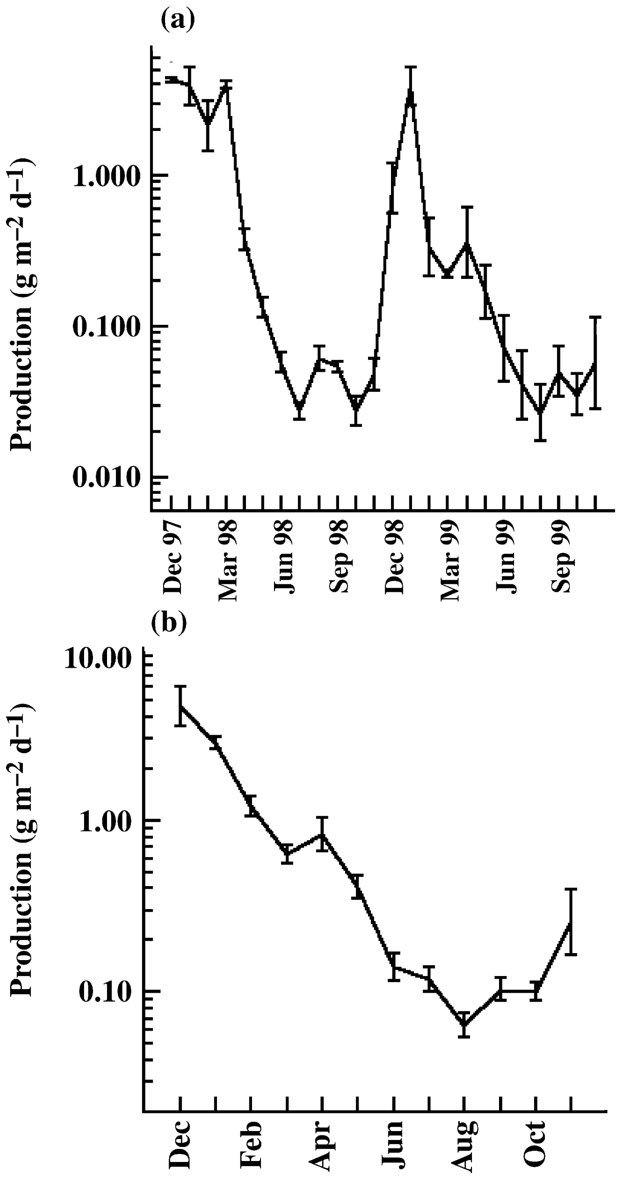


**Figure 2.** Daily above-ground grass production in (a) November 1997 quadrats harvested monthly for 2 y and (b) November 1996 and 1998 quadrats harvested monthly for 1 y. Vertical lines show standard error of mean.

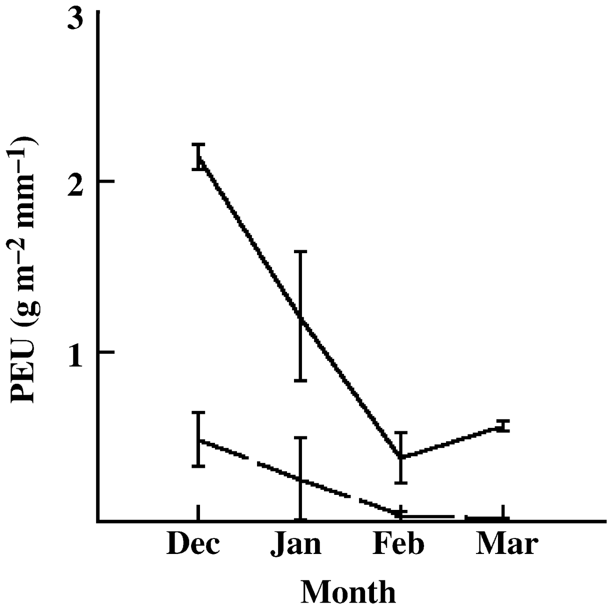


**Figure 3.** Precipitation-use efficiency (PUE) of grasses in November 1997 quadrats (A1 and B1) during 1997/98 (solid line) and 1998/99 (broken line) wet seasons. The low PUE during the second wet season is probably due to the negative effect of monthly harvesting for over 1 y.

in December to 0.7 ± 0.12 g $m^{-2}$ $mm^{-1}$ in January, 0.2 ± 0.04 g $m^{-2}$ $mm^{-1}$ in February and 0.3 ± 0.07 g $m^{-2}$ $mm^{-1}$ in March with significant differences between months ($F_{3,44} = 11.7$, $P < 0.0001$). The PUE in the November 1997 quadrats during two consecutive wet seasons, when the quadrats were under monthly harvesting, was higher in the first wet season than in the second wet season (Figure 3).

## DISCUSSION

End-of-wet-season grass phytomass did not vary significantly from year to year at the study site. Annual burning in July probably contributed to this stability in grass production. Grass phytomass recovered quickly after tillage and attained the levels observed on control quadrats within two wet seasons. *Tristachya superba* was the first grass to appear during the first wet season following tillage in November 1996 and the other recorded grass species appeared in the second wet season. This indicates a rapid species recovery from tillage and supports the observation made by Araki (1992) that *Hyparrhenia*-dominated sward develops rapidly after cultivated fields have been abandoned. There was also evidence of a rapid recovery after cessation of a 2-y monthly harvesting. The grassland community at the study site, therefore, has the potential to recover rapidly from disturbance caused by tillage and over-harvesting. For grasslands, such as the one at the study site, a few years of rest following cultivation or overgrazing may be enough for grass phytomass to recover.

There was no evidence to suggest that end-of-wet-season phytomass was significantly influenced by previous and/or current season precipitation, contrary to what has been observed in semi-arid grassland ecosystems (O'Connor *et al.* 2001, Webb *et al.* 1978). This observation may be explained by the fact that most of the above-ground growth at the study site occurred in December and January and declined sharply afterwards as grasses matured and flowered in February and March. Much of the precipitation that occurs in February and March is therefore not effectively used for above-ground growth by the grasses. This proposition is supported by the rapid

**Table 3.** Linear models that best fitted daily grass production (y, g $m^{-2}$ $d^{-1}$) data at the study site. Independent variables are mean daily precipitation (MDP, mm), minimum daily temperature ($T_{min}$, °C), maximum daily temperature ($T_{max}$, °C), dry season month (MDS) and number of monthly harvests (H). The significance level of $r^2$ is shown by asterisks: * = P < 0.05, ** = P < 0.001, *** P = 0.0001; ns = not significant.

| Quadrats/period | Model | $r^2$ |
|---|---|---|
| November 1996 quadrats clipped monthly for 1 year | | |
| December 1996–November 1997 | $y = 3.72 + 0.73MDS + MDP - 0.08H$ | 0.91*** |
| December 1996–March 1997 | $y = -18.3 + 0.01MDP + 0.66T_{max}$ | 0.80** |
| April–November 1997 | $y = -0.51 + 0.02MDP + 0.03T_{max}$ | 0.51*** |
| November 1997 quadrats clipped monthly for 2 years | | |
| December 1997–November 1999 | $y = 0.034 + 0.123T_{min} - 0.2MDS - 0.04H$ | 0.48*** |
| December 1997–November 1998 | $y = 4.26 + 0.01MDP + 0.96MDS - 1H$ | 0.88*** |
| December 1998–November 1999 | $y = 10.2 + 0.55MDS - 0.61H$ | 0.37*** |
| December 1997–March 1998 | $y = 34.9 + 0.86T_{max} - 3.02T_{min}$ | $0.41^{ns}$ |
| December 1998–March 1999 | $y = 113 - 0.07MDP - 1.04T_{max - 3.75Tmin}$ | 0.83** |
| April–November 1998 | $y = 0.06 + 0.05MDP + 0.01T_{min} - 0.03MDS$ | 0.80*** |
| April–November 1999 | $y = 0.18 + 0.01MDP - 0.03DSM$ | 0.34*** |
| November 1998 quadrats clipped monthly for 1 year | | |
| December 1998–November 1999 | $y = 8.18 + 1.91MDS - 1.95H$ | 0.81*** |
| December 1998–March 1999 | $y = -528 + 35.41T_{min} - 0.25MDP - 2.97T_{max}$ | 0.92*** |
| April–November 1999 | $y = -0.51 + 0.02MDP + 0.03T_{max}$ | 0.51*** |

decline in PUE after January (see Figure 3). Much of the precipitation after January may be regarded as redundant with respect to grass above-ground growth during the wet season. This is probably the reason why end-of-wet-season grass phytomass did not vary significantly among the years in spite of a large annual variation in precipitation of 557–1010 mm during the 5-y study period. However, the observation that previous-season phytomass influenced current-season grass phytomass (Jobbagy & Sala 2000, Osterheld *et al.* 2001) was confirmed. Obviously for perennial grasses, such as those at the study site, previous- and current-season phytomasses are not entirely independent of each other. Hence the significant correlation between previous-season and current-season grass phytomass.

Although some single variables explained a significant proportion of the variation in daily grass production at the study site, it is the interaction between a number of variables that was responsible for the largest proportion of the variation in grass production across a range of temporal scales, with or without disturbance (see Table 3). The observation that the interaction between mean daily precipitation and minimum and maximum temperature explained the largest variation in wet season grass production confirms the finding by Chidumayo (2001) that the interaction of precipitation and temperature has a strong influence on savanna phenology in southern Africa. The significant influence of mean daily precipitation on dry season grass production may be linked to the carry-over effect of stored water in the soil. Thus the more the precipitation in the rainy season, the greater is the likelihood of more available moisture for dry-season grass production. Soil moisture is one of the key determinants of grass production in savanna ecosystems (Frost *et al.* 1986). In savannas of central and southern Africa, topsoil (0–30 cm) moisture drops from 10–15% by weight in the rainy season to < 1% in the dry season (Chidumayo 1997*a*) and within this depth, soil dries out to wilting point early in the dry season (Strang 1969). It is therefore not surprisingly that soil moisture stress, as measured by the harvest-month into the dry season (MDS), had a significant effect on dry-season grass production, especially under conditions of prolonged monthly harvesting that exceeded 1 y. Under the latter conditions, the PUE of the grasses was reduced to less than 25% of the normal values. O'Connor *et al.* (2001) also found that grass in poor condition had the lowest PUE at a semi-arid grassland site in South Africa. The decline in both PUE and daily grass production as the wet season progressed may be related to a number of factors: (1) the temporary depletion of soil nutrients; (2) oxygen deficiency in the soil caused by a high water table close to, or on, the surface in February during above-average-rainfall wet seasons; and (3) flowering that occurred from January to March. In addition, PUE of grasses can be expected to decline gradually as the rainy season progresses as more and more photosynthates are transferred to below-ground parts instead of investment into above-ground parts (Chidumayo 1997*b*). The decline in PUE during the second wet season (Figure 3), after 20 monthly harvests, may therefore be a result of less and less investment in below-ground parts which in turn may cause less and less leaf production and less photosynthetic production.

The increasing tendency of concentrating cattle grazing to wetlands in central and southern African countries (Ingram 1991) is most probably diminishing the productive capacity of grasses through both overgrazing and soil erosion. The progressive decline in PUE of grasses in monthly harvested quadrats at the study site is evidence of this loss in productive capacity. The stress of overgrazing, even in the absence of soil erosion, probably results in reduced production. It is also apparent that mere seasonal shifts in continuous grazing across the catena (Scoones 1991) may not be adequate in sustaining grass production in the long term (see Hood 1972). Nevertheless, because recovery is possible after cessation of monthly harvesting, it is recommended that areas that have been continuously grazed be protected from grazing for 1 or 2 y to restore the productive capacity of grasses. The present study revealed that multiple climate and land-use factors and their interactions affect grass production (see Table 3). These complex interrelationships between independent factors make it more difficult to predict grass production in grazing lands in central southern Africa that has conventionally been based on precipitation alone (Deshmukh 1984).

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