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FINAL REPORT

PROJECT NO. US-997-85

Dynamics of Early-Season Grazing as a Key Process in Range Management

M.M. Kothmann, D.D. Briske, I. Noy-Meir, M. Gutman

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Title

DYNAMICS OF EARLY-SEASON GRAZING AS A KEY PROCESS IN RANGE MANAGEMENT

Investigators' Names
(Principal listed first)

Kothmann, M.M.

Briske, D.D.

Noy-Meir, I.

Gutman, M.

Investigators' Institutions

Texas A&M Research Foundation

Texas A&M Research Foundation

Dept. of Botany, HUJ, Jerusalem

Dept. of Range and Forest Crops, ARC

Project's starting date: 25 August 1986

Type of Report: 1st Annual ☐ 2nd Annual ☐ Final ☒

Signature
Principal Investigator

Signature
Institution's Authorizing Official

630.72 : 333.74 : 636.084.2 : 636.208.5
BAR/KOT

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ABSTRACT

Experiments in Israel and USA investigated the hypothesis that early-season grazing and supplementary feeding in the first weeks of the growing season has substantial effects on range condition, herd nutrition and plant and animal productivity. The research combined field studies with modelling to identify the main biological processes which affect range and animal responses.

Studies in Israel concluded that height-differential grazing by cattle has major and immediate impact on early-season dynamics. Preferential grazing among species is of lesser importance, in the short term. The rate at which cattle canprehend, bite and ingest green herbage between 1-5 cm of height, and the height distribution of green herbage, determine sensitivity of cattle intake and pasture production to stocking rate and deferment during the early season. In *Hordeum bulbosum* dominated grasslands, early season intake by cattle is limited by the height distribution of green herbage. Therefore, primary production is insensitive to changes within and beyond the currently practiced range of stocking rates, even under continuous grazing. This results in only a modest and transient effect of early season deferment on green herbage accumulation. Reductions of range contribution to animal production under heavy continuous grazing, as observed at Karei-Deshe, probably result from increases in unpalatable species over several years, rather than an immediate reduction in primary production.

USA grazing experiment confirmed the importance of forage height in relation to its grazability. Species selective grazing was less important during early-season, but increased as forage matured. Early-season delay of grazing for 30 d reduced animal production without apparent benefit to kleingrass productivity. Grazing intensity had less effect on primary than on secondary production, within a season. The critical level for stocking rate was identified as the point where forage demand and forage growth rates were equal. Stocking above this level severely reduced animal production, both per individual and per hectare.

The tiller population model and associated field experiments provided additional insights into mechanisms of change in plant populations subjected to grazing. Disproportionate utilization of the climax dominant, relative to the associated mid-seral species, is the predominant mechanism contributing to species replacement in these perennial grasslands.

Forage dynamics and diet selection models were developed and tested. Forage model components for age and senescence were shared between U.S. and Israeli investigators and validated for both locations. Data from the Israel study were used to estimate model parameters for forage harvestability in the USA diet model. Experiments conducted using linked forage, diet and animal models demonstrated the ability of the models to simulate forage and animal responses and interactions for grazed pastures. These models are highly mechanistic and will have broad applicability for future research and management. These studies and the cooperative relationships established form a sound basis for future research.

1. INTRODUCTION

Due to the critical dependence of rangeland production and income on management, considerable research effort has been directed towards optimization of management practices on rangelands. Long-term grazing experiments provide the most direct answers to specific management problems, but are seriously limited in the number of management alternatives and environments that can be investigated by land, labor, money and time constraints (Kothmann et al. 1982a). The challenge for research is to extend the results from a limited set of field experiments to the broad range of management alternatives available to the producer. To do this requires a shift from applied research with its very limited range of application to more basic research which identifies and quantifies key processes and casual relationships. These basic relationships can be readily incorporated into models that allow evaluation of a much broader range of alternatives than is possible in a field research program alone.

Plant growth models that have been developed for ecological understanding, watershed evaluation, or crop production are generally not suitable to be linked with a grazing interface to an animal production model. There is a need to develop and evaluate hypotheses and models of plant growth in rangeland which are clearly focused on the interactions of animal intake, diet selection, and animal production. These interactions are complex and involve many processes, but there is evidence that there are a few critical processes which have major effects on performance of the system in response to management. An example which is relevant to the present proposal is the balance of growth and defoliation in the early part of the growing season.

2. HYPOTHESIS

EARLY-SEASON DIFFERENTIAL GRAZING-REGROWTH (EDGR) RESPONSE

The main scientific hypothesis to be evaluated is as follows. The grazing and supplementary feeding schedule in the first weeks of the growing season has drastic effects on range condition, productivity, and herd nutrition:

- a. In the same season, through the defoliation-regrowth balance of foliage as well as its vertical and horizontal distribution, all of which affect forage quality and availability.
- b. In subsequent seasons, through differential defoliation and regrowth of species, affecting population dynamics and species composition (range condition).

The practical corollary of this hypothesis is: Production and income from many rangelands can be substantially increased, in the short and the long term, by developing more precise decision rules for grazing and supplementation management during the early season.

3. OBJECTIVES

1. To evaluate the EDGR hypothesis for cattle range on:
  - a. Mediterranean mixed grassland in Israel.
  - b. Summer rainfall perennial grassland in the USA.
2. To identify the main biological processes and relations involved in range response in both regions, and to develop quantitative models of them.
3. Adapt and validate a dynamic plant population model based on tiller age classes, natality, mortality, and longevity as a tool for determining subsequent range productivity and trend in response to various grazing regimes.
4. To use these models to develop rational, practical, prediction and decision rules, based on field criteria, for early-season grazing.

4. ISRAEL COMPONENT OF RESEARCH

4.1 RESEARCH PLAN

A direct biological evaluation of yearlong vs. early-season deferred grazing was conducted in a long-term grazing experiment set up at Kare-Deshe Experimental Range in Galilee. The site is a natural grassland on basaltic soils and receives 550 mm annual rainfall. Eight plots (25-30 ha each) having known grazing treatments and production records for 24 years were used. Treatments consisting of continuous and early-season deferred grazing at two stocking rates (each replicated twice) were applied to 8 paddocks with balanced herds of 15-25 cows per paddock. The Israel Department of Agriculture supported the infra-structure and standard monitoring of system performance. We used this experiment as the base for an intensive study of the processes involved in early-season grazing dynamics and for the testing and development of relevant hypotheses and models.

The main processes studied were:

1. Defoliation rates by cattle grazing in the early-season as differentiated in relation to height, foliage density and species.
2. The effects of early-season defoliation on rates of regrowth and its distribution between species and vegetation layers.
3. The effects of differential early-season defoliation on plant mortality and reproduction as mechanisms of species composition change.

METHODS

Differential defoliation rates by species and layers were measured in graze-down experiments in short-term (1 week) enclosures. Plant biomass by species and layer, marker disappearance, nutritive value, animal grazing behavior and supplement intake were measured daily. Functions relating defoliation rate of components to availability and quality were fitted to results and parameters estimated. A model of differential defoliation was developed.

Growth/regrowth rates by species and layer were measured in grazed plots and in clipped quadrats in permanent and in temporary small enclosures. Functions relating foliage growth rate and height allocation to sward structure, composition and defoliation were fitted to the results and used in model development.

Species composition trends were monitored in permanent quadrats in grazed plots and in enclosures used in the preceding experiments. Species population counts were conducted at the beginning and end of the growing season in response to grazing or defoliation regime.

Animal production, pasture production, availability, quality and composition were monitored during 3 years. Results were used to evaluate the predictive power of the model

developed in the project. Once reasonable confidence in the predictions of the model is established, it will be used to simulate plant and animal production in different conditions and different early-season management schemes. Simulation experiments will be designed to search for optimal grazing and supplementation schedules which can be defined by practical decision rules based on field estimates.

4.2 GRAZING SYSTEMS EXPERIMENT

DESIGN

The grazing systems experiment which served as reference and validation system for the project included 8 paddocks and herds, in 2 blocks of 4 grazing treatments. The grazing treatments included continuous grazing and early season deferment, each at two stocking rates (Table 1, p 14). In the deferred treatments the cows were removed from the pasture into a small feeding paddock after germination each year and were released back to the main paddock after green biomass there had reached about 80 g/m² (Table 2, p 14). In the continuous treatments the cows were supplemented in the pasture as long as necessary.

CLIMATE

Meteorological data for the years 1986-89 are given in Table 3, p 15. The 1986/87 rain season started early, rainfall was abundant and favorably distributed. In 1987/88 rains started late, but the total amount was about average. The 1988/89 season was relatively dry with a rather irregular rainfall distribution.

HERBAGE DYNAMICS AND PRODUCTION

During the two years of the process studies, 1986-88, the seasonal dynamics of green biomass were monitored in an ungrazed paddock (Table 4, p 16) and in four of the experimental paddocks (one block) (Table 5, p 17).

The 1986/87 growing season started early in October. After a short dry spell, plant growth was continuous until April. Peak herbage mass (and primary production) in the ungrazed plot was the highest ever observed in Karei-Deshe, 576 g/m². Unusually high biomass was also measured in the grazing treatment plots. Early in the season, the deferred plots accumulated more biomass than the continuously grazed ones, but later this difference disappeared or was masked by other differences between plots.

In 1987/88 growth started late, only in December, and was initially very slow. Thus, the deferment period started later and lasted longer than in 1986/87. Biomass at any time was about 100 g/m² lower than in the previous season in both grazed and ungrazed plots. Both the deferred plots built up a considerably higher biomass than the two continuous plots early in the season, but the gap was practically closed by about 45 days after deferment ended.

CATTLE PRODUCTION AND SUPPLEMENTARY FEEDING

Calf weaning weights fluctuated between years, but there were no consistent differences between grazing treatments (Table 6, p 18). The main difference between the treatments was in the amount of supplementary feed (chicken litter, straw and grain) consumed in the deferment period in winter. The herds of the deferred treatments, which were in this period fed in a small holding paddock, consumed, on the average for three years, about 800 Mcal/cow/period of supplements; the continuously grazing herds, which were offered the supplement while grazing on the new green pasture, consumed only about 240 Mcal/cow/period. Since the deferment treatments left no greater amounts of dry herbage at the end of the growing season than the continuous treatments, there was no saving of supplement in the summer period.

4.3 RATE OF GROWTH AND REGROWTH EXPERIMENTS

1986/87 EXPERIMENTS

Six experiments were carried out, between November and March. In the first one, sample size was too small for meaningful results. No serious technical difficulties were encountered, except for high variance between sampling units (625 cm² circles) which was compensated for by increasing the number of units. Estimates of cover, height, herbage volume (cover * height) and mass were generally highly correlated with each other, and the two latter showed the highest correlation with harvested herbage mass. Radiometer values (ir/r reflectance ratio with soil correction) were highly correlated with cover, and in the first experiments also with harvested mass. The selected calibration equations based on non-destructive estimates accounted for 60% to 82% of variance in harvested herbage mass.

Growth rates fluctuated around 50 kg/ha/day and were not consistently different between continuously grazed and deferred treatments. There was no consistent trend in growth rate against mass over the range of 100 to 500 g/m². There is an indication that below 100 g/m² relative growth rate (g) was higher in the continuously grazed plot. This could be explained by the lower biomass in that plot at any date. When g is plotted against biomass, points from both treatments fall close to the same declining curve. Cover, height and herbage volume were always greater in the deferred pasture and increased in the course of the season. Herbage density per unit volume tended to be higher in the continuously grazed pasture.

1987/88 EXPERIMENTS

Five experiments were carried out, between January and March 1988 (Table 7, p 18). Variance between samples was high. As in the previous year, estimates of cover, height, herbage volume (cover * height) and mass were generally highly correlated with each other. The two latter showed the highest correlation with harvested herbage mass. The best regression equations based on non-destructive estimates accounted for 69% to 87% of variance in harvested herbage mass. Absolute daily growth rates fluctuated between 1 and 6 g/m²/day and were not consistently different between continuously grazed and deferred treatments (Table 7, p 18). Growth rates (both absolute and relative) measured at low

herbage mass, early in the season, were considerably lower than those measured in 1986/87. In the range of 100-250 g/m² herbage mass, growth rates were similar in the two years. Relative growth rates (g) varied between 1% and 6% with a declining trend in both treatments. Cover, height, herbage volume and mass were always greater in the deferred pasture and increased in the course of the season (Table 8, p 19). Herbage density per unit volume, again, tended to be higher in the continuously grazed pasture.

ANALYSIS AND PARAMETER ESTIMATION

The absolute and relative growth rate data from all experiments in both years were pooled. Their relations with various sward characteristics and other variables were examined by linear and non-linear regression.

The only significant relationships were the positive asymptotic dependence of absolute growth rate on total plant cover and total green biomass, and the negative asymptotic dependence of relative growth rate on cover and biomass. The residual variation in growth rates around the functions fitted to cover or biomass showed no consistent effect of the year or of grazing history (continuously grazed versus ungrazed). Absolute growth rate was positively correlated also with height, but the correlation was much lower than with biomass and cover and is probably a spurious effect of the correlation between height and biomass in the course of the season.

The relation of relative growth rate to total green biomass fitted best ($R^2 = 0.75$) to a negative exponential function:

$$g = g_{\max} * e^{-v/v_x}$$

in which the parameters values are:

$$g_{\max} = \text{maximum net relative growth rate} = 0.056 \text{ day}^{-1}$$

$$V_x = \text{characteristic biomass for extinction} = 193 \text{ g/m}^2$$

The data for absolute growth rate versus biomass could be reasonably well fitted by the function used in the simulation model:

$$G = g_{\max} * V_x * (1 - e^{-v/v_x}) - m * V_x$$

with parameter values:

$$g_{\max} = \text{maximum gross relative growth rate} = 0.08 \text{ day}^{-1}$$

$$m = \text{relative loss ("maintenance") rate} = 0.01 \text{ day}^{-1}$$

$$V_x = \text{characteristic biomass for saturation} = 90 \text{ g/m}^2$$

4.4 RATE OF DEFOLIATION (GRAZE-OUT) EXPERIMENTS

1986/87 EXPERIMENTS

Eight such experiments were carried out between November 30 and February 6. Four experiments were on a pasture that had been continuously grazed before the experiment and four on deferred pasture. The design and techniques were by and large as

described in the research plan. Certain modifications were made to solve problems of work organization and sampling intensity that appeared in the first two experiments. The experiments produced a large and complex data set, a large part of which was directly recorded on a portable terminal. All data are now stored on computer and have been analyzed intensively.

The patterns of correlation between various non-destructive estimates (cover, height, volume, estimated biomass, reflectance ratio) and harvested biomass, were similar to those reported for the rate of growth experiments. Calibration equations with r^2 of 58% to 89% (usually 79% to 82%) were obtained. In the course of each experiment, plant cover, height, volume, and biomass declined consistently from day to day (except on two days for biomass).

Bare soil cover increased in all experiments, bare rock cover only in some. The cover of annual dicots and their proportion in the harvested biomass usually showed a declining trend through the experiments. By contrast, the cover of the grasses and of the dominant *Hordeum bulbosum* did not show a decreasing trend in most experiments.

Herbage density showed a tendency to increase during the experiment as plant height was reduced more severely than biomass. The decrease in biomass was close to linear in most experiments though in some cases curvilinear functions gave a better fit to the data. Usually biomass disappearance was faster in the upper layer of the sward (5 cm) and particularly the grass component in this layer. Defoliation rate was calculated by adding the estimated growth rate (from the growth rate experiments) to the daily reduction in biomass. The average defoliation rate for experiments varied between 4 and 8 kg dry matter per cow per day. It increased in relation to the mean available biomass in the experiment. Differences between continuously grazed and deferred pastures were not consistent.

1987/88 DEFOLIATION RATE EXPERIMENTS

Eight such experiments were carried out between January 10 and February 25 (Table 9, p 19). Four were on a pasture that had been continuously grazed before the experiment and four on deferred pasture. The design and techniques were as described in the research plan, with modifications made in the first year. The patterns of correlation between various non-destructive estimates (cover, height, volume, estimated biomass) and harvested biomass, were similar to those reported for the rate of growth experiments and in the previous year. Calibration equations with r^2 of 65% to 94% (usually 75% to 84%) were obtained. In the course of each experiment, plant cover, height, volume, and biomass declined consistently from day to day, while bare soil cover increased (Table 10, p 20).

Herbage density showed a significant tendency to increase during the experiments, as in 1986/87. The decrease in biomass was close to linear in most experiments. Biomass disappearance was faster in the upper layer of the sward (above 5 cm) and particularly the grass component in this layer.

Defoliation rate was calculated by adding the estimated growth rate (from the growth rate experiments) to the daily reduction in biomass. This year a much wider range of initial herbage mass was covered by the experiments than in 1986/87. Thus, also the range of defoliation rates obtained was much larger. The average defoliation rate for experiments varied between 1 and 14 kg dry matter per cow per day (Table 11, p 20). It increased in relation to the daily available biomass. The rate in the continuously grazed plot was always lower than in the deferred plot on the same date.

ANALYSIS AND PARAMETER ESTIMATION

The rate of "defoliation" (biomass loss) as estimated in the graze-out experiments included direct intake and loss of biomass trampled into the ground and not recovered by the sampling method. Independent estimate of the latter loss indicated that it was small (less than 5%), except in one experiment conducted in very rainy and muddy conditions. Data from this experiment were excluded from the overall analysis, so that rate of defoliation functions and parameters should closely represent cow intake.

Over the remaining 15 experiments daily grazing rate per cow, c , was related to green biomass V (whether defined as daily, initial or average for the experiment), by an increasing convex function. Of various empirical functions, best fit in regression ($R^2=0.89$) was obtained by a square-root function with a non-zero intercept. A biologically more meaningful non-linear function which gave a reasonable fit was a Michaelis-Menten type saturation function with a residual biomass:

$$c = c_{\max} * \frac{s * (V - V_r)}{s * (V - V_r) + c_{\max}}$$

with parameter values:

$c_{\max}$ = satiated consumption = 14.8 kg/cow/day

s = grazeability coefficient = 0.012 ha/cow/day

V_r = residual ungrazeable biomass = 2.4 g/m²

The estimated $c_{\max}$ is consistent with other estimates of maximal daily intake of cows of similar type in similar conditions.

Further analysis was based on the biomass extinction coefficients in each experiment; i.e., the slope parameter b of exponential regression of biomass against cumulative grazing pressure:

$$V = V_0 * e^{-b * H dt}$$

In the range of biomass where intake is linearly related to biomass, and neglecting simultaneous growth, b estimates the grazeability coefficient s . In general, b can be interpreted as an "apparent grazeability", s' , with dimensions area/animal/day. As such, it can be estimated not only for the total biomass but for each biomass component (by layer and species) the disappearance of which was monitored separately in the graze-out

experiments. The value of the specific s' for each component measures how effectively it was ingested by grazers in relation to its available biomass.

In all experiments, s' values for the upper biomass layer (above 5 cm) were much higher (average 0.023 ha/cow/day) than for the 0-5 cm layer (average 0.008 ha/cow/day). This was true also in experiments in which only a small proportion of the total biomass was above 5 cm. This means that cows highly select for the upper layer and also ingest it much faster. In the course of each experiment, plant height declined much faster and more consistently than all other sward characteristics (including biomass) down to a height of about 2 cm, where it tended to stabilize.

All the evidence from the graze-out experiments shows clearly that grazing behavior and daily intake in the early season are closely controlled by biomass height distribution, particularly as long as most of the green biomass is below 5 cm.

By contrast, botanical composition had a weaker effect on grazing behavior and intake. The values of s' in the upper layer (and overall) in many experiments tended to be higher for grasses than for dicotyledonous annuals (mostly rosette-forming crucifers), indicating a certain preference for grasses. But the difference was not consistent and usually not large. The relative botanical composition of the sward (grasses/annual dicots) usually did not change markedly in the course of an experiment. The perennial thistle *Echinops* was usually not eaten until the third day of the experiment, and the noxious perennials *Ferula* and *Asphodelus* were totally avoided; but none of these were very abundant in the experimental plots.

4.5 MODEL DEVELOPMENT AND EVALUATION

MODEL DEVELOPMENT

A model has been developed describing biomass dynamics in the early growing season in order to test the effects of stocking rate and deferment criteria. The model differs from previous simple models in that biomass is partitioned by height layer and botanical composition. In the initial version, two layers by two species (or species groups) are accounted for separately. The general forms of growth and consumption functions are as in the simple model, but two new functions have been introduced. The allocation function allocates the daily biomass increment for each species between height layers depending on the weighted cover (calculated from biomass) in the respective layer. Allocation parameters may differ between species. Consumption of each species * layer component is calculated by a selection function involving a preference rank (grasses > forbs; upper > lower layer) and optionally different maximal intake and ingestion efficiency parameters for each species * layer component. The model has been programmed in Pascal and is running on the Hebrew University CDC main computer as well as on Olivetti M24 PC.

SENSITIVITY OF DIFFERENTIATED VERSUS SIMPLE MODELS

Initial parameterization of the model was based on the results of the experiments in the 1986/87 season. The sensitivity of the differentiated model to several parameters was evaluated by sets of simulation experiments and compared with the simple model. The two outputs mainly considered were the cumulative herbage growth (primary production) and the cumulative herbage consumption by the herd over a growing season of 150 days. Like in the simple model, the output of the differentiated model is highly sensitive to the values of relative growth rate and grazeability parameters. However, the differentiated model is much less sensitive than the simple one to stocking rate under continuous grazing, and to time of deferment at high stocking rates (Tables 12 and 13, p 21). Simulation experiments with only differentiation by height and only differentiation by species showed that the former was more important in reducing sensitivity. If indeed the lower layer (0-5 cm) of leaves of each species has a much lower grazeability, this is expected to increase the resilience of the range under a wide range of grazing treatments.

SENSITIVITY TO SENESCENCE PARAMETERS

The biomass aging and death by senescence functions used in the TAMU forage balance model were introduced into the growth-grazing model, and the effects of the parameters on simulated biomass dynamics in Karei-Deshe conditions were tested. The ratio dead/live biomass in the early growing season was highly sensitive to the basic senescence rate $T1$, while the ratio later in the season was sensitive to the age-dependent rate $A1$. Evaluation against field observations suggested that realistic values were $T1=0$ and $A1=$ about 0.0015 day^{-2} . In further simulations only age dependent biomass death was considered.

ESTIMATION OF PARAMETERS OF GROWTH ALLOCATION BETWEEN LAYERS

In the model, the allocation of new biomass of each botanical component between layers is determined by the VL parameters, expressing the effect of existing biomass in the lower and the upper layer on the allocation. Simulations with different VL values produced curves of the relation between biomass in the upper and lower layer in the course of the season. These were compared with actual data of initial conditions in the graze-out experiments.

The observed points fell close to simulated curves assuming values of $VL(0-5 \text{ cm}) = 100-120 \text{ g/m}^2$ and $VL(>5 \text{ cm}) = 50-60 \text{ g/m}^2$.

SENSITIVITY TO GRAZEABILITY OF LOWER LAYER

The assumed value of the grazeability coefficient of the 0-5 cm layer $\underline{s}_1$ (all other parameters being constant) had large effects on simulated biomass accumulation and primary production. Under continuous grazing, assuming $\underline{s}_1 = 0.03-0.05 \text{ ha/cow/day}$, there was a sharp decrease in biomass and in seasonal cumulative primary production in relation to stocking rates in the range of 0.5 to 1 cow/ha (Table 14, p 22). However, assuming $\underline{s} =$

0.01 (closer to the values estimated in the graze-out experiments), primary production decreased only moderately in response to stocking rate.

Deferment of grazing until 60-days after germination entirely removed the dependence of primary production on lower-layer grazeability and on stocking rate. Even after only 30 days of deferment the sensitivity was greatly reduced.

GRAZING SYSTEM SIMULATIONS AND EVALUATION

The effect of stocking rate and deferment period on biomass dynamics were examined by simulation, after setting all parameters to their most likely values, based on the process studies and on previously described simulation experiments. The grazeability of the lower layer, s_1 , was set at 0.008 ha/cow/day, based on the graze-out experiments.

The results (Table 15, p 22) showed that under continuous grazing, cumulative seasonal primary production decreased moderately in response to stocking rate, from 370 g/m² without grazing to 337 g/m² at 1 cow/ha. The response to stocking rate was much weaker with 30 days of deferment. Deferment of 60 days made primary production virtually independent of stocking rate. Cumulative herd consumption in the green season increased with stocking rate up to 1 cow/ha, and was somewhat increased by deferment.

The green biomass accumulation curves simulated in conditions of the Karei-Deshe grazing experiments showed an initially faster build-up in the deferred systems, similar to the observed. After 60 days of deferment, their advantage over the continuous systems was 35% in the simulation, compared with 50-60% in the experiment. After the deferred plots were opened to grazing, the biomass difference was gradually reduced in the simulated, as in the experimental systems, becoming negligible by the end of the growing season.

4.6 CONCLUSIONS

1. In mixed Mediterranean grasslands, such as Karei-Deshe, height-differential grazing by cattle has a major and immediate impact on early season dynamics. Preferential grazing of botanical components is of lesser importance, at least in the short term.

2. The rate at which cattle canprehend, bite and ingest green herbage between 1 and 5 cm of height, and the height distribution of green herbage in this range, determine cattle intake in the early season. They also determine the sensitivity of pasture production to stocking rate and early-season deferment period.

3. In *Hordeum bulbosum* dominated grasslands, such as Karei-Deshe, cattle intake in the early season is severely limited by the height distribution of green herbage. Therefore, primary production appears to be fairly robust to changes in stocking rate within and beyond the currently practiced range, even under continuous grazing. Early-season deferment has only a modest and transient effect on green herbage accumulation.

4. Reductions of range contribution to animal production under heavy continuous grazing, as observed at Karei-Deshe, may result from an increase in unpalatable plants over several years, and not from an immediate reduction of total seasonal primary production.

5. Sensitivity of early-season dynamics and of primary production to stocking rate and deferment period is expected to be greater in systems where the grazeability of the early herbage is higher than at Karei-Deshe; for instance, in systems grazed by sheep (as shown for the Migda system in the Negev), or grazed by cattle but dominated by erect annual grasses (e.g., oat) or caespitose perennial grasses (as in many U.S. rangelands).

Table 1. Design of deferment grazing trial.

Treatment	Paddock Number	Stock Density (ha/cow)	Paddock Size (ha)	Number of Cows
Deferred Heavy (DH)	1	1.2	25.5	21
	8	1.2	31.5	26
Deferred Moderate (DM)	4	1.5	27.8	19
	7	1.5	20.0	14
Continuous Moderate (CM)	3	1.5	28.3	19
	6	1.5	27.2	18
Continuous Light (CL)	2	2.0	33.8	17
	5	2.0	28.3	14

Table 2. Periods of grazing deferment in the grazing systems experiment.

Year	Deferred		Deferment Period (days)
	From	Until	
1986/87	10 Nov 86	17 Dec 86	37
1987/88	11 Dec 87	3 Feb 88	54
1988/89	23 Nov 88	16 Jan 89	54

Table 3. Meteorological data for Karei-Deshe weather station (8 AM), 1986-89. Heat days are calculated as ((max. temp. + min. temp.)/2)/25, starting from the first rain.

	Max. temp. avg.			Min. temp. avg.			Heat days		
	86/7	87/8	88/9	86/7	87/8	88/9	86/7	87/8	88/9
September		33.2			19.3				
October	28.1	27.6	28.1	20.8	16.4	16.7	7.5	7.9	7.1
November	19.6	23.4	20.7	12.1	14.4	11.1	5.4	6.8	5.8
December	14.9	17.2	16.6	6.1	10.4	9.4	4.0	5.1	4.8
January	15.6	14.6	11.9	7.3	7.2	5.5	4.1	4.1	3.3
February	21.4	14.4	16.5	8.5	8.1	6.8	5.0	4.1	3.9
March	16.4	18.8	19.0	6.5	10.0	8.9	4.3	5.5	5.2
April	22.0	24.1	29.7	10.1	15.0	13.9	5.8	7.1	7.9
May	30.4	30.7		13.1	18.5		7.7	9.3	
June	32.9	32.5		16.5	16.2		8.9	8.8	
July	35.0			20.4			10.3		

	Relative Hum %			Pan evap. mm.			Rain days			Rain mm.			
	86/7	87/8	88/9	86/7	87/8	88/9	86/7	87/8	88/9	85/86	86/7	87/8	88/9
September		75.8			6.9								
October	72	78.2	65.7	4.6	4.4	5.8	3	4	4	18	59	21	18
November	79	79.6	59.1	2.9	3.7	3.3	10	2	5	17	215	8	50
December	85	91.0	73.4	2.0	1.8	1.8	14	16	10	76	119	175	152
January	79	87.3	76.7	2.1	1.4	2.2	11	16	8	101	146	93	48
February	79	82.6	66.8	2.6	1.7	4.1	10	14	6	120	60	138	37
March	86	84.3	69.2	2.2	2.4	3.9	21	11	7	14	112	93	98
April	72	72.8	56.7	4.3	5.1	7.1	3	3		29	6	14	
May	59	70.0		7.7	8.7					29			
June	65	69.6		8.3	9.1								
July	73			7.9									
Total							72	66	40	404	716	543	403

Table 4. Dynamics of green herbage biomass (g/m²) at Karei-Deshe, in an ungrazed plot.

Year	1985/86		1986/87		1987/88	
date	Days from first rain	Yield g/m ²	Days from first rain	Yield g/m ²	Days from first rain	Yield g/m ²
11 Nov			41	25		
4 Dec			64	66		
12 Dec			72	97		
31 Dec	74	24	91	154		
6 Jan					61	36
18 Jan			109	201		
25 Jan	99	150	116	158		
28 Jan					83	49
11 Feb			133	356	97	74
18 Feb	123	190				
6 Mar					121	150
12 Mar			162	518		
25 Mar					136	361
28 Mar	152	231				
12 Apr					158	470
28 Apr	192	280	209	576		

Table 5. Dynamics of green herbage biomass in the grazing experiment plots at Karei-Deshe.

Treatment		HD	MD	MC	LC
Paddock		8	4	6	5
Year 1986/87	days from first rain	g/m ²			
26 Nov 86	56	32	40	26	26
16 Dec 86	76	79	97	59	67
4 Jan 87	95	137	182	123	133
28 Jan 87	119	144	157	140	155
18 Feb 87	140	191	199	186	202
8 Mar 87	158	310	289		
17 Mar 87	167			256	318
30 Mar 87	180	284	280	326	429
28 Apr 87	209	434	397	367	477
Year 1987/88					
4 Jan 88	59	21	23	17	18
17 Jan 88	72	34	39	32	34
1 Feb 88	87	72	75	58	87
14 Feb 88	100	95	106	77	64
15 Mar 88	130	152	168	150	144
11 Apr 88	158	325	317	317	351
Year 1988/89					
2 Jan 89	52	42	56	35	40
30 Jan 89	80	101	118	80	81
5 Mar 89	114	164	162	135	164
12 Apr 89	152	447	394	301	422

Table 6. Calf weaning weights in the grazing system experiment plots at Karie-Deshe, 1986-89.

Treatment	Paddock	Weaning weight during the trial years (Kg)				
		1986	1987	1988	1989	1986-89 Average
12 D	1	178	148	205	193	181
	8	176	153	215	184	182
	AVG	177	151	210	188	180
15 D	4	172	170	178	201	180
	7	180	153	187	204	181
	AVG	177	162	183	203	181
15 C	3	174	173	184	187	180
	6	175	156	196	191	180
	AVG	174	165	190	189	180
20 C	2	176	161	183	188	177
	5	184	162	190	213	187
	AVG	180	162	187	200	185
All padd.		177	160	192	195	181

Table 7. Growth rate experiments: Absolute & relative growth rates.

Exp. start date	Exp. end date	Treatment	No. of clipped plots	Average yield	Growth rate (Abs.)	Growth rate (Relative)
				g/m ²	g/m ² /day	%/day
6/1/88	14/1/88	Deferred	60	36.1	1.1	2.6
		Continuous	60	12.7	0.8	5.5
22/1/88	28/1/88	Deferred	60	37.1	2.4	5.7
		Continuous	60	28.8	1.2	3.6
5/2/88	12/2/88	Deferred	80	62.8	1.9	2.8
		Continuous	80	36.6	2.0	4.6
29/2/88	6/3/88	Deferred	80	124.3	4.0	2.9
		Continuous	80	67.9	1.6	2.1
14/3/88	21/3/88	Deferred	80	221.2	5.7	2.4
		Continuous	80	113.7	2.5	2.3

Table 8. Pasture variables at beginning of growth rate experiments.

Date	Treatment	Plant cover	Plant height	Volume	Herbage density
		%	cm	l/m ²	g/cm ³
6/1/88	Deferred	64.2	5.9	41.3	0.0008
	Continuous	32.8	3.0	10.5	0.0014
22/1/88	Deferred	55.8	4.9	29.2	0.0018
	Continuous	50.7	4.3	23.6	0.0018
5/2/88	Deferred	64.4	8.0	58.2	0.0013
	Continuous	49.1	5.9	31.5	0.0015
29/2/88	Deferred	73.1	14.4	117.8	0.0014
	Continuous	57.1	6.0	36.1	0.0023
14/3/88	Deferred	86.6	20.8	188.2	0.0013
	Continuous	64.0	6.2	41.7	0.0040

Table 9. Design of 1987/88 defoliation rate experiments.

Treatment	Exp. start	Exp. end	Plot size	No. Of cows
	day	day	(ha)	
Deferred	10/1/88	13/1/88	0.1071	3
Deferred	24/1/88	27/1/88	0.1172	3
Deferred	7/2/88	11/2/88	0.1183	3
Deferred	21/2/88	25/2/88	0.1202	4
Continuous	10/1/88	13/1/88	0.0960	2
Continuous	24/1/88	27/1/88	0.0978	2
Continuous	7/2/88	10/2/88	0.1059	3
Continuous	21/2/88	24/2/88	0.1058	3

Table 10. Changes in pasture variables in one of the defoliation rate experiments (deferred plot no. 3). Numbers are averages of n=200.

Date	Plant cover	Height	Volume	Herbage density	Biomass
	%	cm	l/m ²	g/cm ³	g/m ²
7/2/88	75.7	11.4	93.5	0.0015	127.0
8/2/88	69.7	8.3	64.8	0.0018	96.9
9/2/88	64.9	6.6	46.2	0.0018	69.8
10/2/88	59.0	4.6	29.6	0.0023	53.7
11/2/88	54.9	4.1	24.1	0.0024	48.6

Table 11. Average defoliation rates (kg/cow/day).

Experiment		Deferred plot	Continuous plot
start	end		
10/1/88	13/1/88	0.9	0.8
24/1/88	27/1/88	4.6	2.8
7/2/88	11/2/88	7.4	
7/2/88	10/2/88		3.9
21/2/88	25/2/88	14.2	
21/2/88	24/2/88		7.4

Table 12. Cumulative seasonal herbage growth (g/m^2) over a 150 day period and herbage consumption (g/m^2 in brackets) in response to stocking density (SD) (cows/ha) and time deferred (TDEF) as predicted by a simple growth-consumption model. (NG=not grazed).

SD =	NG	0.50	0.67	0.83	1.00	1.25
TDEF (days)						
0	340	328(61)	314(77)	295(88)	264(95)	193(90)
30		349(62)	350(83)	349(101)	346(118)	336(138)
60		353(53)	357(71)	361(89)	364(107)	368(133)

Table 13. As table 12; but predicted by a growth - consumption model where herbage mass is differentiated into two layers by two botanical components, differing in grazeability and maximum intake parameters. Average parameters are similar to those used in table 12.

SD =	NG	0.50	0.67	0.83	1.00	1.25
TDEF (days)						
0	340	346(55)	346(69)	346(79)	344(87)	340(98)
30		351(56)	353(70)	355(81)	355(91)	356(103)
60		353(55)	356(68)	359(72)	361(91)	364(104)

Table 14. The effects of stocking density (SD, cows/ha) and early season deferment period (TDEF, days from germination), on simulated cumulative seasonal primary production SGT (g/m^2) over a 150 day growing period, at different values of the grazeability coefficient of the 0-5 cm herbage layer, s_1 (ha/cow/day). In ungrazed conditions, $\text{SGT} = 344 \text{ g/m}^2$.

s_1	0.01			0.03			0.05		
TDEF	0	30	60	0	30	60	0	30	60
SD = 0.5	342	348	352	328	346	352	315	344	352
0.67	340	349	354	318	345	354	295	342	354
0.83	337	349	355	306	342	356	269	339	356
1.0	334	348	357	290	339	357	230	334	357

Table 15. The effects of stocking density (SD, cows/ha) and deferment period on simulated cumulative seasonal primary production, SGT, using the most likely parameter values for the Karei-Deshe experimental grazing systems. In ungrazed conditions $\text{SGT} = 370 \text{ g/m}^2$.

TDEF	0	30	60
	(g/m^2)		
SD = 0.5	356	364	370
0.67	350	361	369
0.83	344	358	368
1.0	337	354	367

5. USA COMPONENT OF RESEARCH

5.1 A forage dynamics model for use in range or pasture environments

H. D. BLACKBURN AND
M. M. KOTHMANN

Department of Range Science, Texas
Agricultural Experiment Station, College
Station, Texas, U.S.A.

Abstract

A deterministic model that simulates forage dynamics is described and validation results presented. The model simulates different species of grasses and forbs for a production year and provides the necessary input for a diet selection model. The model does not simulate growth, but does simulate the accumulation of live leaf and stem, the senescence of live biomass, and its transfer to dead mass using growth rates for leaf and stem of each species, which are specified for the model. Using such an approach specific types of years can be simulated. Plant components in the model include live leaf and stem, dead leaf and stem, and old dead leaf and stem which were produced during the previous growing season. These plant components were chosen because of their importance in the diet selection process and their differences in forage quality. Plant species which the model was validated against were *Cynodon dactylon*, *Avena sativa*, *Schizachyrium scoparium* and *Paspalum plicatulum*. Validation results indicated that with adjustment to input growth rates, live biomass could be adequately simulated. Deviations between measured and simulated dead components were observed for *S. scoparium* and *P. plicatulum*. High values observed for dead stem early in the trial resulted from lack of separation of dead and old dead stem material in the field sampling. Variations in dead forage throughout the season were caused by unexplained sources of variation. This indicated a

need for field research to better quantify the dynamics of dead biomass. The model meets its goal of simulating biomass dynamics and forage quality of plant parts and it provides a suitable forage base to interface with diet selection and animal simulation models.

Introduction

Diverse plant species, inconsistent weather patterns, and multitudes of managerial options affect forage biomass dynamics and necessitate the use of simulation models to understand and quantify dynamic rangeland or tame pasture systems. Additionally, when the diet selection processes of grazing herbivores are interwoven with forage dynamics, the situation becomes more complex. Most previous models have simulated net forage production and the total amount of forage removed by the herbivores (Noy-Meir, 1976; Innis, 1978; Christian *et al.*, 1978; Smith and Loewer, 1983). However, this approach does not account for the effects of selective grazing or changes in plant morphology, seasonal changes in plant growth, or animal performance (Noy-Meir, 1976).

Several models with varying levels of resolution have been constructed to address plant-animal interactions (Wright, 1983; Johnson and Parsons, 1985; Laurenroth *et al.*, 1986). Diet selection models need nutritional information about both spatial and species heterogeneity within the available herbage. Previous biomass level models did not provide a suitable level of resolution. Models constructed at a physiological level of resolution cannot be interfaced readily with diet selection models.

This model was constructed to simulate the forage dynamics of mixtures of species. Its level of resolution provides sensitivity to temporal changes in rates of accumulation, senescence and disappearance of plant part components. It

Correspondence: Dr H. D. Blackburn, Department of Animal Science, Texas A & M University, College Station, TX 77843, U.S.A.

partitions the major sources of nutritional heterogeneity among forage biomass components, thereby permitting changes in the sward structures to affect forage quality. Model construction permits evaluation of the major factors controlling the rates of flow of biomass through a system.

The model was designed specifically to simulate dynamics of biomass and forage quality necessary for realistic integration with a diet selection model that, in turn, can be linked to models simulating the performance of beef cattle, sheep and goats (Sanders and Cartwright, 1979; Blackburn *et al.*, 1987).

Model structure

The model was designed for adaption to a wide array of situations; i.e. it is not species, location, or management dependent. State variables partition forage into leaf and stem with each including live, current year's dead and old (previous year's) dead and the amount of crude protein and digestible dry matter in each category. Leaf categories contain only lamina; stem categories include sheath and culm. Major functions controlling the level of state variables include precipitation, age, senescence, and transfer from dead to litter categories. Information on forage biomass is stored in a three-dimensional array comprised of pasture, forage class or species, and plant part. Forage may be simulated by class such as C₃ (cool-season) and C₄ (warm-season) grasses and forbs, or by species, or some combination of the two. Required inputs include mean daily temperature, minimum daily temperature, daily precipitation, and growth rates for leaf and stem. If desired, forage biomass can be initialized to non-zero values. Outputs from the forage model include levels of biomass for plant parts, the chemical composition associated with these parts, and senescence and disappearance rates for the plant parts. The model was structured to allow time step (DT) to vary from 1 d to a longer interval.

Simulated age of live leaf and stem are key components in this model. Age was selected as a key component because it integrates the effect of many physiological processes such as growth and senescence (Leopold, 1961, 1980; Wilson and Mannetje, 1978; Chapman *et al.*, 1984). Detling *et al.* (1979) used leaf age to control leaf death rates. They noted that leaf age directly and indirectly

(through increased moisture stress) influenced plant death rates. In their model, death rate increased from leaf age of 20 to 45 d and then remained constant.

Model functions

The simulated age of plant parts is for the average of the sward. The addition of new plant material (growth) to the biomass pool can reduce the mean age of the pool. The term pool is used in this paper to denote a quantity of biomass. For a single species within a pasture there are six pools (live leaf or stem, dead leaf or stem and old dead leaf or stem). Throughout the paper I, J, and K will refer to pasture, species, and pool respectively. Values for K of 1, 2, 3, 4, 5, and 6 are used to designate live leaf, live stem, dead leaf, dead stem, old dead leaf and old dead stem, respectively. Age is calculated as a weighted average of the new and old forage that is currently in the pool, with the age of the existing biomass increasing with time:

$$\text{AGE}_{(I,J,K)} = \frac{[\text{FORAGE}_{(I,J,K)} - \text{NGRO}_{(I,J)}]}{\text{FORAGE}_{(I,J,K)}} + \text{AGEP}_{(I,J,K)} + \text{DT} \quad (1)$$

where:

I = pasture,

J = plant species,

K = pool of leaf or stem,

FORAGE = biomass in a specific pool (g m^{-2}),

NGRO = growth for the current period (g m^{-2}),

AGEP = previous age of the pool (d),

AGE = new age of the pool (d) and

DT = time step (d).

A major advantage of using age to control senescence and quality is increased ease in adapting the model to different environments, which have different growth patterns. Furthermore, different growth patterns or life spans of different plant species can be incorporated into the model by adjusting functions based on age. This approach also reduces computer memory requirements compared to using a series of age cohorts.

Leaf age is in turn associated with forage quality in that deterioration processes associated with senescence reduce forage quality. During senescence, nutrients are transferred from senescing leaf and stem (Leopold, 1980). Senescence is a physiological process that is mediated genetically.

Senescence in plants occurs part by part; i.e., leaves, apical meristems, stems, and buds. Leaves may senesce while other plant parts remain alive. The model simulates the senescence of leaves and stems separately. Senescence processes are similar for annual and perennial grasses and forbs. The primary difference between perennial and annual herbs is the senescence of all buds in annuals and the survival of buds over the dormant season in perennials. Buds are not considered in this model. Seasonal differences in senescence rates within the same species have been documented (Hunt, 1971; Wilson and 't Mannetje, 1978). Brougham (1958) and Chapman *et al.* (1984) indicated that the survival of leaves is relatively constant within a species. To simulate senescence and to create a survivorship curve similar to Chapman *et al.* (1984) and Wilson and 't Mannetje (1978), difference equations were derived:

$$\begin{aligned} \text{SR} &= \text{T1} + \text{A1}[\text{AGE}(\text{I,J,K})], \quad (2) \\ \text{SENSC} &= \text{FORAGE}(\text{I,J,K}) * \text{SR} \quad (3) \end{aligned}$$

and

$$\text{FORAGE}(\text{I,J,K})_t = \text{FORAGE}(\text{I,J,K})_{t-1} - \text{SENSC} * \text{DT} \quad (4)$$

where:

SR = relative senescence (d^{-1}),
T1 = a basal relative turnover rate, $0.018 (\text{d}^{-1})$,
A1 = the coefficient regulating a per unit change of age, $0.000075 (\text{d}^{-2})$ and
SENSC = senescence rate ($\text{g m}^{-2} \text{d}^{-1}$).

Differential rates of senescence have been reported in the literature. Plant age in the SR function serves to increase or decrease the basal turnover rate. For grasses of different growth patterns it may be necessary to modify T1 and A1. Currently, T1 is the major component of the SR equation. As experience is gained with the model the importance of T1 can be better evaluated. Senescence of live stem uses the same equations; however, T1 and A1 have been modified to reduce senescence rate for stem compared to leaf.

If the minimum temperature (TMIN) drops below 0.0°C , freezing functions override the senescence equations for leaf and stem. The amount of live leaf or stem which is transferred to dead varies as a function of the severity of the freeze. The empirically derived equations describing the effect of a freeze for C_4 and C_3 grasses, respectively, are:

$$\text{SENSC} = \text{TMIN}/50 * \text{FORAGE}(\text{I,J,K}) \quad (5)$$

and

$$\text{SENSC} = \text{TMIN}/100 * \text{FORAGE}(\text{I,J,K}). \quad (6)$$

The processes of translocation and nutrient movement result in a decrease in the nutrient content of plant leaves and stems as they become older. Several studies have documented the decline of forage quality with age for grasses and legumes (Butterworth 1965, Johnson and Pezo 1975, and Wilson and 't Mannetje 1978). Using these published values, regression equations were derived for the model. The equations for proportions of crude protein (CP) and digestibility (DIG) of leaf are:

$$\text{CP}(\text{I,J,K}) = \text{BCPL}(\text{J,K}) + \text{BICPL}(\text{J,K}) * \text{AGE}(\text{I,J,K}) \quad \text{and} \quad (7)$$

$$\text{DIG}(\text{I,J,K}) = \text{BDL}(\text{J,K}) + \text{BIDL}(\text{J,K}) * \text{AGE}(\text{I,J,K}), \quad (8)$$

where

BCPL(J,K) = initial value for crude protein live leaf, 0.12,

BICPL(J,K) = the coefficient controlling the decrease of crude protein as age increases, $-0.0008 (\text{fraction d}^{-1})$.

BDL(J,K) = initial value for digestibility of live leaf, 0.70,

BIDL(J,K) = the coefficient controlling the decrease of digestibility as age increases, $-0.0025 (\text{fraction d}^{-1})$.

Stem quality is calculated by:

$$\text{CP}(\text{I,J,K}) = \text{BCPS}(\text{J,K}) + \text{BICPS}(\text{J,K}) * \text{AGE}(\text{I,J,K}), \quad \text{and} \quad (9)$$

$$\text{DIG}(\text{I,J,K}) = \text{BDS}(\text{J,K}) + \text{BIDS}(\text{J,K}) * \text{AGE}(\text{I,J,K}), \quad (10)$$

where:

BCPS(J,K) = initial value for crude protein of live stem, 0.09,

BICPS(J,K) = the coefficient controlling the decrease of crude protein as age increases, $-0.005 (\text{fraction d}^{-1})$,

BDS(J,K) = initial value for digestibility of live stem, 0.60,

BIDS(J,K) = the coefficient controlling the decrease of digestibility as age increases, $-0.002 (\text{fraction d}^{-1})$.

These equations assume a negative linear relationship between forage age and quality. When age of tissue is low and growth is rapid, forage quality will be high, and as age increases when growth slows or stops, quality will decrease. Currently, the same equation is used with

different coefficients for all forage pools and species. We assume age of plant biomass is the overriding factor affecting forage quality within a pool. The intercept and slope can be adjusted for different forage classes or species. Such flexibility contributes to the ability to use the model in different environments.

After plant material has senesced, it is transferred from the live to dead category. Before adding this material to the dead pool, digestible and nondigestible fractions are separated, and 55% (Z1) of the digestible biomass is transferred to a translocation/respiration sink. The digestibility of the remaining material is recalculated and assigned as the value for dead leaf. Crude protein is estimated in the same manner. The biomass losses for stem material are less for digestible organic matter and crude protein (20% and 10%, respectively). The following equations document how this is achieved:

$$\text{DIGLOS} = \text{SENSC} * \text{DIG}(I,J,1) \quad (11)$$

$$\text{NONDIG} = \text{SENSC} - \text{DIGLOS} \quad (12)$$

$$\text{DIGLOS} = \text{Z1} * \text{DIGLOS} \quad (13)$$

$$\text{FORAGE}(I,J,3) = \text{FORAGE}(I,J,3) + \text{DIGLOS} + \text{NONDIG} \quad (14)$$

where:

DIGLOS = the amount of digestible biomass (g m^{-2}) which is lost in translocation and

NONDIG = non-digestible biomass (g m^{-2}) which cannot be lost in translocation.

Transfer of standing dead biomass to litter is poorly understood. Detling *et al.* (1979) assumed that the physical force of precipitation caused fracturing and transfer to litter. However, work in the Chihuahuan Desert showed absolute quantity of rainfall was not as important as season of occurrence of precipitation for biomass decomposition (Whitford *et al.*, 1986). From this report and the lack of fit of the standing-dead category of the ELM model, which uses only precipitation to transfer standing dead (Innis, 1978), it appears that other factors are involved in the transfer of standing-dead to litter. Therefore, this model assumes two factors are controlling the transfer of dead material: precipitation and temperature. It was hypothesized that these factors act on dead material in the following ways. As with Detling *et al.* (1979), the physical force of precipitation

causes a transfer of standing dead material, according to the following equations:

$$\text{RAIN} = 1.0 - \text{EXP}(R1 * \text{PPT}), \quad (15)$$

where:

R1 = -0.03077 (DT cm^{-1} of precipitation) and
PPT = the amount of precipitation (cm DT^{-1}).

The effects of temperature are combined with precipitation in the following difference equations for the disappearance of dead leaf:

$$\text{DEADIS} = \text{RAIN} + \text{T2}(\text{TEMP}) * \text{DT}, \quad (16)$$

$$\text{DUMP} = \text{FORAGE}(I,J,3) * \text{DEADIS}, \quad \text{and} \quad (17)$$

$$\text{FORAGE}(I,J,3) = \text{FORAGE}(I,J,3) - \text{DUMP}, \quad (18)$$

where:

DEADIS = relative transfer,

DUMP = amount of dead material removed (g m^{-2}),

TEMP = temperature ($^{\circ}\text{C d}^{-1}$) and

T2 = a coefficient used to adjust the loss of dead material owing to temperature, 0.0005 ($^{\circ}\text{C}^{-1}$).

There are different rates of disappearance for dead stem. More precipitation is required to transfer stem to litter compared to leaf.

$$\text{RAINST} = 1.0 - \text{EXP}(R2 * \text{PPT}), \quad (19)$$

where: $R2 = -0.01$ (cm^{-1}).

For dead stem, the relative transfer function (STMDIS) is:

$$\text{STMDIS} = \text{RAINST} + (\text{T3}) \text{EXP}[-0.044454 * \text{AGE}(I,J,4)] * \text{DT}, \quad (20)$$

where: $\text{T3} = 0.005866$ (d^{-1}).

The quality of dead leaf and stem is the weighted average of the previous time step and the amount of digestible or crude protein material that remains in the senescent material after the translocation process occurs. Digestibility and crude protein of dead leaf are calculated as:

$$\text{DIG}(I,J,3) = \text{DLDIG}(I,J)/\text{FORAGE}(I,J,3), \quad \text{and} \quad (21)$$

$$\text{CP}(I,J,3) = \text{CP}(I,J,3) * [1.0 - \text{SENSC}/\text{FORAGE}(I,J,3)] + \text{CPLL} * [\text{SENSC}/\text{FORAGE}(I,J,3)], \quad (22)$$

where:

$DLDIG(I,J)$ = amount of digestible dead leaf ($g\ m^{-2}$),

$SENSC = FORAGE(I,J,1) * SR$, where $SENSC$ is expressed in $g\ m^{-2}\ d^{-1}$ and reduced by the translocation loss and

$CPLL = CP(I,J,1) * Z1$, the result of translocation loss.

Qualities for dead stem are calculated in similar fashion:

$$DIG(I,J,4) = DIG(I,J,4) * [1.0 - SENSC / FORAGE(I,J,4)] - DLGSTM * [SENSC / FORAGE(I,J,4)], \text{ and} \quad (23)$$

$$CP(I,J,4) = CP(I,J,4) * [1.0 - SENSC / FORAGE(I,J,4)] + CPLSTM * [SENSC / FORAGE(I,J,4)], \quad (24)$$

where:

$$DLGSTM = DIG(I,J,2) * Z2$$

$$CPLSTM = CP(I,J,2) * 0.90, \text{ and}$$

$Z2$ = proportion of digestible stem biomass lost in translocation, 0.80.

The fifth and sixth components of forage classes or species, which are simulated are old dead leaf and old stem stem. These pools are carried over from the previous year. The biomass in the dead leaf and stem pools at the end of the simulated year are transferred into the old dead leaf and stem pools at the initiation of a new growing season.

Precipitation is the input parameter which controls the transfer of old dead leaf and old dead stem to litter (thereby leaving the system). For old dead leaf (FALOLD) the equation is:

$$FALOLD = 0.01 + P1(PPT), \quad (25)$$

where: $P1 = 0.021\ (g\ m^{-2}\ cm^{-1})$.

For old dead stem, a similar equation is used except precipitation has a smaller influence upon the movement of old dead stem ($P1 = 0.015$). The decrease in old dead leaf and stem quality is a linear decline from the initial quality of the pool. For leaf these equations are:

$$DIG(I,J,5) = DIG(I,J,5) - D1[DIG(I,J,5) * DT], \text{ and} \quad (26)$$

$$CP(I,J,5) = CP(I,J,5) - C1[CP(I,J,5) * DT], \quad (27)$$

where: $P1 = 0.021\ (g\ m^{-2}\ cm^{-1})$.

For old dead stem the equations are of the same form, but $D1 = 0.002\ d^{-1}$ and $C1 = 0.0002\ d^{-1}$.

Forbs

Simulation of forb dynamics is necessary to add realism to the range situation. Previous models have not adequately simulated forbs, (Innis, 1978). In the description of the grass component, three items were identified as having a major influence on forage accumulation: the input growth rate for leaf and stem, the senescence rate and its associated biomass loss, and the transfer from dead to litter. By adjusting these factors either by changing the input for growth or by increasing or slowing the rate functions, forbs can be simulated. Reports by Brougham (1958) and Chapman *et al.* (1984) also indicate that this approach is feasible. Brougham (1958) reported that white clover leaves reached their maximum weight at a leaf age of 20-26 d and the life cycle of the individual leaves ranges from 28 to 34 d. Chapman *et al.* (1984) showed white clover survival curves to be longer than those found by Brougham (1958), ranging from 56 to 105 d, but they were very similar to the grass species studied simultaneously. Senescence rate of live leaf and stem can be altered in this model primarily by changing $T1$ of Equation 2. Levels of biomass accumulating in dead pools are controlled by senescence and the translocation coefficients $Z1$ and $Z2$. For our initial work with forbs it is assumed that they have a shorter life span. Therefore, the $T1$ value is increased to 0.028 for leaves and stems. In simulating the disappearance of dead leaves and stems it was assumed that forbs would not remain in the standing-dead category as long as grasses. Therefore, the $R1$ parameter in the RAIN equation was increased to 0.05, $T2$ in DEADIS was increased to 0.005, and $T3$ in STMDIS was altered to 0.05.

Johnson and Pezo (1975) showed legumes to be higher in quality than grasses. However, the rate of decline with age was similar. Therefore, the quality parameters changed were: $BCPL = 0.25$, $BDL = 0.80$, $BCPS = 0.20$, and $BDS = 0.70$.

Validation

Three studies using four grass species were used to validate the model: a short-term 36-d study using hybrid bermudagrass (*Cynodon dactylon*), a

Table 1. Net growth rates calculated from standing crop measurements and the adjusted values used for the simulation ($\text{g m}^{-2} \text{d}^{-1}$)

Day	Leaf			Stem		
	Calculated	Adjusted	Deviation	Calculated	Adjusted	Deviation
4-8	7.5	8.0	-0.5	0.6	0.3	0.3
8-12	12.5	13.0	-0.5	4.8	2.0	2.8
12-16	8.7	9.0	-0.3	6.4	6.0	0.4
16-20	18.5	20.0	-1.5	23.3	24.0	-0.7
20-24	0.0	8.0	-8.0	0.0	10.0	-10.0
24-28	12.3	12.0	0.3	17.4	15.0	2.4
28-32	1.9	5.0	-3.1	17.8	10.0	7.8
32-36	4.2	7.0	-2.8	5.1	17.0	-11.9
36-40	0.0	3.0	-3.0	30.1	30.1	0.0

180-d oat (*Avena sativa*) study, and a 1-year study involving little bluestem (*Schizachyrium scoparium*) and brownseed paspalum (*Paspalum plicatulum*). The only model function altered in simulating the four species was T1, which was changed from 0.018 to 0.01 for the bermudagrass and the oat studies. A time step of 1 d (DT) was used for the reported simulations.

Bermudagrass simulations. The bermudagrass experiment evaluated growth with no limitation of nutrients or water. The plots were closely clipped on day zero, the standing crop was measured every 4 d. Biomass was separated into live leaf, live stem and total dead material (M. Hussey, personal communication). The model was set up to stimulate biomass dynamics of the bermudagrass plots. From the standing-crop data, net growth rates for leaf and stem were calculated based on the net change in standing crop. These were used as the initial inputs for simulation. Throughout this section of the paper it will be demonstrated that estimates of net growth rate tend to be lower than the simulated growth rate which is required to have simulated standing-crop equivalent to actual standing crop. A comparison of the calculated net growth rates (based on actual standing crop) and the growth rates used for final validation are presented in Table 1. Differences between calculated and adjusted values are small in the initial stages of the experiment. However, after day 20, the deviation becomes larger. This is an indication that leaf senescence was equal to, or greater than growth rate. Since the model accounts for both processes, the growth rate input for simulation had to be higher than the calculated net growth rate for actual and simulated standing crops to be equal. The comparison of actual and simulated standing

Figure 1. Actual (+) and simulated (solid line) standing crop for bermuda grass.

crops is presented in Figure 1. With the adjusted growth rates, simulated live standing crops agree closely with actual data. Important criteria to evaluate are the feasibility of the growth rates

Table 2. Simulated bermudagrass age^a, crude protein (CP), and digestibility (DIG) for live leaf and stem

Day of Simulation	Leaf			Stem		
	Age (d)	CP (%)	DIG (%)	Age (d)	CP (%)	DIG (%)
4	2.1	11.8	69.5	22.3	7.9	55.5
8	3.3	11.7	69.2	21.8	7.9	55.6
12	5.6	11.5	68.6	17.1	8.1	56.6
16	6.2	11.5	68.5	9.4	8.5	58.1
20	8.7	11.3	67.8	9.8	8.5	58.0
24	12.5	11.0	66.9	13.5	8.3	57.3
28	14.1	10.9	66.5	13.2	8.3	57.4
32	16.4	10.7	65.9	17.2	8.1	56.6
36	20.4	10.4	64.9	15.3	8.2	56.9

^a Age = mean age of the live leaf and stem pools.

used and the age of live leaf and stem biomass. Use of both criteria helps prevent use of growth values which are unrealistic.

This particular aspect of setting model parameters focuses attention on the problems involved in estimating growth rates of plants from experimental data. Using age as a criterion for evaluation provides a variable which can be measured in the field. Simulated plant ages are given in Table 2. A disadvantage to the estimation of growth inputs and the subsequent adjustment of these values upward is that there is no unique solution to a particular year's growth rates or biomass. However, absolute values are perhaps not as important as the trend and magnitude of changes in growth rates.

Oat simulations. The next validation study was with oats. The oats were planted in late September, and measurements were taken on a uniform cohort of plant material. Data were collected at approximately 30 d intervals. Standing crop was estimated from 1.0 m² plots clipped to ground level. Individual plants were also harvested and separated by forage pool to determine the proportion of plant parts. This information was used for validation. Results from the validation are presented in Figure 2.

Growth rates for model input were adjusted so actual and simulated live plant material were in close agreement. The interesting comparison in this series of validations is that of dead materials. Until day 60 for dead leaf and day 90 for dead stem, there was close agreement between actual and simulated data. After day 60 there was a greater accumulation of simulated dead leaf; the

difference occurring at day 90 remained constant for the duration of the study. This implies that the difference generated at this time was due to a causative factor in the physical world. If this is indeed the case, there may be two causes. First, senescence may have slowed. Alternatively, disappearance of dead material may have increased for the 60 to 90 d time interval and then slowed after the causative factor was relaxed. The difference between actual and simulated dead stem occurred near day 120; at this time the actual accumulation of dead stem levelled, but the simulated value decreased by approximately one-third of the previous value. After day 120, both actual and simulated values responded in the same direction and with similar magnitudes of increase for the duration of the study. These results indicate that the model may not be accounting for all factors controlling the transfer of dead material in the system. They also demonstrate the need for more comprehensive information detailing how dead material is affected by alterations in plant biomass and age structure and how environmental variables are affecting the accumulation of biomass. Previous documentation of the problems relating to simulating dead material have been reported (Innis, 1978).

Bluestem and paspalum simulation. The third study used for validation involved two native species, little bluestem and brownseed paspalum. The data were collected for a complete year and Figure 3 and Figure 4 show the comparison between actual and simulated plant parts for both species. Generally, the actual and simulated live leaf and stem are in close agreement. There is divergence between actual and simulated dead components. It should be noted that these two species differ in the form and seasonality of their growth. Little bluestem has more stem biomass and has a more erect growth form than brownseed. These different growth forms should be translated into differences in biomass, and this was the case. For both species, agreement between actual and simulated data improves with time. Early disagreement between dead leaf and stem components is largely due to the actual dead components being a summation of recent dead and old dead material. As the year progresses, old dead material decays and leaves the system, and the recent dead material starts to accumulate. The dead leaf component of little bluestem remains relatively close to actual data in the later part of

Figure 2. Actual (+) and simulated (solid line) standing crop for oats.

Figure 3. Actual (+) and simulated (solid line) standing crop for little bluestem.

Figure 4. Actual (+) and simulated (solid line) standing crop for brownseed paspalum.

Table 3. Simulated values for little bluestem and brownseed paspalum age^a, crude protein (CP), and digestibilities (DIG)

Day of Simulation	Little Bluestem						Brownseed Paspalum					
	Live Leaf			Live Stem			Live Leaf			Live Stem		
	Age (d)	CP (%)	DIG (%)	Age (d)	CP (%)	DIG (%)	Age (d)	CP (%)	DIG (%)	Age (d)	CP (%)	DIG (%)
30	11.7	12.0	72.0	—	—	—	7.1	12.4	74.1	6.4	8.5	57.6
90	25.3	11.0	66.5	12.9	8.0	54.9	26.1	10.9	66.2	19.4	7.4	52.4
140	29.1	10.7	64.9	28.1	6.8	49.1	32.7	10.4	63.4	29.2	6.7	48.7
180	38.5	9.9	60.9	35.6	6.3	46.5	38.1	10.0	61.1	49.7	5.4	41.9
230	51.1	8.9	55.6	42.6	5.9	44.1	36.3	10.0	61.9	54.2	5.2	40.5
280	54.3	8.7	54.3	59.3	4.9	39.0	54.3	8.7	54.3	72.3	4.3	35.5
330	69.1	7.5	48.1	84.5	3.8	32.4	75.8	6.9	45.3	83.1	3.9	32.7

^a Age = mean age of the live leaf and stem pools.

the year. The dead stem component of the same species shows extremely close agreement in the middle portion of the study. However, the simulated dead stem decreases in the later time periods while the actual value increases. This difference was largely generated by a larger proportion of live stem being transferred to dead material than was simulated. The most probable cause of this increased rate of transfer was that the actual stem was more vulnerable to freezing than was simulated.

Comparison of brownseed dead components shows a different pattern of biomass accumu-

lation. Biomass accumulation of brownseed dead leaf was of a lower magnitude than that of little bluestem. Simulated values for dead leaf were lower in the initial portion of the year, for reasons already discussed above with little bluestem, and higher than the actual values by year's end. With the values for live leaf in such close agreement it would appear that dead material is moving out of the system at a faster rate than was simulated. However, for this particular year, this rate appears to be relatively constant. Brownseed dead stem is less consistent in biomass present at various times during the year. The simulated

values had a much greater consistency and showed an accumulation much more like the live biomass accumulations.

Evaluation of age function

As stated in the methods section, the age function has permeating effects throughout the model. This concept was used to make the model as robust as possible. The age of biomass in a live pool can increase or decrease depending upon how much growth occurs at a given point in time. This approach has several advantages over using phenological classes. Although phenological classes can be easily associated with real world characteristics of a plant, they tend to be rigid in their structure and change the characterization from a continuous function, as it is in reality, to a discrete variable. Furthermore, the inclusion of such characters in a model reduce the dynamic nature of the program. A second advantage results from relating forage quality to an age function. Quality becomes a continuous function increasing with young material and decreasing as biomass ages. Therefore, it is possible for quality in a given pool to either increase or decrease over time.

Age of leaf and stem and their qualities are presented in Table 2 and Table 3 for little bluestem, brownseed paspalum and bermudagrass. Comparing all three species, it is apparent that age varied as a function of growth rate. Perhaps of greatest interest is how at various points in time the growth rate was high enough to keep age relatively constant with time (e.g., day 90 to day 140 for little bluestem, day 140 to day 230 for brownseed) and with decreased age the corresponding increase in quality (e.g., bermudagrass live stem).

Conclusions

This model takes a different approach to simulating forage systems than previously constructed simulation models. Its primary emphasis is the flow of biomass through the forage or range system. It is not intended to simulate growth. The deterministic nature of the model allows evaluation of the rates of change in the system of interest without stochastic variation influencing the model's response. This has an advantage; it allows scientists to focus on cause and effect

relationships that control the flow of plant material through the system. From the results presented, it is apparent that evaluations of forage production systems based upon net forage accumulation can be misleading. This is primarily a result of increased senescence rate as forage matures. When growth and senescence are equal, net growth is zero. Models based on net growth may overlook a highly dynamic series of plant processes. Furthermore, non-consideration of these processes may lead to erroneous conclusions when trying to evaluate different levels of herbivory. In addition, the approach taken in constructing the model will enable it to be used to evaluate rates obtained from physical experiments which will have evaluated senescence rates and transference of dead material to litter.

The validation results show that with minimal data for growth rates, the model can emulate physical world results of plant biomass and provide realistic quality values to serve its primary function of providing data suitable for interfacing with a diet selection model. The concepts used in model construction are shown to be of a general nature, allowing the model to be robust in simulating a variety of forages. This is important if the model is to be useful for simulating rangeland and mixed forage systems. In addition to the model's primary function, the validation results demonstrate the model's capability to address questions concerning the factors controlling transfer of biomass from live to dead to litter. This provides researchers with a new capability to address hypotheses concerning the properties of forage dynamics. The validation shows the model to have difficulty in consistently simulating dead material. We believe this to be more a statement of the lack of biological knowledge concerning dead biomass dynamics than a criticism of the model.

Besides an interest in simulating biomass for diet selection purposes, the model has utility for addressing questions concerning plant growth and sward structure. Planned applications for the model are to link it with various plant growth models, representing different hypotheses of plant growth, to test these models and evaluate forage growth and senescence in grazed as well as ungrazed situations.

Acknowledgments

Dr D. Scarnecchia contributed to the early

conceptual development of the model. Members of the Grazing Management Research Team, and particularly Drs Heitschmidt, Briske, and Stuth contributed suggestions during initial model development. Actual bermudagrass data were provided by Dr M. Hussey. The work was supported in part by Grant No. US99-7-85 from BARD, the United States-Israel Bi-national Agricultural Research and Development Fund. Texas Agricultural Experiment Station manuscript number TA-23576.

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(Received 16 May 1988; revised 21 November 1988)

5.2 DIET SELECTION MODEL

SUMMARY

A mechanistic simulation model was developed which provides an interactive interface between plant and animal simulation models. It incorporates recognized diet selection concepts with animal intake control mechanisms to produce an effective quantitative representation of diet selection and intake by herbivores. Preference is defined by an index calculated from forage crude protein and digestibility and a user assigned avoidance scalar. Palatability is related to potential restrictions to forage intake by anti-quality components. Dietary restrictions arising from low forage availability are simulated using a Michaelis-Menten type function. Inputs of forage quality and availability are obtained from a forage dynamics model and output from the diet model goes to an animal production model. Sensitivity analyses were conducted to determine the diet selection and intake responses to variations in selected model inputs and functions. Diet selection and nutrient intake were highly responsive to changes in forage growth rates, stock density, forage availability, and the forage quality functions in the desirability index. The model provides a working hypothesis for evaluating biological cause and effect mechanisms of diet selection and intake by grazing ruminants. Additionally, the level of resolution of the combined forage-diet-animal models is appropriate to provide a basis for developing management recommendations.

INTRODUCTION

Attempts to simulate the grazing behavior of herbivores have been diverse and the degree of complexity dependent upon the purpose of the model (Rice et al., 1983; Loewer et al., 1987; Ungar and Noy-Meir, 1988; Sneft, 1989). Studies have approached diet selection at many levels of spatial and temporal hierarchies (Sneft et al., 1987), and at different levels of resolution with respect to biomass classification (Arnold and Dudzinski, 1978). McNaughton (1984) evaluated diet selection in terms of coevolution of plants and animals, while tactical aspects of diet selection have been considered by Ellis et al. (1976). It is apparent that no one hypothesis describing diet selection accounts for all significant sources of variation across environments. Instead, animals blend elements of foraging theory, hierarchical theory, etc. (Sneft et al., 1987; Sneft, 1989). The concept of herbivores maximizing dietary energy may be valid; however, strategies for maximizing energy intake are complex. Range herbivore diets commonly contain a large number of plant species and plant parts indicating that they do not harvest forage in a purely hierarchical manner (Demment and Greenwood, 1988).

Few models have attempted to bridge the gap between theory and management (Sneft, 1989). There is a need to integrate concepts for botanical selection with those for forage quality and intake to simulate plant/animal interactions at a management scale of resolution. For such an effort to be successful, the major components driving diet selection and nutrient intake must be incorporated into the diet selection routine. The model of diet selection reported here differs from previously reported models in level of resolution and conceptual design. Forage species (or species group), quality, and availability are considered. Animal factors dealing with preference, palatability, and foraging ability have

been incorporated into the model. It provides for interactions between forage quality and availability. The interaction between plants and animals can be observed as a dynamic process reflecting changes in the physiological condition of plants, animals and herd structure.

This model was developed to apply diet selection theory to generate management level data, allowing grazing management concerns to be addressed. Generalized diet selection protocols were developed, giving the model broad applicability. This allows evaluation of interactions and feedback between animals and forages. Utilization of such models can greatly increase understanding of grazing behavior in dynamic environments. The objectives here are to report the model structure and function and to demonstrate its ability to simulate plant/animal interactions at a management level of resolution.

MODEL DESCRIPTION

The diet selection model was constructed to interface a dynamic forage model with dynamic animal production models (Figure 1, p 45). It receives input from the forage model described by Blackburn and Kothmann (1989) and provides inputs for the cattle production simulation model described by Doren et al. (1985) and the sheep or goat production simulation models described by Blackburn et al. (1987). The forage model simulates species or species groups partitioned into leaf and stem with live, recent dead, and old dead, referred to as forage pools. The number of forage pools simulated is determined by the objectives of the researcher and the level of resolution of data available to validate both forage and diet models. With this model, species with similar structural and growth characteristics can be simulated separately or as a group. Diverse species in the plant community should be partitioned to account for major sources of structural and nutritional heterogeneity.

The diet selection model has no state variables. It determines the amounts of dry matter, crude protein (CP), and digestible dry matter (DDM) to be transferred from each forage pool of the forage model to the animal model. We adopted the approach that large ruminant herbivores are basically generalist foragers. Concepts for preference, palatability, and harvestability have been implemented in the diet model in a unique approach which allows interactions between these components. Preference relates to factors affecting relative choice (not intake). Palatability addresses anti-quality factors which limit voluntary intake of a particular forage pool. Harvestability determines restrictions to the potential ingestion rate of each pool based on availability. Harvestability is a function of structural characteristics of the forage and the animal's prehensile ability. This mechanistic approach is responsive to a wide variety of forages and is readily adaptable to different animal species and locations.

Inputs for the diet model are from three sources: (1) potential intake (kg) of the combined herd, from the animal production model, (2) availability (gm^{-2}) and quality (percentages of CP and DDM) of each forage pool, from the forage model, and (3) values for avoidance, palatability, ungrazable residual, and KM for each forage pool, from user inputs. Both animal and forage inputs can vary across time. To illustrate the logic flow of the model, a summary of the steps used to determine a diet follows:

- Step 1. Calculate desirability of each forage pool based on CP, DDM and avoidance index.
- Step 2. Based on desirability index, calculate desired proportions for each forage pool.
- Step 3. If desired proportion exceeds palatability rating, limit intake from forage pool and re-proportion excess to other forage pools.
- Step 4. Determine total potential intake of desired diet using the weighted average of DDM and CP from the forage model and the physical limit equations and number of animals from the animal model.
- Step 5. Multiply desired proportions by total potential intake to determine desired intake of each forage pool.
- Step 6. Calculate harvestability of each forage pool. Evaluate for restricted availability of forage pools. If harvestability equals one for all forage pools or iteration equals 3, proceed to step 7, if not, return to step 1 and adjust desirability indexes of each forage pool using respective harvestability coefficient.
- Step 7. Calculate proportions of each forage pool based upon harvestable forage. Then calculate weighted average digestibility and percentage of crude protein of the diet and the animal intake correction factor; proceed to the animal model.

Model Components

Preference. An initial step in diet selection is determining which plants and plant parts will be more intensively sought. A desirability index is calculated;

$$DESIND_i = CFDIG_i * CFCP_i * AVOID_i \quad (1)$$

where,

$DESIND_i$ = desirability index for the i^{th} forage pool,

$$CFDIG_i = 1.67 * (DDM_i - 0.20), \quad (2)$$

DDM = digestible dry matter proportion of the i^{th} forage pool,

$$CFCP_i = 3.509 * (CP_i - 0.015), \quad (3)$$

CP = crude protein proportion of the i^{th} forage pool and

$AVOID_i$ = avoidance scaler for the i^{th} forage pool (0.0 to 1.0).

Avoidance is a scalar that is designed to reflect negative preference factors. Preference may be reduced by chemical and/or physical characteristics of forage that are not reflected in CP or DDM. The avoidance coefficient is used to adjust for these differences by assigning an avoidance value less than 1.0. The coefficients CFDIG and CFCP can be adjusted for different animal species by adjusting the intercept and slope and/or by raising them to a power greater than 1.0. This alters the sensitivity of diet selection to forage quality.

Desired dietary proportions (PROP) are calculated from the desirability indexes (Equation 4). The equation for desired proportion for each forage pool is,

$$PROP_i = DESIND_i / \sum (DESIND_i). \quad (4)$$

$$i = 1, n$$

Palatability. Palatability is a scalar ranging from 0.0 to 1.0. Palatability reflects factors other than DDM and CP which restrict potential intake of forage. The proportion of forage taken from any pool can not exceed its palatability rating. If a desired proportion is greater than its palatability rating, the difference between desired proportion and the upper limit set by palatability is re-proportioned among forage pools with no or unmet palatability limits. Examples of range species with potential palatability limitations are sagebrush (*Artemisia* spp.) and juniper (*Juniperus* spp.) which contain large amounts of phenolic compounds. Livestock grazing these species will not consume to their potential intake, even if an adequate amount is available and no other forage is present.

Intake. The model calculates a weighted average digestibility of the desired diet and uses the physical limit equations presented by Sanders and Cartwright (1979) or Blackburn et al. (1987) to simulate potential forage demand for each class of livestock. The values are multiplied by animal numbers per class and summed across animal classes to determine total potential intake. Potential intake of each forage pool is calculated as the product of the total potential intake and the desired proportion for that pool. If potential intake is not restricted by availability of any forage pool, the diet model passes the weighted average DDM and CP of the diet and an animal intake correction coefficient (AIC) of 1.0 to the animal model.

Harvestability Coefficient. Potential forage intake and standing crop are used to calculate a harvestability coefficient for each pool. The harvestability coefficient determines the proportion of desired intake that can be obtained from a forage pool. If the harvestability coefficient of any pool is less than one, the model adjusts the desirability index of each forage pool by multiplying by its harvestability coefficient and then makes another iteration through the diet selection process. If a deficit still exists after three iterations, the accumulated intake is divided by the potential intake calculated during the third iteration to determine the AIC value. An AIC value less than 1.0 reduces intake simulated by the animal model for each animal by the complement of the AIC. It should be noted that the harvestability coefficient is associated with individual forage pools; whereas, AIC is associated with the total diet.

Several hypotheses have been proposed as to the possible shape of the function relating forage availability and intake. Noy-Meir (1978) suggested that the shape of the function could be sigmoidal, a saturation curve or a ramp function. We used a saturation curve, in the form of a Michaelis-Menten function (Figure 2, p 46). The Michaelis-Menten equation (5) used to calculate the harvestability coefficient (range 0.0 to 1.0) is,

$$\text{HARVEST}_i = (1.1 * \text{FORAGE}_i) / (\text{KM}_i + \text{FORAGE}_i) \quad (5)$$

where,

FORAGE_i = the biomass ($\text{kg} \cdot \text{ha}^{-1}$) present for the i^{th} forage pool,

KM_i = the Michaelis constant, and

1.1 = the asymptotic value allowing HARVEST_i to exceed 1.0.

If $\text{HARVEST}_i > 1$, then HARVEST_i equals 1.

The Michaelis-Menten equation allows flexibility in varying the rate of forage harvestability by changing the value of KM. Restrictions to intake may result from low forage density and/or low plant stature which reduce bite size. The input coefficient KM represents the relationships between availability of a forage pool, bite size of the grazing species and prehensile ability of the grazing species. The value used for KM varies depending upon the animal species and plant species, part and growth form. The KM value for leaves of a grass with erect growth form may be quite small; whereas, a grass with decumbent or prostrate growth form would have a larger KM value. The value selected for KM will also need to consider the animal's prehensile ability.

In some situations there may be an ungrazable residual for a forage pool. This occurs because the forage is above or below the potential grazing height or otherwise inaccessible to the animal being simulated. In such situations, the user specifies the quantity of ungrazable residual forage, and this value is subtracted from the existing forage biomass before the diet selection procedures are initiated. Different values for KM and ungrazable residual may be specified for different animal species on the same pasture.

Two approaches can be used to determine values for KM. The selection of method depends upon the kind of information available. The first approach involves the basic assumptions made in the calculation of harvestability. If the minimum level (FMAX) where a forage pool has a harvestability of 1.0 is known; i.e., the minimum level of freely available forage, then equation (6) can be solved for KM. Algebraic manipulation of the harvestability equation yields KM for a specific forage pool:

$$\text{KM}_i = 0.1 * \text{FORAGE}_i \text{ (at FMAX}_i\text{)}. \quad (6)$$

The second approach is to utilize the Lineweaver-Burk plot (Bohinski, 1976) or a transformation/weight model (Ruppert et al. 1989). These procedures may give a precise estimate of KM, but they require estimates of harvestability at different levels of forage biomass availability. Because KM, specified for each forage pool, is a new concept, few researchers have collected biomass data at this level of resolution. However, this provides an opportunity to better quantify the forage resource.

If harvestability is less than 1.0, the amount of forage taken from the pool is determined as follows. All forage above the point of restricted availability (FMAX) is considered completely available. Demand for forage of restricted availability will be adjusted downward to the proportion indicated by the harvestability coefficient. This results in a deficit in the animal intake function. As in the physical world, when a deficit occurs, the animal, given time, will search for a replacement. To simulate this activity, desirability indexes are recalculated and adjusted by multiplying them by the harvestability coefficient. This allows animals to take increments from the deficit pool but shifts the diet selection emphasis to pools with greater harvestability.

Time step. The forage and diet models are usually run on a 1-day time step. The sheep and goat models operate on a 15-day time step and the cattle model on a 30-day time step. Simulated daily intake from the diet model is used to update state variables in the forage model daily. Intake is accumulated over 15 or 30 days and passed to the animal model with the weighted average values for DDM, CP, and AIC.

SENSITIVITY ANALYSIS

Methods

A series of 86 simulation experiments were conducted using the diet model as the interface between a forage dynamics model (Blackburn and Kothmann 1989) and a sheep production model (Blackburn et al. 1987). The simulated experiments formed a 2 X 2 X 3 X 7 factorial with two plant growth scenarios, two expressions of the preference function, three levels of KM, and seven levels of stocking density, respectively. In addition, there was one simulation of forage biomass dynamics with no grazing (a control) for each plant growth scenario.

All simulations were run for 210 days. The initial age of live leaf present on day 1 was set to 6.8 days. Avoidance and palatability scalars were set at 1.0 for all forage pools for all runs. This eliminated them from consideration in this sensitivity analysis to allow primary attention to be focused on the desirability and availability functions.

Plant growth was constant during growth periods. The first plant growth treatment consisted of one species growing at the rate of $3.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from day 1 to 150 with initial live leaf biomass set at $10.0 \text{ g} \cdot \text{m}^{-2}$. The second treatment consisted of two species with the one growing at the rate of $1.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from day 1 to 150 (initial biomass of $10.0 \text{ g} \cdot \text{m}^{-2}$) and the other growing at the rate of $1.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from day 31 to 180 (initial biomass set at zero).

Eight stock densities (0, 5, 8, 10, 12, 15, 18, and 20 head $\cdot \text{ha}^{-1}$) were evaluated to assess the effects of increasing forage demand. Grazing began on day 1 and continued through day 210 with constant stock density throughout all simulations.

Two versions of the desirability function were used. The first version (DESIND1) was reported in Eqn. 1. In the second version, CFDIG and CFCP were each raised to the third

power (DESIND2). The effect of this was to increase the model's sensitivity to forage quality.

Three levels of KM (10, 50, and 100) were evaluated to determine their effects on forage and diet dynamics. These values of KM were assigned to each forage pool of live and dead forage for each species.

Response variables evaluated were standing crop (SC) of live and dead leaf biomass, desired proportions of diet components, composition of diet actually selected, diet digestibility, AIC, and digestible nutrient intake per sheep (kg). Response surfaces were generated from output at 15-day intervals with time and stock density as the independent variables. The response surfaces were created by connecting the data points generated from the simulations, not by mathematical fitting. Separate response surfaces were generated for each plant growth treatment, KM value, and desirability function. Since the models are deterministic, output data were not evaluated statistically.

Simulation Results

Standing crop. Figure 3 (p 47) presents the standing crop (SC) of live leaf for species one for all simulations using the adjusted desirability index. Stock density and growth rate were the dominant influences. At zero stock density, SC increased until about day 90 when growth and senescence reached equilibrium. After growth stopped on day 180, SC of live leaf declined to near zero by day 210. As stock density (SD) increased, SC of live leaf decreased. There was very little accumulation of dead leaf, indicating that very little live leaf was senesced at high SD.

There was an interaction of SD and KM. At SD less than $12 \text{ hd} \cdot \text{ha}^{-1}$ and with 1 or 2 species, SC of live leaf was similar across KMs. However, as SD increased above 15 hd , SC was strongly influenced by KM. In these situations, SC increased as KM increased.

Diet selection. The proportion of live leaf one desired in the diet for simulations with one species on the first iteration of the model varied as the DESIND index function was changed to increase diet sensitivity to CP and DDM (Figure 4, p 48). With low sensitivity (DESIND1), the desired diet initially contained only 74% live leaf compared to 96% with the high sensitivity function (DESIND2). Obviously, the model is very responsive to changes in this function, indicating its potential usefulness in simulating different sensitivity to diet quality by different herbivores. For example, small ruminants can be expected to graze more selectively than large ruminants; thus, the low sensitivity may be more appropriate for cattle and the high sensitivity more appropriate for small ruminants such as sheep, goats, and deer.

Simulation of two plant species of comparable preference and palatability resulted in diet shifts to approximately equal amounts of both species in the diets when SC became large enough to allow unrestricted grazing. After growth stopped for both species, initial preference for live leaf differed between the two preference functions. The reduced proportion of live leaf requested with DESIND2 indicates that remaining live leaf of species one was of lower quality than had previously been encountered.

Actual proportions of live leaf in the diet are presented in Figure 5, p 49. Proportions selected in early stages of simulation indicated no differences between desirability equations. These results differ from the initial desired proportions (Figure 4, p 48). The difference was due to low availability of dead material desired by equation one. This caused a shift in diet components selected resulting in very similar diets. With lower KM, the response surfaces between the two desirability equations were different at points due to alterations of plant age and quality. Differences between other portions of the factorial were primarily observed as KM was altered. As KM decreased, less live leaf was available to be selected in the diet as a result of smaller accumulations of live leaf.

To better illustrate how the model emulates the dynamics of diet selection, the proportions of all four simulated forage pools are presented in Figure 6, p 50, for the two species, DESIND2 runs. The selection of live leaf of species one and two were nearly equal between days 30 and 150 while there was constant growth. After species one stopped growth, consumption of live leaf of species two increased as did dead leaf of both species. Dead leaf increased because of the limited availability of live leaf. Live leaf of both species was rapidly depleted under all stocking densities after growth stopped. From these results the dominant impact of leaf growth on diet selection is high-lighted, indicating the need for understanding both plant and animal components of the grazing system.

Based on these results and to conserve space, only the results of simulations with desirability function two (DESIND2) are presented for the remaining variables.

Diet digestibility. Diet digestibility remained relatively constant while forage was growing (Figure 7, p 51). The additional growing period in the two species simulations provided a higher quality diet for a longer period of time. As KM increased, the rate of decrease in digestibility for high SD was slowed due to a larger accumulation of SC. However, when KM was large, digestibilities for all SD were lower during the entire simulation.

Before day 150 in the one species simulations, a slight quadratic response was observed for digestibility with highest levels observed for SDs of 15 and 12 for KMs of 10 and 50, respectively (Figure 7, p 51). This response was mediated through high demand keeping live leaf age low resulting in higher quality, and the limits placed on harvestability by KM. High demand reduced leaf aging, thus reducing senescence. The responses to diet digestibility were amplified in the process of calculating digestible dry matter intake. Thus, while the variations in diet digestibility may appear relatively small, the animal model was very sensitive to changes in this variable.

Animal intake correction factor. All of the independent variables studied had a marked influence on AIC (Figure 8, p 52). AIC for the one and two species simulations differed markedly and interacted with the level of KM and SD. Because there were four forage pools with the two species simulation and only two forage pools with the one species simulation and the same amount of total growth, the KM of 50 on the two species was similar to the KM of 100 for the one species. This response implies that the appropriate value for KM may decrease as SC is partitioned into more forage pools. This hypothesis needs to be evaluated in field trials.

At KM of 10 and SD of 5 head per ha, AIC remained at 1 throughout the 210 days for both the one and two species simulations. As both SD and KM increased, restrictions to forage intake based on availability increased. AIC was much more sensitive to rate of plant growth at high SD than at low SD. With KM of 100 for two species, there was a notable interaction of SD with time after plant growth stopped at day 180. At low SD, AIC increased; whereas, at high SD AIC decreased. At the low SD, diets shifted to the readily available dead forage, but at high SD, all forage was limiting. Even though AIC increased at this time, digestible dry matter intake was decreasing (Figure 9, p 53). This clearly illustrates the ability of the model to deal separately with the several factors that influence diet selection and intake while integrating all of them in an interactive process.

Digestible dry matter intake. The response surfaces for digestible dry matter intake (DDMI) differ from those for the other variables studied (Figure 9, p 53). DDMI integrates the effects of diet selection, forage quality, and forage availability; thus, it reflects more complex interactions. As expected, SD is a major factor affecting DDMI. Considering the effect of number of forage pools on AIC (as discussed previously) the responses for one and two species were generally similar during the period when both species were growing. The most variation occurred when only one of the two species was growing.

The importance of KM and its interaction with SD is clear when DDMI is examined (Figure 9, p 53). The highest DDMI occurred for KM of 10 with SD of 15 head*ha⁻¹. There was a quadratic response of DDMI to increasing SD at KM of 10 and 50; however, at KM of 100 this changed to a linear decline in DDMI with increasing SD. The one species simulations with KM of 100 produced a plateau up to SD of 8 head*ha⁻¹, followed by a near linear decline with further increases in SD.

DISCUSSION

This model incorporates several major biological principles which regulate diet selection by grazing herbivores. The model was constructed to simulate diet selection in different environments by different kinds of animals. Such flexibility increases the utility of the model, and more importantly, allows basic hypotheses concerning diet selection to be evaluated across a wide range of environments and seasonal conditions. The integration of forage availability and quality in this model represents a significant step in the simulation of diet selection by herbivores.

The diet model provides insight into the causes for discrepancies between the actual and desired diets. The linked forage, diet, and animal models provide information at several levels of resolution. Information includes response data for forage standing crop and quality over time, the composition and quality of desired and final simulated diets, and animal natality, growth, body condition, and mortality. This allows thorough evaluation of the outcome from simulation of management alternatives and environmental conditions.

The sensitivity analysis of selected model components demonstrated the model's responsiveness to alterations in desirability index, harvestability of plant material as expressed by KM, and stock density. By changing the desirability index, diet composition

was altered. This function will allow different levels of selectivity to be simulated for sheep, goats and cattle with the same model. As more experience is obtained with the model and it is evaluated with field data, more precise parameterization of the model functions will be possible. Altering accessibility of plant material by changing KM caused shifts in simulated diet composition and nutrient intake. This was a result of changing harvestability due to altered sward structure. The model was highly sensitive to the third variable evaluated, stock density. Even though each of these components was capable of altering model response, the interactions which occurred between model components are perhaps more interesting and important than the main effects.

CONCLUSIONS

The diet model provides a suitable interface between animal and plant models to allow evaluation of grazing livestock production systems. This is a significant step in the development of a mechanistic management level model to simulate plant/animal interactions regulating diet selection and intake. The level of resolution of the three models will allow researchers to probe deeper into plant-animal interactions.

We feel this model will have two primary uses. First, as a basic research tool and second as a management decision aid. Model use as a research tool will center upon evaluation of underlying assumptions related to the effects of forage quality and availability on diet selection and intake. The form and coefficients for equations and algorithms used will need further evaluation through biological research. The model will be useful to evaluate the design of proposed grazing experiments and will suggest the kinds of data and levels of resolution required from field studies to test specific hypotheses incorporated as functions in the model. Use as a management tool will require that the model and input parameterization be thoroughly tested at a specific location over an extended period of time.

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Figure 1. Diagram of diet model which controls diet selection and quality. It also evaluates restrictions to intake resulting from low forage availability.

Figure 2. The harvestability coefficient is calculated from a Michaelis-Menten function. This example shows the curve for KM of 100, with free availabilities above 1000 kg ha⁻¹. The curve defines a progressively increasing restriction to intake as forage availability declines. Ungrazable residual forage equals zero for this example. See Figure 2, p 126 for an example fit with real data.

1 SPECIES, DESIRABILITY = 2

2 SPECIES, DESIRABILITY = 2

Figure 3. Standing crop of live leaf reached equilibrium after about 90 days of constant growth under light stocking density. Under the highest stocking density, live leaf standing crop was directly proportional to K_m .

Figure 4. The proportion of live leaf desired in the first iteration of the diet model using two different desirability functions. The initial desired proportion of live leaf was lower for desirability-1 than for desirability-2, demonstrating how this function can be altered to adjust sensitivity to forage quality.

Figure 5. Comparison of the proportions of live leaf actually selected in the diets using desirability-1 and -2. Initial small amounts of dead forage restricted selection with desirability-1. As dead leaf accumulated on the lighter stocking densities, it increased in the diets. Desirability-2 better reflects the selectivity expressed by sheep. Live leaf was depleted more rapidly after growth stopped at the low values for KM.

SPECIES 1

SPECIES 2

Figure 6. Dietary proportions of live and dead of two species (using DES2) having different growth periods demonstrate the model's responsiveness to changes in sward composition. Growth rates of forage were the dominant factor affecting diet selection.

1 SPECIES, DESIRABILITY = 2

2 SPECIES, DESIRABILITY = 2

Figure 7. Diet digestibility reflected the proportions of live and dead. K_M had little effect on diet digestibility. When all forage growth stopped, diet digestibility declined sharply.

1 SPECIES, DESIRABILITY = 2

2 SPECIES, DESIRABILITY = 2

Figure 8. Animal intake correction (AIC) was strongly influenced by both K_m and stocking density. During early season, increasing K_m caused greater reductions in AIC at higher stock densities, but during late season, AIC decreased more rapidly at low K_m . This reflects the depletion of available forage through increased intake earlier in the season. K_m of 50 with two species was equivalent to K_m of 100 with only one species.

1 SPECIES, DESIRABILITY = 2

2 SPECIES, DESIRABILITY = 2

Figure 9. Digestible nutrient intake of simulated sheep. At low stocking densities, accumulation of dead reduced diet quality, and at high stocking densities, availability of live leaf restricted intake. There was a strong interaction between K_m and SD.

5.3 TILLER DYNAMICS MODEL

SUMMARY

This research evaluated objective three of the proposal. This objective proposed to adapt and validate a dynamic plant population model based on tiller age classes, natality, mortality, and longevity as a tool for determining subsequent range productivity and trend in response to various grazing regimes. The research was conducted in three parts: (1) an architectural model was developed and parameterized with data previously collected in the field, (2) a field experiment was conducted to verify the significance of the spatial arrangement of tillers within the field to grazing tolerance and productivity, and (3) a field experiment was conducted to examine the mechanism(s) contributing to herbaceous retrogression in response to grazing. Each of the three experimental approaches are reported independently in this chapter and then are integrated with other work in chapter V, Evaluation of Research Achievements.

Architectural simulation models of tiller dynamics indicated that the effects of grazing on tiller dynamics were less direct than the immediate reduction of tiller recruitment from parental tillers. Plants became proportionately less productive per unit area as they expanded because of decreasing tiller density per unit of basal area. The predominant effect of grazing on tiller density may be to influence plant basal area, because the greatest number of tillers and axillary buds are located on the plant periphery. Consequently, if grazing causes fragmentation of large plants, it may increase tiller production by increasing tiller density per unit of basal area.

Results of a field experiment indicated that tiller dispersion did not significantly affect aboveground production in either defoliated or nondefoliated populations. However, populations constructed with large numbers of small plants (maximum tiller dispersion) displayed greater relative increases in tiller density and basal area than populations composed of fewer larger plants. These responses were apparently mediated through a mechanism regulating tiller recruitment, as opposed to the efficiency of resource acquisition, because annual aboveground production was comparable across the range of tiller dispersion evaluated.

Plant species do not grow or respond to grazing as isolated individuals, but rather as members of a population and community. Therefore, competitive interactions are important in determining both production and species composition. Disproportionate species utilization and differential regrowth capabilities among species following comparable intensities of defoliation are both potential mechanisms contributing to herbaceous retrogression in grasslands. Field experiments indicated that intraspecific neighborhoods provided a more competitive environment for the climax dominant than neighborhoods composed of seral species which replace it following long-term grazing. Therefore, disproportionate utilization appears to be the primary mechanism contributing to the replacement of the climax dominant by lower seral species in the southern true prairie. The managerial implications of these findings are that species composition and, to some extent, production are under the control of grazing managers by determining the frequency, intensity and seasonality of defoliation among individual species populations.

EXPERIMENT 1: CONSTRUCTION OF AN ARCHITECTURAL MODEL TO SIMULATE BUNCH GRASS GROWTH

INTRODUCTION

The developmental morphology of grasses originates from the successive production of phytomers from meristems. The accumulation of successive phytomers differentiated from a single apical meristem defines the tiller (Briske 1986). Tillers are initiated from the axillary buds of ontogenetically, older parental tillers. Following a juvenile period of development tillers are potentially capable of initiating additional tillers from axillary buds differentiated with each phytomer. The number of available apical meristems and axillary buds determines the production potential for a species population at a point in time. Grazing can influence meristem availability by affecting plant density, individual plant basal area and tiller demography (Butler and Briske 1988, Olson and Richards 1988a). Consequently, growth may be restricted by meristematic limitations in some species and systems (Watson and Casper 1984).

The predictable developmental pattern of grass growth is well suited to modeling. The developmental pattern or "growth rules" can be used to construct models simulating the recruitment, development and death of individual tillers within plants (Bell et al. 1979). The use of models provides the capability of observing plant development through time while circumventing the long generation times of individual plants. The objective of this investigation was to construct an architectural model simulating the growth of individual clones of the bunchgrass (*Schizachyrium scoparium*) to evaluate the consequences of grazing on meristem availability. *S. scoparium* is characteristic of numerous species possessing the bunchgrass or caespitose growth form.

MODEL CONSTRUCTION AND OPERATION

The model was developed to simulate bunchgrass growth by the successive recruitment of tillers from a single tiller or set of tillers. The modeling approach is based upon work describing clonal plant architecture by Bell et al. (1979). The model simulates the number and two-dimensional spatial distribution of tillers within the bunchgrass growth form. Growth rules governing tiller recruitment, branching angles, inter-tiller distances, duration of anatomical attachments, and tiller longevities were based upon data collected in the field for this species (Butler and Briske 1988)(Figure 1, p 69). Spatial requirements of the model are recorded as coordinates within a grid system. Values determining tiller recruitment and mortality are generated with a Monte Carlo probability technique within the range of values based on data recorded in the field (Figure 2, p 70). Recruitment is restricted to a total of eight grid sites directly associated with the parental tiller. A mature parental tiller can produce a maximum of three juvenile tillers in any one month. Tiller longevity does not exceed 12 months and crown decomposition occurs 24 months following tiller death. The model subcomponents interact through a series of system loops (Figure 3, p 71).

The model generates both statistical and graphical output. Statistical output includes the number of live, dead and decomposed tillers produced by generation from the initiation of the simulation (Figure 4, p 72). Plant basal area is also calculated monthly. Graphical output represents the total number and spatial location of live and dead tillers within the plant. Tiller decomposition is essential to make space within the plant for subsequent tiller recruitment. Tiller growth is simulated in increments associated with chronological tiller age and phenological status (vegetative or reproductive). Plant production is based on the cumulative weight and number of tillers within an individual plant.

RESULTS AND DISCUSSION

Simulations indicated the strong dependence of production and survival on the continuous availability of meristems within the plant. Many plants died at a very young age when tiller mortality progressed more rapidly than tiller recruitment. Simulated plants began to form hollow centers (interior of the plant possessed a low tiller density) after 3-4 years of growth, but continued tiller recruitment on the plant periphery (Figure 4, p 72). These hollow centers were only infrequently recolonized. Prolonged decomposition times for tiller crowns accentuated the formation of this growth pattern. Several generations of recalcitrant crowns appear to form a mechanical barrier preventing tillers on the plant periphery from recruiting tillers within the interior. This developmental pattern may contribute to fragmentation of the initial plant into smaller subunits within a 5-10 yr period. This appears to be a natural progression of plant development within this growth form as opposed to a consequence of excessive grazing or other environmental stresses. This pattern of developmental morphology has been observed to occur in *Deschampsia cespitosa* within approximately 60 years of establishment (Gatsuk et al. 1980).

Grazing did not directly inhibit the recruitment of new tillers on a parental tiller basis. The potentially detrimental effects of grazing on meristem availability appear to be less direct. Large plants became proportionately less productive per unit area because of decreasing tiller density per unit area. Therefore, the more predominant effect of grazing on tiller density may be its influence on plant basal area because the greatest number of tillers and axillary buds are located on the plant periphery. Consequently, if grazing increases fragmentation of individual large plants, it may increase production by increasing tiller density per unit of basal area (i.e., the hollow crown would be eliminated). However, a substantial decrease in basal area induced by grazing will undoubtedly limit tiller density per unit area and thereby reduce plant production. Field experiments were conducted to evaluate the potential responses of plant production to tiller distribution and defoliation.

EXPERIMENT 2: TILLER DISPERSION WITHIN POPULATIONS OF THE BUNCHGRASS *SCHIZACHYRIUM SCOPARIUM*: IMPLICATIONS TO HERBIVORY TOLERANCE

INTRODUCTION

The ability of plants to cope with herbivory is dependent upon two broad categories of resistance mechanisms. Avoidance mechanisms reduce the probability of defoliation (e.g., biomass accessibility and mechanical deterrents) while tolerance mechanisms facilitate growth following defoliation (e.g., meristem availability and resource allocation patterns;

Briske 1986). The ability of plants to survive grazing undoubtedly results from a combination of these two broad resistance mechanisms, but one mechanism may predominate over another in certain species and under specific environmental conditions. The relative expression of resistance mechanisms among species subjected to various frequencies and intensities of herbivory will eventually manifest themselves at the population and community levels of vegetation organization (e.g., Archer and Tieszen 1986).

Although, herbivory resistance is most frequently viewed as an organismal attribute, species populations may also display structural attributes which influence their ability to cope with herbivory. For example, the density, size class distribution and spatial arrangement of plants and tillers within and among populations may potentially influence herbivory avoidance by influencing plant appearance and biomass accessibility (Norton and Johnson 1983). Similarly, population structure could potentially affect herbivory tolerance by influencing tiller recruitment (Butler and Briske 1988), resource acquisition (Nobel 1981), and inter-and intra-specific competitive interactions within the community (Briske and Butler 1989).

Herbivory reduced individual plant basal area and concomitantly increased plant density within populations of the perennial bunchgrass *Schizachyrium scoparium* (Butler and Briske 1988). Intensive herbivory apparently increased plant density and tiller number per unit of plant basal area by fragmenting individual large plants and eliminating areas of low tiller density within the plant interior. These herbivore-mediated modifications in population structure collectively influence the number and spatial distribution of tillers within the population. Similar responses have been observed in other bunchgrass species, including *Festuca idahoensis* (Pond 1960), *Agropyron desertorum* (Hickey 1961) and several grasses in the pampas of Argentina (Sala et al. 1986). However, the ecological consequences of herbivore-mediated modifications in population structure remain unexplored. This investigation was designed to test the hypothesis that a population modified structurally by herbivory, into a configuration consisting of a high density of small plants, would possess greater herbivory tolerance than a population composed of a low density of large plants at comparable tiller densities.

STUDY SITE AND PROCEDURES

Transplant Garden and Abiotic Variables

Individual, intact plants of *Schizachyrium scoparium* var. *frequens* F. T. Hubb. were collected from a remnant southern true prairie community near Caldwell, Texas in February 1986, and established in a transplant garden located at the Texas A&M University Native Plant and Animal Conservancy. The Conservancy is located 2 km west of the Texas A&M main campus, College Station, Texas and is classified as part of the Post Oak Savanna natural resource region (Gould 1975). The collection site was located 45 km west of Texas A&M University, and had been intensively grazed by cattle for approximately 20 years. Plants that did not survive the initial transplanting during February were replaced in March. Sprinkler irrigation was used to augment natural precipitation during February and March to increase transplanting success.

Long-term (30 yr; 1951-1988) and actual precipitation received during the investigation were recorded at a weather station 2 km south of the transplant garden. Long-term average annual precipitation is 993 mm and is bimodally distributed with maxima in the spring and fall (NOAA 1986-1988). Total annual precipitation during 1986 and 1987 approximated the 30-year average, but distribution was proportionately greater during May through July (Figure 5, p 73). Total annual (351.0 mm) and May through August precipitation (151.8 mm) in 1988 were 58 and 50% less than the 30-year average, respectively. The entire garden was irrigated during May and June 1988 with a total of 50 mm of water to insure plant survival and maintain live biomass throughout the season. The 30-yr mean daily temperature was 20.0C with the minimum occurring in January (9.4C) and maximum in July (29.4C). Temperatures during the investigation did not deviate appreciably from the 30-year mean.

Soils in the garden were a Lufkin fine sandy loam with an A horizon not exceeding 23 cm in depth (USDA 1958). The B horizon is characterized as a dense clay with limited permeability to water. The transplant garden was tilled to a depth of approximately 15 cm in preparation for transplanting. Interspaces between plots were tilled periodically for weed control.

Treatments and Experimental Design

Tiller dispersion treatments were designed to represent decreasing plant basal areas and increasing plant densities associated with intensive herbivory in this species (see Butler and Briske 1988). Three patterns of tiller dispersion were established by transplanting two plants with basal areas of 120 cm² (minimum dispersion), four plants with basal areas of 60 cm² (intermediate dispersion) or eight plants with basal areas of 30 cm² (maximum dispersion) into 0.25 m² plots at a constant tiller density of approximately 250 tillers. The number of live tillers per plant was proportional to the basal area estimates in cm² (i.e., approximately one tiller per cm²). Each of the 0.25 m² plots was confined on all sides by a metal barrier to a depth of 35 cm to standardize the soil volume accessible to each dispersion treatment. Lateral root development below the metal barriers was assumed to be minimal because of the dense clay pan at this depth.

Approximately 70% (by weight) of the above-ground biomass was removed with hand clippers from all plants within one-half of the plots in mid-April, early June, mid-August and early October to simulate herbivory. Height-weight relationships were constructed from 15 tillers per treatment at three stages of phenological development (vegetative, culmed and flowering) by regressing cumulative height against cumulative percent weight on an incremental basis. These relationships were used to implement a uniform intensity of defoliation. The remaining plots containing non-defoliated plants served as controls.

Data Collection

Baseline data were collected in September 1986, 8 months after transplanting. Plant responses were monitored by estimating tiller number and basal area on each plant within a plot in June (peak production period) and October (end of growing season) of both

years. Tiller number per plant was determined by counting all tillers that had attained the two leaf stage. Plant basal area was calculated from the circumference of the plant base. Tiller number and basal area were analyzed on the basis of percent change from their respective September 1986 values to account for variation among plants at the initiation of the experiment. Absolute values for tiller density and basal area per plot did not differ significantly among dispersion treatments on this date ($P>0.10$). Production from defoliated plants was estimated by determining the amount of biomass removed from each plant at each of four harvests throughout the year. Production from nondefoliated plants was estimated from a single harvest in October.

The experiment was established as a 3 (dispersion treatments) x 2 (defoliation treatments) complete, random factorial design with three replications (all plants within an individual plot). Water relations data were collected on an individual replication per day to limit the duration of the sampling period and thereby minimize diurnal variation in abiotic variables. These data were blocked by collection date to account for variation in daily environmental conditions. Analysis of variance procedures were used to test for factor level and treatment differences.

RESULTS

The intermediate and maximum dispersion treatments exhibited greater increases in relative tiller densities per plot than the minimum dispersion treatment at all sampling dates ($P<0.001$, Figure 6, p 74). Relative increases in tiller density per plot were 61, 56 and 6%, respectively, for maximum, intermediate and minimum dispersion at the end of the investigation (October 1988). Relative tiller densities in the intermediate and maximum dispersion treatments increased 125% in June 1988, but by the conclusion of the study, density had decreased to values 60% greater than those observed in September 1986. Relative tiller density in the minimum dispersion treatment increased 70% in June 1988, but then decreased to density values comparable to those at the initiation of the study. Tiller density decreased below the September 1986 value in only the minimum dispersion treatment in October 1987.

Defoliated plants initially responded with higher relative tiller densities (October 1987) than did the non-defoliated plants (Figure 6, p 74, $P=0.016$). This trend was reversed in 1988 when relative tiller densities within the non-defoliated plants exceeded those of the defoliated plants by 50% on the last two sampling dates. Seasonal fluctuations in tiller density were observed within all treatments with the maximum occurring in the spring (June) and the minimum in the fall (October). No significant defoliation by tiller dispersion interactions were observed ($P>0.10$).

Dispersion treatments significantly influenced relative increases in basal area per plot (Figure 7, p 75, $P<0.001$). Mean relative basal area within the maximum, intermediate and minimum dispersion treatments increased 220, 170 and 130%, respectively, over the course of the investigation. A reduction in the relative rate of increase over time suggests that basal area expansion was beginning to diminish in response to resource limitations. Defoliation did not significantly affect the rate of basal area expansion or create a significant defoliation x basal area interaction ($P>0.10$).

Tiller dispersion did not significantly affect annual aboveground production per plot ($P>0.10$), although maximum and intermediate dispersion treatments tended to produce more biomass than did the minimum dispersion treatment (321, 436 and 297 g per plot for nondefoliated plants and 376, 391 and 298 g per plot for defoliated plants, respectively). Defoliation did not significantly affect total annual production (352 and 355 g per plot, $P>0.10$).

DISCUSSION

Tiller dispersion did not significantly affect aboveground production in either defoliated or nondefoliated populations. Consequently, the hypothesis that a population characterized by a high density of small plants confers greater herbivory tolerance than a population composed of a low density of large plants was rejected. The spatial arrangement of tillers within populations of the bunchgrass *S. scoparium* was inconsequential in mediating plant responses to herbivory within the range of plant sizes and tiller densities utilized in this investigation. A more severe defoliation regime may have magnified differences among dispersion treatments. Plant production and tiller weights were not significantly affected by the defoliation regime imposed.

Bunchgrass populations with greater tiller dispersion expressed proportionately greater increases in tiller recruitment and basal area (Figures 6, p 74, and 7, p 75). Greater increases in tiller density and basal area were presumably mediated through a mechanism regulating tiller recruitment, as opposed to the efficiency of resource acquisition, because comparable levels of aboveground production occurred over the range of tiller dispersion treatments evaluated. Proportionately greater tiller recruitment has been documented on the periphery, as opposed to the interior, of two perennial bunchgrasses, *S. scoparium* (Butler and Briske 1988) and *Agropyron desertorum* (Olson and Richards 1988a). The mechanism associated with this response is unknown, but radiation quality has been implicated (Deregibus et al. 1985). Consequently, greater plant periphery in populations with intermediate and maximum tiller dispersion may have increased the opportunity for tiller recruitment. Rapid tiller recruitment on the plant periphery would also account for proportionally greater increases in basal area.

Relative tiller density responded differently to defoliation between years of the investigation. Defoliated plants recruited a greater number of tillers than nondefoliated plants in 1987 regardless of the degree of tiller dispersion. However, in 1988 nondefoliated plants showed relative increases in tiller density 50% greater than those of defoliated plants (Figure 6, p 74). This response cannot be entirely attributed to the limited precipitation received during 1988 (50% of the long-term norm; Figure 5, p 73), because both defoliated and nondefoliated plants made the greatest relative increases in tiller density between October 1987 and June 1988 (Figure 6, p 74).

A reduction in tiller recruitment within defoliated populations during the second year of the study supports the conclusion of Ellison (1960) that grazing generally inhibits tillering in grasses over the long-term. Although defoliation may stimulate tillering by alleviating apical dominance in the short-term, the repeated removal of photosynthetic area eventually

minimizes the availability of resources for tiller growth. This interpretation is supported by the observation that neither *S. scoparium* or *Agropyron desertorum*, a grazing-tolerant perennial bunchgrass, displayed increased tiller recruitment following 2 years of livestock grazing (Butler and Briske 1988, Olson and Richards 1988b). However, short-term increases in tiller recruitment have been observed in both *S. scoparium* (Jameson and Huss 1959, Vogel and Bjugstad 1968) and *A. desertorum* (Olson and Richards 1988c) when defoliation coincided with reproductive culm elongation.

Although the spatial distribution of tillers did not influence aboveground production following defoliation (i.e., herbivory tolerance), it represents only one aspect of herbivore-mediated modifications in population structure. Herbivory also modifies plant size class distribution and alters absolute tiller densities within and among various species populations which comprise the community (e.g., Butler and Briske 1988). Consequently, small plants will very likely be at a competitive disadvantage with neighboring large plants (e.g., Liddle et al. 1982). Similarly, populations possessing the greatest tiller densities would be anticipated to acquire the greatest proportion of available resources within the community (Caldwell et al. 1987). The population attributes of plant size class distribution and absolute tiller density appear to be of greater significance to herbivory tolerance than tiller dispersion within perennial bunchgrass populations.

EXPERIMENT 3: SPECIES REPLACEMENT IN RESPONSE TO HERBIVORY: THE ROLE OF COMPETITIVE INTERACTIONS

INTRODUCTION

Grazing-induced modifications in species composition have been documented in numerous grasslands throughout the world (Noy-Meir et al. 1989, Williams 1969, Ellison 1960). Compositional changes frequently involve the replacement of higher successional species by lower successional species (Canfield 1957). The lower successional species are often mid- or shortgrass species held in a subordinate position by competition from species possessing greater stature (Belsky 1986, Arnold 1955). Grazing reduces the competitive ability of the mid- and tallgrasses thereby increasing the relative abundance of lower successional grasses and forbs and establishing the potential for shrub invasion. This scenario of species replacement in response to grazing has frequently been inferred from field observation, but has not been experimentally verified.

Herbivore-induced modifications in competitive interactions may be created by either disproportionate utilization of the climax dominant (herbivory avoidance) or superior regrowth ability of lower seral species following grazing (herbivory tolerance) (Briske 1986). In cases where these imbalanced competitive interactions are maintained over one or more growing seasons they will eventually manifest themselves in plant architecture, tiller demography and population structure (Butler and Briske 1988). If the climax dominant proves to be the superior competitor when all species are proportionately defoliated, then herbaceous retrogression can be assumed to result from disproportionate species utilization rather than differential regrowth abilities.

This investigation was conducted to test the hypothesis that competitive ability and herbivory tolerance of the climax dominant is equal or superior to that of lower seral species which replace it in response to long-term herbivory when all species are defoliated equally. This would imply that herbaceous retrogression is under the direct influence of resource managers by influencing the frequency, intensity and seasonality of herbaceous plant defoliation within the community.

STUDY SITE AND PROCEDURES

Plant Material

Plant material was collected from unbroken remnants of native Southern True Prairie communities near Caldwell, Texas. The Caldwell site, 45 km west of Texas A&M University, is considered a Blackland inclusion within the Post Oak Savannah region (Gould 1975). Precipitation and temperatures are similar to those described for the transplant garden area (Figure 5, p 73), but the soil is classified as the Dimebox series, fine montmorillonitic, thermic, Udic Pellustert.

Entire, undivided plants were collected from pastures intensively grazed for over 20 years. Three perennial grass species, *Stipa leucotricha* (Texas wintergrass), *Bothriochloa saccharoides* (silver bluestem) and *Schizachyrium scoparium* (little bluestem), were used to establish monospecific competitive neighborhoods. *Schizachyrium scoparium* represents the sole climax dominant with this community and was used as the target plant. Plants were taken from the Caldwell sites in January and February 1986 and established in specific arrangements in the transplant garden on the Texas A&M campus (see Experiment 2 for description). Plants that did not survive the initial transplant were replaced with plants from the same populations through the end of March 1986.

Sprinkler irrigation at the time of transplanting was essential for transplant survival, but was discontinued as of April 1, 1986. Extremely low precipitation in the early months of 1988 prompted supplemental irrigation (total of 50 mm) during May and June 1988 to insure plant survival and physiological activity through the growing season (Figure 5, p 73). Periodic hand weeding within plots and tilling between plots kept interference from plants not involved in the investigations at a minimum.

Procedures

Experimental Design

Monospecific competitive neighborhoods of *Stipa leucotricha*, *Bothriochloa saccharoides* and *Schizachyrium scoparium* were created from plants transplanted from the Caldwell site. Each plot contained four target plants and nine neighbors and each treatment combination was replicated four times. The initial basal area for both the target plants and neighbors ranged between 50 and 70 cm². Spatial arrangement was constant initially such that each *Schizachyrium* target plant was positioned in the center of four neighbors (approximately 21 cm from center of a neighboring species to center of target).

The neighborhoods were not confined on the plot periphery and were separated by a 2-3 m boarder to separate the plots.

Data were collected on two of the four target plants within each plot (additional target plants were established to complete the experimental design). Data were also collected on the central neighbor enclosed by the *Schizachyrium* target plants in 1987, but high mortality of the central neighbors late in the year and early in 1988 prohibited continuation. Data were collected in mid-April, early June, mid-August and early October of 1987 and 1988. Baseline data were taken in September 1986 eight months after transplanting. Each sampling period was approximately two weeks in duration.

Intensive herbivory was simulated by removing 70 percent (by weight) of above-ground biomass of the target plants during each collection period. A proportional amount of above-ground biomass was removed from the associated neighboring plants when this treatment was imposed. Standard height-weight relationships were established for each species by phenological stage. This was accomplished by dissecting a tiller into segments of a known length, weighing each segment, and then regressing the cumulative height against the cumulative percent weight on an incremental basis.

Three patterns of defoliation were imposed. First, defoliation of all plants within a plot, including both the target plants and the respective neighborhoods, representing proportionate utilization by mammalian herbivores. Second, defoliation of only the target plants representing disproportionate utilization of the climax dominant. Finally, a control in which no plants were defoliated representing the non-grazed climax community.

Data Collection

Tiller number and basal area per plant were recorded in June and October of both years on both the target and neighboring plants. This provided estimates near the period of maximum biomass production and the end of the growing season. Tiller number per plant was determined using a double sampling procedure. The direct measure was a full count of all tillers per plant on every fourth plant of a species. The indirect measure was a count of tillers in one quarter of the basal area of each plant established by bisecting the basal area with two rods perpendicular to one another. Plant basal area was estimated by a measure of circumference (assuming a circular shape) at the base of each plant. Since the size of target plants varied at the initiation of the experiment, tiller numbers and basal area were analyzed on the basis of percent change from their respective September 1986 values.

Regrowth was estimated by determining the amount of biomass removed from the target plants at each of the four harvests throughout the growing season. Target plant biomass harvested at the end of the growing season yielded an estimate of total annual production for a comparison between non-defoliated and defoliated treatments (cumulative annual regrowth). Regrowth estimates very likely provided more accurate estimates because senescence losses were minimized.

Statistical Analysis

This experiment was established as a 3 (levels of competitors) x 2 (levels of target defoliation) x 2 (levels of competitor defoliation) incomplete factorial design. The design was incomplete because one potential factor combination, defoliation of seral species but not the climax dominant, was deemed ecologically inappropriate and omitted from the study. Since the design was incomplete, two balanced submodels were analyzed using basic analysis of variance techniques to determine factor level and treatment differences. In cases where the elements unique to the individual submodels (neighborhood defoliation and target plant defoliation) were not significant the data were pooled.

RESULTS

Target plants in *Stipa* and *Schizachyrium* neighborhoods expressed a seasonal oscillation in tiller number per plant about the initial September 1986 values while plants in *Bothriochloa* neighborhoods exhibited a progressive decline in tiller numbers per plant throughout the study (Figure 8, p 76). An abnormally high amount of precipitation was received during the establishment phase of the experiment which resulted in high tiller numbers per plant when baseline data was taken. The negative percent change in tiller numbers reflects a decrease in tiller numbers per plant in reference to the baseline data. The neighborhood defoliation and target plant defoliation treatments had no significant effects on tiller numbers per target plant.

Basal area per target plant was not affected by neighborhood treatments (Figure 9, p 77). However, the general tendency was for target plants in *Stipa* neighborhoods to display the greatest increase in basal area while those in the *Schizachyrium* neighborhoods displayed the smallest. Plants grown in defoliated neighborhoods had greater increases in basal area than those grown in non-defoliated neighborhoods (Figure 9, p 77). A parallel response in target plants was observed across neighborhood defoliation treatments in 1987, but a divergence occurred in 1988 resulting in 160 percent greater increase in basal areas in target plants associated with defoliated neighborhoods. Target plant defoliation did not significantly affect the change in basal area.

Target plants produced the greatest regrowth and annual production in *Stipa* neighborhoods, intermediate amounts in *Bothriochloa* neighborhoods and lowest amounts in *Schizachyrium* neighborhoods (Figure 10, p 78). Target plants in the *Stipa* neighborhoods produced four times the regrowth biomass and annual production as did target plants in the *Schizachyrium* neighborhoods. Plants grown in defoliated neighborhoods produced greater amounts of regrowth and annual production than plants grown in non-defoliated neighborhoods (Figure 10, p 78).

DISCUSSION

The hypothesis indicating that the climax dominant is the superior competitor in this grassland under conditions of equivalent defoliation was not rejected. Defoliated target plants grown in defoliated neighborhoods of *Schizachyrium* exhibited 75 and 60 % lower amounts of regrowth and annual production than plants grown in defoliated neighborhoods

of either *Stipa* or *Bothriochloa*, respectively. Production of target plants was suppressed to the greatest extent when grown in *Schizachyrium* neighborhoods irrespective of neighborhood defoliation.

As indicated by plant production, the *Schizachyrium* neighborhood is the superior competitive environment, irrespective of neighborhood defoliation, relative to both *Stipa* and *Bothriochloa* neighborhoods. Given proportionate defoliation, replacement of the climax dominant with either *Stipa* or *Bothriochloa* would result in a reduction in the competitive environment for the remaining climax dominants. A reduction of the competitive environment would suppress the replacement of the climax dominant rather than promote it, indicating that this mechanism does not contribute to species replacement in this system.

The alternative mechanism explaining species replacement is the disproportionate utilization of the climax dominant relative to its associated competitors. When the target plants were defoliated and grown in a non-defoliated neighborhood, annual production, change in tiller number and basal area change did not differ significantly. These results suggest that the defoliation regime imposed was not sufficiently severe to elicit plant responses in a two year period. Frequent, intense defoliation, particularly early in the growing season, may represent a defoliation regime that would lead to species replacement in the field. The defoliation treatments imposed in this investigation apparently allowed defoliated plants to maintain sufficient photosynthetic surfaces to sustain a positive carbon balance.

Disproportionate species utilization and differential regrowth capabilities among species following comparable intensities of defoliation are both potential mechanisms contributing to herbaceous retrogression in grasslands. Either or both mechanisms may establish an imbalance in competitive interactions, initially manifested in reduced physiological function, between or among species relative to the intensity of competitive interactions operating in the absence of herbivory. Disproportionate utilization appears to be the primary mechanism contributing to the replacement of the climax dominant by lower seral species in the southern true prairie. Intraspecific neighborhoods provided a more competitive environment for the climax dominant than neighborhoods composed of either seral species. Consequently, the defoliation tolerance of the climax dominant equals or exceeds that of the seral species which replace it under intensive herbivory. These data minimize the importance of differential regrowth as a mechanism driving species replacement in this system. Alternatively, it can be concluded that disproportionate utilization of the climax dominant, relative to the associated interspecific competitors, is the predominant mechanism promoting herbaceous retrogression.

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GROWTH RULES

Recruitment

- age dependent probabilities
- recruitment in two zones (85/15%)
- random branching angle;
tillers abort if grid site not available
- 2 month juvenile period;
3 month winter quiescence

Mortality

- age dependent probabilities
- increases with age; 12 month maximum

Decomposition

- all tillers decompose at 24 months of age
- grid site becomes unoccupied

Physical structure

- grid system (showing generations:)

Figure 1. Growth rules governing the recruitment, mortality, decomposition and spatial arrangement of tillers in an architectural model designed to simulate tiller dynamics within bunchgrasses.

RECRUITMENT PROBABILITIES

	number of tillers recruited during current month			
	0	1	2	3
1	1.00	0.00	0.00	0.00
2	1.00	0.00	0.00	0.00
3	0.30	0.45	0.25	0.00
4	0.25	0.45	0.20	0.00
5	0.20	0.50	0.20	0.10
6	0.15	0.55	0.20	0.10
7	0.20	0.55	0.20	0.05
8	0.25	0.40	0.15	0.00
9	0.45	0.40	0.15	0.00
10	0.60	0.30	0.10	0.00
11	0.60	0.30	0.10	0.00
12	1.00	0.00	0.00	0.00

Figure 2. Monte Carlo technique used to generate probabilities for tiller recruitment from parental tillers within the architectural model. Probability values are based on field data (Butler and Briske 1988) and vary with tiller age and number of juvenile tillers recruited.

Figure 3. Flow diagram illustrating the location and sequential interaction among the five subcomponents forming the architectural simulation model.

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*****
*****
Month:    60
*****
*****

Live units:  143
Dead units:   92
Decomp units: 129
Area (based on 2 units / linear cm):  99.4 cm ^ 2

Generation:  0  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15
Total:       1  3 11 16 24 32 40 43 60 53 48 28 5  0  0  0
Live:        0  0  0  0  0  0  1  8 21 36 44 28 5  0  0  0
Dead:        0  0  0  0  0  2 12 18 39 17 4  0  0  0  0  0
Decomp:      1  3 11 16 24 30 27 17  0  0  0  0  0  0  0
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*****

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Figure 4. Statistical and graphical output from the architectural simulation model. Statistical output indicates the number and generation of live, dead and decomposed tillers and basal area of the plant. Architectural output indicates the spatial arrangement of tillers within the plant as it develops.

Figure 5. Mean monthly precipitation for (a) 1986, (b) 1987, and (c) 1988 and the long-term average annual precipitation at the study site where experimental populations of *Schizachyrium scoparium* were established.

Figure 6. Relative change in tiller densities of *Schizachyrium scoparium* on a per plot basis during 1987 and 1988 as influenced by (a) tiller dispersion ($P < 0.001$) and (b) defoliation ($P = 0.016$). Percentages are based on absolute values of 233, 298 and 255 tillers per plot for maximum, intermediate and minimum dispersion treatments and 242 and 249 tillers per defoliated and nondefoliated plots, respectively, in September 1986.

Figure 7. Relative change in basal areas of *Schizachyrium scoparium* on a per plot basis during 1987 and 1988 as influenced by tiller dispersion ($P < 0.001$). Percentages are based on absolute values of 233, 289 and 257 cm² per plot for maximum, intermediate and minimum dispersion treatments, respectively, in September 1986.

Figure 8. Relative change in tiller numbers of *Schizachyrium scoparium* target plants during 1987 and 1988 in reference to September 1986 values as influenced by *Stipa leucotricha*, *Bothriochloa saccharoides* and *Schizachyrium scoparium* neighborhoods ($P=.009$). Percentages are based on absolute values of 101, 84 and 63 for the three species, respectively, in September 1986.

Figure 9. Relative change in basal area of *Schizachyrium scoparium* target plants during 1987 and 1988 in reference to September 1986 values as influenced by (a) *Stipa leucotricha*, *Bothriochloa saccharoides* and *Schizachyrium scoparium* neighborhoods ($P > .10$) and (b) neighborhood defoliation ($P = .023$). Percentages are based on absolute values of 82, 66, and 31 cm² for the three species, respectively, and 54 and 64 cm² for defoliated and non-defoliated neighborhoods, respectively, in September 1986.

Figure 10. Mean cumulative regrowth of *Schizachyrium scoparium* target plants during 1987 and 1988 as influenced by (a) *Stipa leucotricha*, *Bothriochloa saccharoides* and *Schizachyrium scoparium* neighborhoods ($P < .001$) and (b) neighborhood defoliation ($P = .013$). The neighborhood x neighborhood defoliation interaction was significant ($P = .08$).

5.4 KLEINGRASS STUDY

SUMMARY

The responses of kleingrass standing crop, tissue fluxes, tiller heights, and livestock gains and intake to early-season grazing treatments were investigated at McGregor, Texas. The study evaluated the growth, production, and utilization of kleingrass to develop improved strategies for early-season grazing management. Specific objectives included: a) Identifying phenological development and rate of growth of kleingrass during the spring; b) Quantifying the growth and senescence characteristics of kleingrass under different early-season grazing treatments at the tiller and sward levels; c) Monitoring animal gains and intake; and d) Relating animal responses to plant growth responses.

The peak SC of annual grasses occurred near 30 April. Peak production of kleingrass had not been reached by 1 June. Stem elongation had only started on some reproductive tillers. Little growth of kleingrass resulted from internode elongation during this study. Kleingrass growth was exponential at the beginning of the study but was linear during the latter part. Kleingrass presented an early tiller recruitment pattern that started 4 wk after initiation of growth and well before peak production was reached. Early-season grazing increased tillering. Tertiary tillers and tillering from the upper nodes occurred only in the grazed plants.

High-intensity grazing reduced forage availability. The 0-delay and 14-day delay, medium-intensity grazing treatments allowed a good harvest of annual grasses before they reached maturation with low utilization of kleingrass during April. The low-intensity treatments with 0-delay and 14-day delay and all 30-day delay treatments utilized annual grasses less efficiently. Competition from annual grasses reduced kleingrass production during April and intensified selective grazing for kleingrass during May. Grazing intensity was the dominant factor affecting kleingrass production.

Average daily gains and gains per hectare were optimized by early grazing with forage demand rate set less than or equal to forage growth rate (medium-intensity). All 30-day delay treatments resulted in lower average daily gains and gains per hectare. Early grazing at low-intensity gave good average daily gains but low gains per hectare. Early-season grazing, with forage demand rate set equal to growth rate, reduced competition of annual grasses with kleingrass, and gave maximum animal gains per head and per hectare. Gain per hectare of the 0-day delay, medium-intensity treatment was nearly 500 percent greater than for the 30-day delay, high-intensity treatment. This indicates the high sensitivity of animal production to variations in early-season grazing.

INTRODUCTION

Kleingrass is a leafy upright warm-season perennial bunchgrass which has been planted on many farms and ranches in the central Texas region. It is used for both hay and grazing, but most acreage is grazed by beef cattle. It is a nutritious forage and generally supports better livestock gains than Coastal bermudagrass. However, kleingrass is susceptible to damage from improper or excessive grazing and many stands have

deteriorated. Productivity of stands declines because of reduced plant densities and invasion of weeds such as cool-season annual grasses.

MATERIALS AND METHODS

Study Area

The study was conducted at the Texas A&M Agricultural Research Center at McGregor (97°27'10"W, 31°22'30"N), approximately 8 km south of McGregor, Texas. This location is on the boundary of the subtropical, subhumid and the subtropical, humid regions of Texas (Larkin and Bomar 1983). It is in the transition zone between the Blackland Prairies and the Cross Timbers and Prairies vegetational areas, specifically between the Blackland Prairie and the Grand Prairie (Gould 1975a). The Center is 213 m above sea level.

The study site (Pasture T-2), was selected based on the apparent homogeneity of density and vigor of the kleingrass stand. The study site contained four soil types: San Saba clay, 0 to 2 % slopes (Sa), Crawford clay, 1 to 3 % slopes (Ch), Crawford clay, shallow variant, 1 to 3 % slopes (Ck) (Templin et al. 1958), and the Crawford silty clay, 1 to 3 % slopes (Cwb), all Udic Chromusterts (McCaleb et al. 1985). Vegetation was composed of kleingrass (*Panicum coloratum* L.), a warm-season perennial grass, and cool-season annuals, Japanese brome (*Bromus japonicus* Thunb.), little barley (*Hordeum pusillum* Nutt.), and Darnel (*Lolium temulentum* L.) with only trace amounts of forbs.

The annual precipitation on the Research Center for 23 years (1965-1987) averaged 855 mm (Table 1, p 102). Rainfall pattern is bimodal with peak occurrences in May and October. Average frost free growing season is 254 days, extending from mid March to mid November.

The daily air temperatures range from winter lows of -10° C to summer highs over 38° C. The last frost for 1987 occurred on 4 April. Average precipitation during the growing season is 637 mm (75 % of the average annual precipitation). Total precipitation for 1987 was 784 mm, 71 mm below the average. The study site received only 72 % (174 mm) of the average (242 mm) for the period 2 April to 8 June.

Experimental Design

A 32.16 ha pasture with a 20-year-old, well established stand of Kleingrass 75 was divided into 10, 3.17 ha paddocks. A small area in the center of the pasture was used as a central management area from which the 10 paddocks radiated in a cell fencing design. The 10 treatments were randomly assigned to the paddocks. In February the total area was staged by shredding and fertilized with 112 kg N and 45 kg P per hectare.

A total of nine grazing treatments were applied along with one ungrazed control (U). The grazing treatments consisted of three grazing intensities (GI) applied at three grazing initiation dates (GID).

The grazing initiation dates (2 April, 15 April, and 1 May of 1987) will be referred to here as 0-delay, 14-day delay, and 30-day delay respectively. The 0-delay treatments, were set to coincide with the approximate initiation of kleingrass growth.

Grazing intensities were calculated considering the potential rate of forage demand (Scarnecchia and Kothmann 1982), based on the dry matter intake requirements from the NRC (1984). The steers were equivalent to 0.75 animal-units (AU), based on a 362 kg average. The cows varied from 0.77 to 1.0 AU, depending on their weight (397-700 kg). Animal-units were multiplied by days to determine the animal-unit-days per hectare (AUD/ha).

Grazing intensity was maintained at three levels (low, medium, and high) using the put and take technique (Mott and Lucas 1952). Animal numbers were adjusted weekly, thus grazing intensities were continuous but variable. The low-intensity (L) allowed the forage growth rate to exceed the demand rate, the medium-intensity (M) maintained a balance of growth and demand rates (Noy-Meir 1975) and in the high-intensity (H) forage demand rate exceeded growth rate. Grazing initiation dates and grazing intensities are presented in Table 2, p 102. Stocking density varied from 1.6 to 6.6 animal-units per hectare, thus comprising the range of stocking proposed in the literature (Holt 1969, Norris et al. 1969, Chmielewski 1981, Guerrero et al. 1984).

Sward Measurements

Standing Crop. Standing crop (SC) was sampled every 15 days in the ungrazed control and every 30 days in the nine grazed treatments. Eleven quadrats (1.0 m²) per treatment were randomly placed along a transect and clipped to ground level at each sampling (2 April, 29 April, 2 June 1987). The samples were sorted into categories of kleingrass and annual grasses which included cool-season annual grasses and forbs; forbs contributed less than 1% of total. Samples were dried at 55° C until constant weight.

Utilization. Movable livestock exclosure cages (Hinnant and Kothmann 1982) were used on the three 0-delay treatments (Pastures 2, 5, and 8). Caged plots were paired with adjacent randomly located unprotected plots (Klingman et al. 1943). The caged plots were clipped on the same dates as the paired uncaged plots. At the end of each sampling period, new plots were selected as before. Utilization was determined in the 0-delay treatments by difference in dry weight between the grazed and the ungrazed (caged) plots (Pieper 1978).

Tiller Height. Height of 100 tillers each of kleingrass and annual grasses was measured in each pasture on four dates. Tillers were randomly selected and the relaxed height measured. Tillers were recorded as grazed or not grazed.

Growth. Growth characteristics were calculated from paired plots in the ungrazed control and the three pastures with cages. Net growth (NG) was calculated by subtracting the standing crop of the previous sampling period of non-caged plots from the average dry weight of the current period caged plot. Net growth rate (NGR) was estimated by dividing net growth by number of days between clippings. Net growth rate was only calculated for

the second and third sampling periods because the date of growth initiation was not determined.

Tiller Measurements

Tillers were sampled every 15 days from the ungrazed control and inside the cages in the 0-delay high-intensity grazing treatment. Two pairs of tillers were randomly selected at each of 11 random sampling locations in both pastures at the beginning of the study. Twenty two tillers were collected from each of the two pastures at each sample date. Tiller dynamics and tissue fluxes were determined from the harvested tillers.

Tiller Dynamics. Daughter tillers were recorded as secondary, tertiary and aerial. Tillers were recorded as reproductive if they had any measurable elongation of internodes (Johnson and Parsons 1985b). Stage of inflorescence development followed Latting (1972).

Tissue Fluxes. Measurements were made of tissue turnover in individual tillers to determine tissue fluxes (Davies 1981, Grant et al. 1983). A system of double labeling was used. A new tiller was selected as a pair for each harvested tiller within location. A painted wire ring was placed at the base of each tiller (Hodgson 1966) and the last fully expanded leaf marked on the back of the collar with latex paint (Davies and Calder 1969). Kleingrass leaves were undifferentiated during the first days of growth and were first marked on 1 April. Tissue fluxes were measured for four sampling periods: (1-14 April, 14-30 April, 30 April-21 May, and 21 May-2 June). The marked leaf served as a reference point to match phytomers for calculation purposes. Each leaf of the harvested tillers was separated, numbered acropetally (Klepper et al. 1982) and divided into dead and live tissue. The crown, culm, and inflorescence were also separated. The crown consisted of the lower 2 mm of the culm with the roots removed.

Positive and negative changes in biomass of live and dead leaf, by phytomer, were measured by weight difference between paired tillers across sampling dates. The sum of positive increments of live leaf estimated growth and the sum of negative increments of green leaf estimated senescence. The sum of positive increments of dead estimated transfer from green to dead. The sum of negative increments of dead represented transfer from dead standing crop to mulch and detritus. The difference between senescence and transfer into dead was the biomass loss associated with senescence. All calculations were based on the assumption of no consumptive losses or transfer from green directly to mulch. Cumulative growth, senescence, addition to dead and disappearance from dead were calculated.

Animal Measurements

Animal Gains. Steers were the tester animals on which weight, body condition, and fecal output were measured as response variables to the treatments. They were sorted so the average weight of each treatment group would not vary more than 2 % from the overall average. The steers averaged 362 kg when the study began with a range from 326 to 424 kg. Seven steers were assigned to the low-intensity treatments and eight steers to the medium-and high-intensity treatments.

Weights were taken to coincide with the grazing initiation dates (2 April, 15 April, 1 May), and the end of the experiment (9 June). Steers were removed from the pastures and weighed without fasting. Gains are reported as average daily gains (ADG) by dividing the difference in weight from two weighing dates by the number of days. Total gains were calculated by extending gains of tester animals using total animal-unit-days for each treatment (Mott and Lucas 1952). Cows were not used to measure animal response variables. They were added or removed to adjust grazing intensities to desired levels.

Body Condition. Body condition scores, based on visual appraisal were estimated by experienced individuals according to the guidelines provided by Herd and Sprott (undated). These were used with weights (Houghton et al. 1986) to provide uniformity between lots of animals (Cook and Stubbendieck 1986) and as an alternative to monitor the grazing animal's nutritional status (Anderson 1987).

Forage Intake. Forage intake was estimated using a pulse dose of forage marked with lanthanum acetate (Pond et al. 1985). The forage obtained from the samples clipped for standing crop measurements was coarsely chopped through a Wiley mill with the screen removed. It was soaked for 24 h in a 0.01 M acetic acid solution to provide 100 mg of lanthanum as acetate per 10 ml of solution per gram of forage dry matter to be marked. Marked forage was rinsed thoroughly in 0.01 M acetic acid solution to remove unbound rare earth and dried. Each steer was orally dosed with two gelatine capsules loaded with 8 g of marked forage (16 g/animal) on 11 May and 9 June. Cows were removed from all treatments at the time when the steers were dosed.

Composite fecal samples, with at least four animals per sample, were collected from the sward at 15-18, 24-30, 36-38, 48-50, and 72 h post dose. Samples were collected after the animals were observed to defecate. The samples were dried immediately after collection at 60° C, ground through a Wiley mill fitted with a 1-mm screen and prepared for analysis by the neutron activation analysis procedure (Ellis and Houston 1968). Analyses were conducted by the Nuclear Science Center at Texas A&M University. Concentration of lanthanum in feces with respect to hours post dose was analyzed using the nonlinear procedure (PROC NLIN) of SAS (1988), based on the one compartment model with gamma 2 residence time distribution (Ellis et al. 1984, Pond et al. in press). This procedure produced fitted curves which estimated initial concentration of the marker and turnover rate, assuming instantaneous mixing of the marker. Fill and daily fecal output (FO) were calculated. FO was calculated assuming an age dependency rate (Matis 1972) and a fast turnover rate of 0.65 (Ellis et al. 1979).

Fill = dose of the marker/initial concentration.

FO = fill x (turnover rate x 0.65) x 24 h.

Percent fecal N (FN) was analyzed by the micro-Kjeldahl method (AOAC 1975) and used to estimate g fecal nitrogen output per 24 h (FNO), g organic mater intake per 24 h (OMI), and g digestible organic matter intake per 24 h (DOMI) (Kothmann and Hinnant 1987).

$$\begin{aligned} \text{FNO} &= \text{FO} \times \text{FN}(\%) \\ \text{OMI} &= 3,085 + 103\text{FNO} \\ \text{DOMI} &= 89\text{FNO} - 99 \end{aligned}$$

These results were compared to other indirect estimations of intake. Percentage FN was also used to estimate organic matter digestibility (OMD), as an indirect evaluation of diet quality (Kothmann and Hinnant 1987).

$$\text{OMD} = 31 + 16.6\text{FN}(\%).$$

Botanical Composition. Botanical composition of the feces was determined by microhistological analysis at the Diet Laboratory at Texas Tech University, following the procedures described by Hansen et al. (1971) and Scott and Dahl (1980). Proportion of kleingrass, annual grasses, and other species leaf and stem (including seed) was calculated for May and June based on the fecal analysis.

Data Analysis

The treatments were not replicated; however, the design permitted the data to be analyzed as a response surface using regression techniques. The response variables were analyzed as a 3x3 factorial in a response surface design (Cochran and Cox 1957). Analysis of the linear and quadratic effects were determined using the Stepwise Regression Procedure (SAS 1988) in order to apply the response surface analysis using pasture effects as residual. This allowed determination of optimal treatment responses (Montgomery 1984).

Grazing intensity and grazing initiation date were the independent variables, each at three levels. Standing crop, forage intake, and animal gain were the dependent variables. Utilization, growth, and tiller measurements were used as complementary variables since they were not determined in all the treatments. These variables were analyzed using the General Linear Model (SAS 1988) with the analysis of variance.

The response surface procedure provides information about model fitting in the form of analysis of variance. Duncan's New Multiple Range Test (Snedecor and Cochran 1980) was used for separation of means. Unless otherwise stated, all the statistical differences are accepted at alpha probability equal to or less than 0.05.

RESULTS

Standing Crop

Forage SC during the observation period was directly related to the phenology of the species. Annual grasses germinated during late fall and winter and began rapid growth during March, and attained their peak SC by 30 April (sampling period 2), then declined (Table 3, p 103). At that date, Darnel was drying and shedding seeds, and little barley was at its peak SC with most of the plants setting seed. However, Japanese brome was still vegetative and reached peak SC with most plants setting seed about 10 May and shedding seeds and senescing by 15 May. SC of kleingrass increased throughout the study.

Internode elongation (reproductive stage) was first recorded on 14 April. Inflorescence development was detected on 21 May and at the end of the study 9 % of the kleingrass tillers had an inflorescence.

Averaged across pastures, SC reached a maximum on 30 April of 435 kg/ha for kleingrass and 2,280 kg/ha for annual grasses, for a total of 2,715 kg/ha (Table 4, p 104). There was not a significant difference between treatments; however, there was a significant difference between sampling periods and forage categories and significant interactions for treatment by period, treatment by forage categories, period by forage categories and treatment by period by forage categories. Because of the significant interactions, standing crop will be presented within periods.

Sampling Date 1. There was no significant difference between pastures for annual grasses and total but kleingrass SC differed significantly (Table 3, p 103). This sampling was carried out before any grazing was applied; therefore, the differences for kleingrass are considered to be pasture/site effects.

At sampling date 1 there were no significant linear or quadratic effects due to grazing intensity or grazing initiation date in any of the forage categories. The grazing intensity by grazing initiation date interaction was not significant. Thus, while pastures differed significantly in kleingrass SC prior to grazing, there was no bias related to grazing treatment.

Sampling Date 2. Treatment 0-H had a significantly lower SC of annual grasses and total than the rest of the pastures (Table 3, p 103). Average kleingrass SC of grazed treatments was approximately twice that of the ungrazed control and 30-day delay treatments. Treatment 30-H had significantly higher SC of annual grasses and total than the rest of the pastures. Except for treatment 14-L, the non-grazed pastures had the highest yields for annual grasses.

Kleingrass showed significant quadratic effects due to grazing intensity ($-0.004GI^2$) and significant quadratic effects due to grazing initiation date ($-0.067GID^2$). Annual grasses ($-10.467GI$) and total SC ($-10.334GI$) showed significant linear effects due to grazing intensity and a significant grazing intensity by grazing initiation date interaction ($+0.468GI \cdot GID$, $+0.462GI \cdot GID$, respectively).

Sampling Date 3. A covariance analysis was carried out in order to test the effects of initial SC of kleingrass on the SC at sampling date 3. The effect of date one on date three was not significant ($P > 0.55$), indicating that the pre-grazing pasture/site effects were not related to after-grazing treatment effects. Therefore, pasture/site effects were not considered to be seriously confounded with the grazing treatments.

Availability of annual grasses decreased in all pastures (Table 3, p 103). By this time, annuals were mature, shedding seeds, and senescing. Treatment 14-L had the highest annual grasses SC (2,362 kg/ha), but was not significantly different from treatments 30-H and 30-M. Treatment 0-H had the lowest SC for annual grasses (152 kg/ha), but was not significantly different from treatments 14-H, 0-L, and 14-M. Kleingrass SC was

significantly higher in treatment 14-M (789 kg/ha) than in the rest of the treatments. The ungrazed control produced the third highest SC of kleingrass after treatments 14-M and 14-L but was sixth in total SC, superior only to the three 0-delay treatments (0-L, 0-H, and 0-M). The three high-intensity treatments produced the three lowest kleingrass SC.

Treatment 14-M was the only treatment in which annual grasses and total forage increased continuously during the three sampling periods, and treatment 0-H was the only treatment in which they decreased continuously. Kleingrass production, however, increased continuously in treatments U, 14-M, 30-M, and 30-L.

The ungrazed control produced significantly higher total SC than the average of all grazed pastures. Grazing intensity, grazing initiation date, and grazing intensity by grazing initiation date interaction were significant for the three forage categories. Kleingrass, annual grasses, and total SC were significantly lower when grazed without delay at high-intensity. Averaged across grazing initiation dates, SC of kleingrass, annual grasses, and total were significantly lower for the high-intensity treatments than for the ungrazed control and the low- and medium-intensities (Table 5, p 104). Other treatments did not differ significantly.

Averaged across grazing intensities, the 0-delay grazing treatments had significantly lower SC of kleingrass, annual grasses, and total than the other grazing initiation dates and the ungrazed control (Table 6, p 105). Kleingrass SC exhibited a significant quadratic effect due to grazing intensity ($-0.007GI^2$). Annual grasses showed a linear effect due to grazing initiation date ($+78.379GID$), a quadratic effect due to grazing intensity ($-0.022GI^2$), and a quadratic effect due to grazing initiation date ($-1.042GID^2$). Total SC showed a quadratic effect due to grazing intensity ($-0.041GI^2$) and a significant grazing intensity by grazing initiation date interaction ($+0.275GI*GID$).

Utilization

There were no significant effects for utilization due to treatments, species or periods. There were significant treatment by species, and treatment by period interactions; therefore, results are presented by sampling period for each species.

Sampling Period 2. Utilization of kleingrass increased as grazing intensity increased during sampling period 1-30 April (Table 7, p 105). Treatment 0-L had the lowest utilization and treatment 0-H had the highest utilization of kleingrass. Utilization of annual grasses increased as grazing intensity increased. Treatment 0-H had significantly higher utilization of annual grasses than the other two treatments. Treatment 0-H had significantly higher total utilization (72.2 %), than treatments 0-M (30.5 %) and 0-L (13.3 %).

Sampling Period 3. Utilization of kleingrass was significantly greater at the medium- and high-intensities than for the low-intensity (Table 7, p 105). There was no significant difference between treatments for annual grasses, but utilization tended to decrease as grazing intensity increased. Treatments did not differ for total utilization.

From 30 April to 1 June, utilization of annual grasses and total increased in treatments O-L and O-M and decreased in treatment O-H. Utilization of kleingrass increased in all three pastures from period two to period three.

Tiller Heights

Tiller heights in the ungrazed enclosure (pasture 1) averaged 28.4 and 27.7 cm for kleingrass and annual grasses, respectively, on 2 June. Ungrazed tillers in the grazed pastures (pastures 2-10) averaged 13.5 and 12.2 cm, respectively, for kleingrass and annual grasses. The average heights of the grazed tillers was 9.3 and 9.5 cm for kleingrass and annual grasses, respectively. There was a significant grazing delay by grazing intensity by species interaction for the grazed tillers (Table 8, p 106). Only the O-H treatment significantly reduced tiller height. Average grazed height in this treatment was 7.9 cm, compared to 10.3 cm in the other treatments.

The percentage of tillers grazed increased asymptotically with time (Table 9, p 107). Differences between grazing intensities decreased at the last two sampling dates as all treatments approached the same level.

Net Growth of Sward

As described for SC, NG was directly related to the phenology of the species (Table 10, p 108). Net growth of kleingrass increased during the study; whereas, net growth of annual grasses decreased with time (Table 11, p 109). NGR (kg/ha/day) of kleingrass, annual grasses, and total for the three pastures with cages and the ungrazed control at two sampling periods is presented in Table 12, p 109. This reflects the more advanced maturity of annual grasses compared to kleingrass. There was a significant difference between sampling dates and forage categories, and significant treatment by date, treatment by forage category, date by forage category, and treatment by date by forage category interactions; therefore, data are presented within periods.

Sampling Period 2. Because production was measured in caged plots, NG and NGR for period 2 are without grazing. Treatments O-H and O-M had significantly higher NGR of kleingrass than treatments O-L and the ungrazed control (Table 10, p 108). There were no significant differences for annual grasses and total because of high variation within treatments. Treatment O-L had the highest NGR of annual grasses and treatment O-M had the highest total NGR (Table 12, p 109). Treatment O-H had the lowest NGR of both annual grasses and total.

Sampling Period 3. The maximum NGR of kleingrass occurred in treatment O-H and the minimum occurred in the ungrazed control (Table 12, p 109). Annual grasses presented negative NGR in all treatments. The ungrazed control had significantly lower NGR of annual grasses than the other pastures and treatment O-H was significantly higher. Total NGR was negative in all pastures except for treatment O-H which was significantly higher than the rest of the treatments. The ungrazed control was significantly lower than the rest of the treatments. NGR of annual grasses and total decreased, and kleingrass increased from one sampling date to the next in all treatments.

Tiller Growth Rate

Growth rates of kleingrass tillers for leaf, stem and inflorescence, daughter (secondary and tertiary) tillers, and total for the ungrazed control and the 0-delay, high-intensity grazing treatment (0-H), for four sampling periods are presented in Table 13, p 110. There were significant differences between treatments for leaf and total. There were also significant differences between sampling periods for the four components, and significant treatment by period interactions for leaf, tiller, and total; therefore, discussion of growth rate will be within sampling periods.

Sampling Period 1. There were no significant differences between treatments for any of the components (Table 13, p 110). Tillering had not started by period 1.

Sampling Period 2. There was no significant difference between treatments for daily growth rate of stem, but growth rate of leaf was significantly higher in the ungrazed control than in the grazed pasture (Table 13, p 110). This resulted in a significant difference of total growth rate, with higher tiller growth rates in the ungrazed pasture than in the grazed pasture. Tillering had not started by sampling period 2.

Sampling Period 3. There were no significant differences between treatments for any of the components (Table 13, p 110, and Figure 1, p 116). Tillering had started by date 3 but there was no difference between treatments for daughter tillers.

Sampling Period 4. Growth rate of leaf was significantly higher in the ungrazed control than in the grazed treatment (Table 13, p 110). This resulted in a significant difference for total growth rate, with higher growth rates in the ungrazed control than in the grazed treatment. Growth rate of secondary tillers was greater (not significant at $p=0.05$) in the grazed treatment.

Growth of Stem

At sampling date one, 18 % of the kleingrass tillers in both pastures had elongated stems. At sampling date two, the stems in both pastures weighed approximately the same; however, in the grazed pasture there were 13 % more tillers with stems. At sampling date three the grazed pasture had 14 % more tillers with elongated internodes than the ungrazed control. At the end of the study, stem growth in the grazed pasture was greater than in the ungrazed control. All the tillers in both pastures presented elongated stems. However, none of the apical meristems on the harvested tillers had been removed by grazing during the early-season grazing.

Growth of Secondary Tillers

Secondary tillers were first recorded on sampling date three (21 May). At this date secondary tillers were present on 9 % of the kleingrass tillers in both pastures. The grazed pasture presented very small tillers in the upper nodes. The growth rate of secondary tillers

was the same for both pastures, indicating that tillering started at approximately the same time.

During late May, the grazed pasture had higher growth rate of tillers than the ungrazed control due to a greater number of secondary tillers in the grazed pasture. In the ungrazed control, 9 % of the tillers had secondary tillers while in the grazed pasture 40 % of the tillers presented secondary tillers, 13 % of the tillers presented tertiary tillers, and 4.5 % tillered from the upper nodes.

Senescence Rate

Senescence rates of kleingrass tillers for leaf, stem and inflorescence, daughter tillers, and total for the ungrazed control and the 0-delay high-intensity grazing treatment for four sampling periods are presented in Figure 2, p 117. Stem and daughter tillers did not senesce. There was no significant difference between treatments for leaf. Tiller senescence rate increased during the study.

Addition to Dead Rate

Additions to dead of kleingrass tillers for leaf, stem and inflorescence, daughter tillers, and total for the ungrazed control and the 0-delay, high-intensity grazing treatment, for four sampling periods are presented in Figure 2, p 117. There was no addition to dead in stem and daughter tillers. There was significantly more addition to dead leaf for the ungrazed than for the grazed treatment. Addition to dead leaf was significantly higher in periods one and two than in periods three and four. Sampling period one had significantly higher daily addition to dead for the ungrazed control than the grazed treatment. There was no significant difference between treatments for periods two, three, or four.

Disappearance Rate of Dead

Disappearance rates of dead kleingrass for leaf, stem and inflorescence, daughter tillers, and total for the ungrazed control and the 0-delay, high-intensity grazing treatment for four sampling periods are presented Figure 2, p 117. There was no dead stem or daughter tillers; thus, there was no disappearance rate for these plant components. There was no significant difference between treatments for leaf. There was a significant difference between sampling dates for leaf, and a significant treatment by period interaction. Daily disappearance rate of dead was significantly higher for periods three and four. It reached a maximum at date three (2.7 mg/tiller/day) and a minimum at period two (0.6 mg/tiller/day).

Cumulative Growth, Senescence, Addition to Dead, and Disappearance

Cumulative growth, senescence, addition to dead, and disappearance of dead for leaf, stem and inflorescence, daughter (secondary and tertiary) tillers, and total for the ungrazed control and the 0-H treatments for four sampling periods are presented in Figures 3, p 118, and 4, p 119, respectively. Cumulative growth of kleingrass leaf was greater in treatment U than in 0-H during the entire study (Figure 3, p 118), but cumulative growth of stem and daughter tillers was greater in treatment 0-H. Cumulative senescence of

kleingrass leaf was greater in treatment 0-H (Figure 4, p 119). Cumulative addition to dead was greater in treatment U and cumulative disappearance of dead was greater in treatment 0-H (Figure 4, p 119).

Animal Gains

Average daily gains (ADG) of the tester animals on nine grazing treatments are presented for two periods (Table 14, p 111 and Figure 5, p 120). There were significant grazing intensity and grazing initiation date effects for both the 2 April to 9 June and the 1 May to 9 June periods. The grazing intensity by grazing initiation date interaction was non-significant. Treatments 0-M, 0-L, 14-L, and 14-M produced the highest ADG during the 2 April to 9 June period (Table 14, p 111). Treatment 30-H was significantly lower than the rest of the treatments, except for 14-H during the period 1 May to 9 June. The three high-intensity grazing treatments had the three lowest ADG.

ADG for 2 April to 9 June showed a significant quadratic grazing intensity effect and a significant grazing intensity by grazing initiation date interaction. ADG for 1 May to 9 June showed a significant quadratic effect due to grazing intensity.

Treatments 0-M and 15-M produced the highest gains. The lowest gains per hectare were produced in treatment 30-H (29.3 kg/ha)(Table 15, p 112). ADG for 0-delay and 30-day delay treatments did not differ between low-and medium. Gains per hectare were highest for the three medium-intensity treatments within GID. Within grazing intensities, gain per hectare were significantly lower for the three 30-day delay treatments. Gains per head for the 14-day delay treatment decreased from low-to high grazing intensity (Figure 5, p 120).

Averaged across grazing intensity the 30-day delay treatments produced significantly lower ADG than the 14-day delay and the 0-day delay treatments. Averaged across grazing initiation dates, the high-intensity treatments produced significantly lower ADG than low- and medium-intensities (Table 16, p 113).

Body Condition

There were no significant treatment effects for BCS.

Forage Intake

Organic matter intake of the tester animals, estimated by fecal nitrogen output (FNO) and by organic matter digestibility (OMD), for the nine grazing treatments at two sampling dates is presented in Table 17, p 114. Percent fecal nitrogen is presented in Table 18, p 115.

At date 1 there were no significant linear or quadratic effects of grazing intensity or grazing initiation date, but at date 2, organic matter intake by both FNO and OMD showed significant negative quadratic effects due to grazing intensity.

The botanical composition determined by microhistological analysis (Figure 6, p 121) showed that kleingrass in the feces increased from an average of 50 % in early May to an average of 75 % in early June. Annual grass stem which included the seed heads decreased markedly from May to June. There was more variation among treatments in May than June.

DISCUSSION

Standing Crop

Several factors contributed to the low production of kleingrass. The study only encompassed two spring months and kleingrass is a warm-season grass. Leaf was the primary source of kleingrass production in April and May. Stem elongation had just started in some tillers and at the end of the study only 9 % of kleingrass tillers had formed an inflorescence. Kleingrass production during this study (1 April - 9 June) represents only 11 to 40 % of the potential total annual production that has been reported (Conrad 1976, Holt et al. 1985). Also, N from the early fertilization (February) was used primarily by the annual grasses, restricting early growth of kleingrass as reported by Chmielewski (1981). Fertilization with N in early May could have promoted kleingrass growth.

Precipitation was only 72 % of the average during the study and occurred mainly after May 10. Competition for moisture probably occurred between the annual grasses and kleingrass. At sampling period 2, kleingrass production was reduced in the pastures where delayed grazing allowed annual grasses to grow unchecked, compared to the 0-delay grazed treatments in which the competition was reduced through grazing. The ungrazed pastures produced an average 20 % less kleingrass than the pastures which had already been grazed. After sampling period 2, annual grasses completed their life cycle and senesced, reducing competition, even without grazing.

Although kleingrass production was inhibited by competition from annual grasses, carrying capacity was increased by early-season grazing since the annual grasses produced as much as 5,143 kg/ha (treatment 30-H). This early-season production would not have been available if annual grasses had been controlled with herbicides or if grazing had been delayed.

Treatments 0-L, 0-M, and 0-H (the three early grazed treatments) and treatment 14-H had the lowest SC of annual grasses at the end of the trial. Kleingrass SC tended to be lower in these treatments. In treatment 0-L the animals were observed to pull up, but not consume, most of the Japanese brome, thus considerably reducing the annual grasses SC.

Treatments 0-H, 14-H, and 30-H, the three high-intensity treatments, produced the three lowest kleingrass SC at the end of the trial. Treatments 14-M and 14-L had the highest kleingrass SC because grazing reduced annual grasses competition without heavy use of the kleingrass. Thus, early grazing was very effective in reducing annual grasses (Chessmore 1979). Chmielewski (1981) reported that grazing from mid-May through early July had little effect on the cool-season annuals. This study indicated that delayed grazing allowed annual grasses to senesce and contribute little to the diet.

Early grazing extended the growing period and increased tillering in annual grasses (Laude 1957). On average, 0-delay and high-intensity treatments utilized annual grasses more completely than other treatments. Treatment 30-H had a strong pasture/site effect which was manifested in the highest annual grasses SC during sampling periods 1 and 2. At the end of the trial, treatment 30-H had the second highest annual grasses standing crop; however, it was mostly stems from Darnel. When grazing was initiated for the 30-day delay treatment, the forage was stemmy and tall. Animals trampled much of the tall grass, laying it on the ground and making it unavailable.

Utilization

During April, grazing pressure was primarily on annual grasses with significant kleingrass utilization only on the 0-H treatment. The 0-M treatment had less standing crop of annual grasses than the 0-L treatment. Higher grazing intensity and lower quantity of total forage on 0-M reduced standing crop of kleingrass compared to 0-L treatment. The high-intensity grazing treatment reduced standing crop of annual grasses and utilization shifted to kleingrass.

During May, the low-intensity grazing treatment (0-L) had the highest utilization of annual grasses, but the lowest utilization of kleingrass. Uprooting of Japanese brome during May increased the utilization of annual grasses from the lowest during April to the highest during May.

The 0-H treatment had the lowest utilization of annual grasses during May although it had the highest grazing intensity. SC of annual grasses in 0-H was very low during May and stocking density had to be reduced by 50 % before the end of the study. Kleingrass utilization was the highest in treatment 0-H. The intensity of grazing in this treatment was so severe that at the end of the study total forage availability limited animal intake.

Use of cages may distort the estimation of utilization (Cook and Stubbendieck 1986). Increased yields inside the cages have been reported for periods as short as 30 days due to modification of microclimatic conditions and differences in live leaf area between caged and grazed plants. This can lead to significant errors in estimating forage utilization (Cowlshaw 1951, Grelen 1967).

Tiller Height

Analysis of tiller height data indicated a similar grazed height for kleingrass and annual grasses except for the 0-delay high-intensity treatment. The primary variable was the proportion of tillers grazed. However, even under the most intense grazing, there appeared to be an upper limit (near 60%) on the proportion of grazed tillers. This resulted from the production of greater numbers of small tillers in the intensively grazed swards. In the 0-H treatment the average height of ungrazed tillers was less than for grazed tillers in the other treatments. These data provide strong evidence that cattle tend to graze swards in a top-down manner when palatability of the available forage is relatively uniform.

Sward Growth

Net growth of annual grasses decreased continuously after sampling period one because most matured and started shedding seeds and leaves by late April. At the end of the study negative net growth rates reflected reduced senescence losses with increased utilization (Parsons et al. 1988).

Net growth of kleingrass increased significantly from period one to period two and then remained constant during period three. Net growth was greatest in the high and medium-intensity treatments probably because competition from surrounding vegetation was reduced by grazing. The lowest net growth of kleingrass occurred in the ungrazed control.

Tiller Dynamics

Kleingrass growth was retarded by freezing temperatures on March 31 and April 4 and the tillers did not reach the four-leaf stage until 3 wk after aboveground growth had initiated. Secondary tiller formation started 4 wk after growth had initiated and occurred only after the shoots presented at least four leaves (Langer 1963). Tertiary tiller formation started 10 days later. Tillering from the upper nodes, or branching, confirmed the report by Evers (1970).

Production of daughter tillers began after internodes elongated (reproductive stage) but before the inflorescence elongated above the vegetative leaves, and before kleingrass reached peak production. Patterns of tiller production and of death are dominated by flowering (Robson 1968), which occurs early in kleingrass. This early pattern of tiller recruitment reduces the opportunity for removal of all active apical meristems by grazing (Butler and Briske 1988). The ability to tiller without the apical meristem being removed is considered an indication of an efficient forage producer (Dahl and Hyder 1977).

Tiller Tissue Fluxes

Growth rate of leaf of kleingrass tillers increased continuously from date 1 to date 4 in both pastures. Growth rate increased with herbage mass in the grazed pasture in an asymptotic manner (Bircham and Hodgson 1981), but did not become asymptotic in the ungrazed control during the study (Figure 7, p 122).

At sampling date two, the annual grasses reached their peak growth and were competing with kleingrass. The tillers in the grazed pasture were caged, but had less competition from the surrounding vegetation than the tillers in the ungrazed control in which the surrounding canopy had not been reduced by grazing (Mueggler 1972). At date 2 there were 13 % more tillers with elongated internodes in the grazed pasture than in the ungrazed control, indicating that more tillers had reached the reproductive stage.

The cages were moved to new plots on 1 May. Of the marked tillers in the cages on the grazed pasture, 41 % had been defoliated compared to 58 % defoliated tillers outside the cages. Although the grazed pasture had a higher leaf growth rate than the ungrazed control, the difference was not significant. There were 14 % more tillers with

elongated internodes in the grazed than in the ungrazed treatment. Kleingrass tillers in the ungrazed treatment were slim and long due to competition for light from the annual grasses. Defoliation of marked tillers was not severe and regrowth was rapid from intercalary meristems at the base of the blades (Dahl and Hyder 1977).

During May, annual grasses in the ungrazed pasture were dry and shedding leaves; whereas, annual grasses were still green and actively growing in the cages on the grazed pasture. Growth of kleingrass increased markedly in the ungrazed pasture. In the grazed pasture, growth rate of kleingrass tillers was reduced, perhaps due to greater competition. The apparent difference in growth rates at the sward and tiller levels reflected the different growth forms. In the ungrazed pasture there were fewer large tillers that had a greater growth rate. The grazed pasture had a larger number of small tillers with less growth per tiller, but a greater net growth rate for the population.

Increased tillering is a common response to grazing (Jones et al. 1982). Since none of the apical meristems in the sampled tillers had been removed by grazing, the increased tillering in the grazed pasture was not induced by elimination of apical dominance (Leopold 1949). Reduction of competition from surrounding vegetation also increases the number of flower stalks produced (Mueggler 1972). Increased tillering may also occur in response to increased red light at the base of the plants resulting from a sparser canopy (Deregibus et al. 1985, Butler and Briske 1988). In the ungrazed control the annual grasses produced a dense stand that reduced light intensity on many kleingrass tillers. Some tillers may die when the whole plant is subjected to a stress such as shade. The smallest tillers generally die first (Ong 1978). Thus, reduced light intensity probably contributed to the lower tillering rate in the ungrazed pasture.

Senescence of Live Leaf

Senescence of leaf lagged growth following the same pattern (Grant et al. 1983, Parsons et al. 1988). Senescence in the ungrazed control and grazed pasture was comparable. Because all marked tillers were protected from grazing, differences between treatments were minimal.

Addition to Dead Leaf

Inclusion of dead sheaths from the previous year that surrounded the newly emerged tillers increased addition to dead leaf on date one. The parts of the leaves that died from the last frosts (31 March and 14 April) also increased the amount of dead material at the beginning of the study in addition to the increased rate of appearance and death of leaves as temperature increased (Anslow and Green 1967, Vine 1983, Chapman et al. 1984). The significant difference between pastures at date one resulted from pasture/site differences. Treatment U was in the lowest part of the study site and was more affected by the last frosts. This increased the amount of dead material. The significant decrease in addition to dead leaf after date two coincided with the initiation of the reproductive stage (Booyesen et al. 1963).

Disappearance of Dead Leaf

Disappearance of dead leaf increased as precipitation increased in May. Rain may act as a physical force that causes fracturing and transfer of dead to litter (Detling et al. 1979).

Animal Gains

ADG produced by 0-L, 0-M, 14-L, and 14-M for the 12 April - 9 June period were similar to the gains reported by Norris et al. (1969) and Conrad (1976). Reduction in ADG by the 30-day delay treatments reflected a decline in forage quality. In these treatments, grazing was initiated (1 May) when the annual grasses were mature. This indicates that to optimize the use of annual grasses, grazing must be initiated before they reach maturity. Reduction in ADG by the three high-intensity treatments reflected a decline in forage availability (Mott 1960, Hart 1988). In these treatments, forage demand exceeded growth rate of forage.

The lowest ADG resulted from the 30-H, in which forage had grown tall and stemmy. When the animals grazed the pasture, they trampled the forage and made it unavailable. ADGs were similar for the 0-delay and the 14-day delay treatments. However, ADG during the 1 May to 9 June period, show that gains for the 0-M treatment declined significantly at the end of the study. This decline was associated with low SC of annual grasses and kleingrass at the last sampling date.

Livestock production in terms of gains per hectare were also significantly reduced by the 30-day delay treatments. Gains per hectare were similar for the 0-delay and the 14-day delay treatments and were highest at medium-intensity grazing. They were reduced at both the low-and high-intensities (Mott 1960). Although ADGs were higher at low-intensity, these treatments were stocked too lightly to maximize livestock production in terms of gains per hectare. Therefore, the best gains for both ADG and gains per hectare were produced by the medium-intensity with 0-delay or 14-day delay.

Treatment 14-M produced only 2 % less gain per hectare than treatment 0-M, and at the end of the trial it had a high availability of total forage (2098 kg/ha) with an increasing production of kleingrass (789 kg/ha). However treatment 30-M had significantly lower gains per head and per hectare with no benefit to the kleingrass. Thus, it is clear that timing of grazing is very critical to achieving high levels of animal production.

Grazing at medium-intensity can start earlier if annual grasses are available than on pure stands of kleingrass. This can increase animal production from the pasture and provide a viable alternative to the use of herbicides for control of cool-season annual grasses (Chessmore 1979).

Body Condition

The lack of significant differences between dates and treatments indicates that body condition scores were not as sensitive a measure as animal gains for a short term study.

The steers entered the study in good condition coming off high quality winter pasture. Changes in body condition occurred within a narrower range than live weight (Russel et al. 1969); therefore, short term changes in body condition, such as those measured in this study, are not likely to be significant.

Forage Intake

Intake was limited when availability of forage was below 850 kg/ha (Johnston-Wallace and Kennedy 1944). At low forage availability, animals were observed to increase time spent grazing in order to balance intake (Arnold and Dudzinski 1978). A low OMI in treatment 0-H was associated with limited forage availability since this pasture had only 589 kg/ha of total available forage. ADG in this treatment was very low.

Treatment 30-H had the lowest OMI and ADG. Although forage availability was high, the sward was mostly tall, stemmy annual grasses. These animals had the highest proportion of annual grasses in the diet. Kleingrass availability was low and SC was declining. OMI appeared to be restricted primarily by low quality of annual grasses and low availability of green kleingrass leaf (Minson 1981).

OMI was lower for all treatments in June compared to May. Annual grasses had few live leaves and were shedding dry leaves. Standing crop of kleingrass was still low also, thus availability of high quality green leaf was low in all treatments. The negative quadratic effects of grazing intensity indicated that OMI tended to decrease more rapidly from medium- to high-intensity than from low- to medium-intensity. Treatments that had the highest OMI generally had the highest ADG.

Proportion of kleingrass in the microhistological analysis of the feces increased from May to June. The low amounts of kleingrass stem reflected low availability of stem, since spring growth was primarily leaf. Increased consumption of annual grass stem/seedhead in May compared to June, reflected differences in maturity. As annual grasses matured during May, stems became tough and seeds shattered. The low palatability of mature stem is evidenced by the low proportion of annual grass stem in the 30-H treatment during June. The steers on 30-H had reduced OMI even though mature annual grass stems were readily available.

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Table 1. Monthly total precipitation (mm) for 1987 and the 23-year average for the period 1965-1987, from Agricultural Research Center at McGregor, Texas.

	1987	Average (1965-1987)
January	36	40
February	78	62
March	43	61
April	47	82
May	107	120
June	146	80
July	17	49
August	15	55
September	60	84
October	4	103
November	144	67
December	87	52
Total	784	855

Table 2. Grazing initiation dates (GID) and grazing intensities (GI) applied to kleingrass pastures under early-season grazing at McGregor, Texas.

GID (Days)	GI (Level)	GI (AUD/ha)	Pasture
0	Low	113	2
0	Medium	177	8
0	High	219	5
14	Low	105	6
14	Medium	175	3
14	High	217	10
30	Low	97	9
30	Medium	169	4
30	High	199	7
68	Control	0	1

Table 3. Mean standing crop (kg/ha) of kleingrass (K), annual grasses (AG), and total (T), for the ungrazed control (U), the three grazing initiation dates (GID), and the three grazing intensities (GI), at the three sampling dates^A.

GID ^B	GI ^C	Sampling Dates								
		1			2			3		
		K	AG	T	K	AG	T	K	AG	T
U	U	58 ^d	1773 ^a	1831 ^a	294 ^b	2895 ^b	3189 ^{bc}	553 ^b	1530 ^{bc}	2083 ^b
0	L	64 ^{cd}	1413 ^a	1477 ^a	580 ^a	1888 ^{cd}	2468 ^{de}	475 ^{bc}	346 ^d	821 ^c
0	M	61 ^d	1555 ^a	1616 ^a	422 ^{ab}	1536 ^d	1958 ^e	336 ^{cde}	449 ^d	785 ^c
0	H	91 ^{abc}	1765 ^a	1856 ^a	377 ^{ab}	370 ^e	747 ^f	272 ^{def}	152 ^d	424 ^c
14	L	83 ^{bcd}	1689 ^a	1772 ^a	567 ^a	3051 ^b	3618 ^b	554 ^b	2362 ^a	2916 ^a
14	M	112 ^a	1304 ^a	1416 ^a	499 ^{ab}	1508 ^d	2007 ^e	789 ^a	1309 ^c	2098 ^b
14	H	55 ^d	1674 ^a	1729 ^a	388 ^{ab}	1488 ^d	1876 ^e	144 ^f	251 ^d	395 ^c
30	L	68 ^{cd}	1596 ^a	1664 ^a	398 ^{ab}	2392 ^{bc}	2790 ^{cd}	443 ^{bcd}	1708 ^{bc}	2151 ^b
30	M	97 ^{ab}	1515 ^a	1612 ^a	473 ^{ab}	2879 ^b	3352 ^{bc}	528 ^b	1810 ^{abc}	2338 ^b
30	H	67 ^{cd}	1880 ^a	1947 ^a	350 ^b	4793 ^a	5143 ^a	193 ^{ef}	1947 ^{ab}	2140 ^b

^A Sampling dates 1, 2, and 3 correspond to 1 April, 30 April, and 1 June, 1987, respectively.

^B Grazing initiation dates 0, 14, and 30 correspond to 0-day, 14-day delay, and 30-day delay, respectively.

^C Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

abcdef Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 4. Mean standing crop (kg/ha) of kleingrass (K), annual grasses (AG), and total (T), at the three sampling dates, averaged across pastures.

Sampling Date ^A	K	AG	T
1	76 ^b	1617 ^b	1693 ^b
2	435 ^a	2280 ^a	2715 ^a
3	429 ^a	1186 ^c	1615 ^b
Mean	288	1694	2008

^A Sampling dates 1, 2, and 3 correspond to 1 April, 30 April, and 1 June, 1987, respectively.

^{abc} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 5. Mean standing crop (kg/ha) at sampling date three^A of kleingrass (K), annual grasses (AG), and total (T), for the ungrazed control (U), and the three grazing intensities (GI), averaged across grazing initiation dates.

GI	K	AG	T
U	553 ^a	1530 ^a	2083 ^a
LOW	491 ^a	1472 ^a	1963 ^a
MEDIUM	551 ^a	1189 ^a	1740 ^a
HIGH	203 ^b	783 ^b	986 ^b

^A Sampling date three corresponds to 1 June.

^{ab} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 6. Mean standing crop (kg/ha) for sampling date three^A of kleingrass (K), annual grasses (AG), and total (T), for the ungrazed control (U), and the three grazing initiation dates (GID), averaged across grazing intensities.

GID	K	AG	T
U	553 ^a	1530 ^{ab}	2083 ^a
0 DAY-DELAY	361 ^c	316 ^c	677 ^b
14 DAY-DELAY	496 ^{ab}	1307 ^b	1803 ^a
30 DAY-DELAY	388 ^{bc}	1822 ^a	2210 ^a

^A Sampling date three corresponds to 1 June.

^{abc} Means in the same column with a common superscript are not significantly different at the 0.05 level of probability.

Table 7. Utilization (%) of kleingrass (K), annual grasses (AG), and total (T), for the three caged pastures, grazing initiation dates (GID), and the three grazing intensities (GI), for two sampling periods.

GID ^A	GI ^B	Sampling Period					
		April 1-30, 1987			April 30-June 1, 1987		
		K	AG	T	K	AG	T
0	L	-104.6 ^b	24.6 ^b	13.3 ^b	35.3 ^b	64.6 ^a	54.1 ^a
0	M	8.0 ^a	29.9 ^b	30.5 ^b	63.5 ^a	47.7 ^a	57.2 ^a
0	H	37.9 ^a	81.9 ^a	72.2 ^a	68.2 ^a	31.2 ^a	66.8 ^a

^A Grazing initiation date 0 corresponds to non-delayed.

^B Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

^{ab} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 8. Mean height (cm) and standard deviations (SD) of grazed kleingrass (K) and annual grass (AN) tillers on 2 June 1987 for three grazing intensities and three grazing delay treatments. Main effect means are presented with mean separation indicated.

Intensity	Delay								
	0-day			14-day			30-day		
	K	(SD)	AN	(SD)	K	(SD)	AN	(SD)	Mean
L	11.1	(4.2)	11.5	(5.6)	9.8	(3.6)	9.5	(3.7)	10.3 ^a
M	9.7	(5.3)	10.5	(4.7)	9.6	(3.6)	8.5	(4.1)	10.2 ^a
H	5.5	(2.9)	4.5	(2.4)	8.1	(3.4)	9.7	(3.8)	7.9 ^b
Mean	8.6 ^b			9.2 ^a			10.7 ^a		

^{ab} Means not having the same superscript differ significantly ($p < 0.05$).

Table 9. Percent kleingrass tillers defoliated at three grazing intensities, three grazing initiation dates, at four sampling dates.

		Delay			Mean
Intensity		0-day	14-day	30-day	
4/20/87	L	16	7	-	11
	M	29	7	-	18
	H	56	15	-	36
	Mean	34	10	-	22
5/01/87	L	20	41	-	31
	M	47	51	-	49
	H	70	39	-	55
	Mean	46	45	-	46
5/21/87	L	63	51	32	49
	M	49	63	48	53
	H	58	43	35	45
	Mean	57	52	38	49
6/02/87	L	51	63	38	51
	M	56	69	36	54
	H	62	62	53	59
	Mean	56	65	42	55

Table 10. Mean net growth (kg/ha) of kleingrass (K), annual grasses (AG), and total (T), for the three caged pastures and the ungrazed control (U), the grazing initiation date (GID), and the three grazing intensities (GI), for the three sampling periods^A.

GID ^B	GI ^C	Sampling Period								
		1			2			3		
		K	AG	T	K	AG	T	K	AG	T
U	U	58 ^b	1773 ^a	1831 ^a	236 ^b	1122 ^a	1358 ^a	259 ^c	-1365 ^c	-1106 ^d
O	L	64 ^b	1413 ^a	1477 ^a	266 ^b	1150 ^a	1416 ^a	287 ^{bc}	-861 ^b	-574 ^c
O	M	61 ^b	1555 ^a	1616 ^a	500 ^a	997 ^a	1497 ^a	525 ^{ab}	-604 ^b	-79 ^b
O	H	91 ^a	1765 ^a	1856 ^a	528 ^a	415 ^a	943 ^a	560 ^a	-21 ^a	539 ^a

^A Sampling periods 1, 2, and 3 correspond to all growth prior to 1 April, April 1-30, and April 30-June 1, 1987, respectively.

^B Grazing initiation date 0 corresponds to 0-delay treatment, and U is the ungrazed control.

^C Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

^{abcd} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 11. Mean net growth (kg/ha) of kleingrass (K), annual grasses (AG), and total (T), for the three sampling periods, averaged across treatments.

Sampling Period ^A	K	AG	T
1	68 ^b	1627 ^a	1695 ^a
2	382 ^a	921 ^b	1303 ^b
3	408 ^a	-713 ^c	-305 ^c

^A Sampling periods 1, 2, and 3 correspond to prior to April 1, April 1-30, and April 30-June 1, 1987, respectively.

^{abc} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 12. Mean net growth rate (kg/ha/day) of kleingrass (K), annual grasses (AG), and total (T), for the three treatments and the ungrazed control (U), for two sampling periods^A.

GID ^B	GI ^C	Sampling Period					
		2			3		
		K	AG	T	K	AG	T
U	U	8.4 ^b	40.1 ^a	48.5 ^a	7.8 ^b	-41.4 ^c	-33.6 ^d
0	L	9.8 ^b	42.6 ^a	52.4 ^a	8.4 ^b	-25.3 ^b	-16.9 ^c
0	M	18.5 ^a	36.9 ^a	55.4 ^a	15.5 ^{ab}	-17.8 ^b	-2.3 ^b
0	H	19.6 ^a	15.3 ^a	34.9 ^a	16.5 ^a	-0.6 ^a	15.9 ^a

^A Sampling periods 2, and 3 correspond to April 1-30, and April 30-June 1, 1987, respectively.

^B Grazing initiation date 0 corresponds to 0-delay, and U is the ungrazed control.

^C Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

^{abc} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 13. Mean growth rate (mg/tiller/day) of kleingrass leaf (L), stem and inflorescence (S), daughter tillers (T), and total (TL) for the ungrazed control (U) and the O-delay, high-intensity treatment (O-H), for four sampling periods^A.

Treatment	Sampling Periods											
	1			2			3			4		
	L	S	TL	L	S	TL	L	S	TL	L	S	TL
U	1.8 ^a	0.2 ^a	0.0 ^a	2.0 ^a	3.2 ^a	0.0 ^a	3.4 ^a	4.0 ^a	1.4 ^a	0.1 ^a	5.5 ^a	14.7 ^a
O-H	1.2 ^a	0.4 ^a	0.0 ^a	1.6 ^a	1.5 ^b	0.0 ^a	2.0 ^b	5.4 ^a	1.8 ^a	0.1 ^a	7.3 ^a	7.6 ^b

^A Sampling periods 1, 2, 3, and 4 correspond to April 1-14, April 14-30, April 30-May 21, and May 21-June 2, 1987, respectively.

^{ab} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 14. Mean average daily gain (kg/day) of the tester animals on nine grazing treatments for two periods.

GID ^A	GI ^B	Period	
		2 April to 9 June	1 May to 9 June
0	L	0.614 ^{ab}	0.558 ^a
0	M	0.615 ^{ab}	0.319 ^{bc}
0	H	0.393 ^c	0.322 ^{bc}
14	L	0.712 ^a	0.609 ^a
14	M	0.612 ^{ab}	0.497 ^{ab}
14	H	0.419 ^{bc}	0.063 ^d
30	L	0.484 ^{bc}	0.484 ^{ab}
30	M	0.498 ^{bc}	0.498 ^{ab}
30	H	0.110 ^d	0.110 ^{cd}

^A Grazing initiation dates 0, 14, and 30 correspond to 0-delay, 14-day delay, and 30-day delay, respectively.

^B Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

^{abcd} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 15. Gain per hectare (kg/ha) calculated by extending the ADG of the tester animals to the total animal-unit-days for each treatment for the period April 2-June 9, 1987.

GID ^A	GI ^B	Gain/Hectare (kg/ha)
0	L	92.4
0	M	145.6
0	H	114.7
14	L	99.7
14	M	142.6
14	H	121.3
30	L	62.6
30	M	111.9
30	H	29.3

^A Grazing initiation dates 0, 14, and 30 correspond to 0-delay, 14-day delay, and 30-day delay, respectively.

^B Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

Table 16. Mean average daily gain (kg/day) of the tester animals, averaged across grazing intensities and grazing initiation dates for the period 2 April-9 June 9, 1987.

Average Daily Gain	
GID ^A	
0	0.537 ^a
14	0.575 ^a
30	0.358 ^b
GI ^B	
L	0.603 ^a
M	0.574 ^a
H	0.307 ^b

^A Grazing initiation dates 0, 14, and 30 correspond to 0-delay, 14-day delay, and 30-day delay, respectively.

^B Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

^{ab} Means in the same column with a common superscript are not significantly different at the .05 level of probability.

Table 17. Organic matter intake (kg) estimated by fecal nitrogen output (FNO) and by organic matter digestibility (OMD) for the nine grazing treatments at two sampling dates^A.

GID ^B	GI ^C	Sampling Dates			
		1		2	
		FNO	OMD	FNO	OMD
0	L	9.439	8.825	8.577	7.437
0	M	10.358	9.967	6.679	4.887
0	H	9.089	8.420	6.813	5.066
14	L	10.028	9.666	8.674	7.658
14	M	9.887	9.408	7.869	6.489
14	H	9.437	8.837	7.135	5.501
30	L	9.802	9.348	7.371	5.875
30	M	10.221	10.080	7.857	6.606
30	H	8.189	7.174	6.362	4.615

^A Sampling date 1, and 2 correspond to 15 May and 12 June, 1987, respectively.

^B Grazing initiation dates 0, 14, and 30 correspond to 0-delay, 14-day delay and 30-day delay, respectively.

^C Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

Table 18. Percent fecal nitrogen for the nine grazing treatments at two sampling dates^A.

GID ^B	GI ^C	Date 1	Date 2
0	L	1.7	2.1
0	M	1.8	1.9
0	H	1.7	2.2
14	L	1.7	1.8
14	M	1.8	2.0
14	H	1.7	1.9
30	L	1.7	1.8
30	M	1.7	1.7
30	H	1.7	1.6

^A Sampling date 1, and 2 correspond to 15 May and 12 June, 1987, respectively.

^B Grazing initiation dates 0, 14, and 30 correspond to 0-delay, 14-day delay and 30-day delay, respectively.

^C Grazing intensities L, M, and H correspond to low, medium, and high, respectively.

Figure 1. Response surface of total standing crop (kg/ha) to grazing intensity and grazing initiation date at three sampling periods. (Sampling periods 1, 2, and 3 correspond to April 1, 2, 3, April 28, 29, 30, and June 1, 2, 3, 1987, respectively) ($P < 0.15$).

Figure 2. Senescence, addition to dead and disappearance rates of dead kleingrass leaf (mg/tiller/day) for the ungrazed control (U) and the non-delay, high intensity grazing treatment.

Figure 3. Cumulative growth of leaf, stem and daughter tillers of kleingrass for the ungrazed control (U) and the non-delay, high intensity treatment.

Figure 4. Cumulative senescence, addition to dead and disappearance of dead kleingrass leaf for the ungrazed control (U) and the non-delay, high intensity treatment.

Figure 5. Gain per head and gain per hectare for early-season grazing treatments.

Figure 6. Botanical composition of the feces (%) determined by microhistological analysis for the nine grazing treatments at two sampling dates.

6. EVALUATION OF RESEARCH ACHIEVEMENTS

Research associated with this project achieved the objectives identified in the original project proposal. Main processes involved in plant-animal interactions associated with early season grazing were identified, quantified, and integrated in a predictive theory. The hypothesis that early season processes, and management decisions affecting them, are major determinants of forage production and range trend were tested in two important range types: Mediterranean annual in Israel and perennial grassland in Texas. The approach and methodology of integrating field studies with modelling and the results obtained will contribute in a broader context towards understanding the biological mechanisms controlling both plant and animal responses in grazed ecosystems.

The models developed as part of this research are being used in Texas to extend the results of grazing trials. Extensive research has been conducted to validate the linked forage-diet-animal models for sheep grazing in the Edwards Plateau region. This research thrust is being continued with other funding. A new initiative is being proposed to integrate these models into a complex bio-economic model developed by Agriculture Canada. The Canadian model is used as a management decision-aid. Inquiries have been received from several outside research locations about possible cooperative research endeavors using these models.

Continued research and development of the simulation models will play a significant role in directing the design of future grazing management field studies. These models suggest which variables should be measured in field studies, the desired frequency of measurements, and the required levels of precision. Furthermore, they can be used to formulate and test complex hypotheses and simulate expected responses for a large number of potential treatments. Field studies can then be designed to collect validation data for critical regions to test the simulation hypothesis. Grazing management research utilizing empirical field studies can be greatly enhanced by integrating simulation. Simulation is required to formulate the complex, time-dynamic hypotheses for the main effects and interactions of the many variables involved in grazed ecosystems.

Concepts developed in this project led to an associated research endeavor by Texas scientists which resulted in the production of a management decision-aid. The decision-aid consists of three computer templates for use with Lotus 123. These will be released during the spring 1990. The "Grazing Management Stock Adjustments Decision-Aid" has been tested for the past year with ranchers and extension specialists. It promises to be a very useful tool for balancing forage demand with forage production. The balancing of forage demand rate with forage production rate was a key process identified in the kleingrass grazing trial. We anticipate that this decision-aid will find world wide acceptance as a grazing management tool.

7. DESCRIPTION OF COOPERATION

This study fostered extensive collaboration and cooperation between USA and Israel scientists which will have significant long range impacts on the development and conduct of their research. Discussions during the development of the proposal promoted an exchange of concepts on the importance of early season grazing in very different ecosystems.

Both Israeli scientists visited the USA immediately after the project was approved. Dr. Noy-Meir stayed for 10 days and Dr. Gutman stayed for 3 months. During their visit, extensive discussions were held to develop detailed research plans. Visits were made to the USA field research site. Dr. Gutman participated in the planning and early phases of an oat grazing study that was used in the development and parameterization of the USA forage dynamics model. During this time we shared research techniques for measurement of sward and tiller level forage variables, and discussed the selection of variables to be studied. Modeling approaches were compared and discussed.

At the beginning of year 3, Dr. Noy-Meir made a short visit to USA and plans were discussed for collaboration during the final phase of the study. Model development was discussed and compared. During January of 1989, Dr. Kothmann spent two weeks in Israel. This provided an opportunity to visit the study site and review the research program at Karei-Deshe Research Station. Extensive discussions were conducted evaluating the research that had been completed and planning for future research. Several areas of common interest were identified as areas of future cooperative research. During Kothmann's visit, he was afforded an opportunity to visit several other research sites and to discuss research programs and problems with all of the range scientists in Israel. This opportunity provided significant new insights into the kinds of range ecosystems, their management, and the research approaches used in Israel.

During the final phase of the research there was exchange of data and models between the USA and Israel. Two examples of the integration of the research will serve to illustrate cooperation. Based upon USA research, a senescence function was incorporated into the Israeli forage model. Lack of fit led to revision of the function with new estimation of the parameter. Simultaneous work in the USA (Spangler, unpublished Dissertation) reached the same conclusion (Figure 1, p 125). The new function with only one parameter is more robust and fits real world data better. A second example is the sharing of data to estimate parameters for model functions. Forage height, standing crop, and forage disappearance (estimated intake) data from Israel were used to estimate parameters for the harvestability function in the USA diet model (Figure 2, p 126).

Cooperative efforts have been initiated to pool the data and modeling efforts to evaluate forage-animal interactions, not only for early-season grazing but in a broader context. It is anticipated that one or more joint publications will be developed over the next year or two as a direct result of this project. It is the intention of the scientists to maintain regular communication and to pursue opportunities for future cooperative research.

Figure 1. Comparison of two senescence rate functions for runs with a constant growth rate of $2 \text{ g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ for 60 days starting with an initial age of 30 days and $15 \text{ g} \cdot \text{m}^{-2}$ of live leaf. The function without the constant (only the age parameters) is more responsive to forage age, and also goes to zero when standing crop goes to zero.

Karei-Deshe Trial (7-11/2/88)

Figure 2. Data from Israeli grazeout trial is used to estimate K_M and F_{MAX} parameters for USA diet model. Data indicate presence of an ungrazable residual of about 450 kg/ha or 360 mm height.

8. LIST OF PUBLICATIONS

Journal Papers

Anderson, V.J., and D.D. Briske. 1990. Stomatal distribution, density and conductance of three perennial grasses native to the southern true prairie of Texas. *American Midland Naturalist* 123:152-159.

Blackburn, H.D., and M.M. Kothmann. 1989. A forage dynamics model for use in range or pasture environments. *Grass and Forage Science* 44:283-294.

Journal Papers Submitted

Blackburn, H.D., and M.M. Kothmann. 1990. Evaluating plant/animal interactions: Modelling diet selection and intake of grazing herbivores. *Ecological Modeling* (Submitted February 1990)

Briske, D.D. and V.J. Anderson. Tiller dispersion within populations of the bunchgrass *Schizachyrium scoparium*: Implications to herbivory tolerance. *Oikos* (Revision submitted April 1990).

Proceedings

Briske, D.D. 1990. Vegetation dynamics in grazed systems: A hierarchical perspective. Proceeding of the XVI International Grassland Congress, Vol. III, Nice, France. (reprints not yet available).

Kothmann, M.M., D. Forbes, and H. Blackburn. 1989. Approaches to simulating intake of range animals. Proc. 3rd Int. Workshop on Modelling Digestion and Metabolism in Farm Animals. Lincoln College, NZ. (Reprints not yet available)

Abstracts of Papers Presented

Kothmann, M.M., H.D. Blackburn, and A.M. Spangler. 1989. Preference, palatability and availability in grazing systems simulation. Proc. Society Range Management, Billings, MT. (Abstract)

Kothmann, M.M., H.D. Blackburn, and A.M. Spangler. 1989. Simulation of sheep production in intensive grazing systems. Proc. American Society of Animal Science, Lexington, KY. (Abstract)

Spangler, A.M., H.D. Blackburn, and M.M. Kothmann. 1989. Simulating diet selection of sheep grazing on rangeland. Proc. Ecological Modelling Society, Ontario. (Abstract)

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- Briske, D.D. and V.J. Anderson. 1988. Implications of plant and population structure to herbivory tolerance in *Schizachyrium scoparium*. Proc. Society for Range Management, Corpus Christi, TX.
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- Anderson, V.J. and D.D. Briske. 1989. Herbivory-induced species replacement in the southern true prairie: A case of herbivory tolerance or avoidance? Proc. Ecological Society of America, Toronto, Canada.
- Anderson, V.J. and D.D. Briske. 1989. Species replacement in response to herbivory: An evaluation of potential mechanisms. Proc. Society for Range Management, Billings MT.
- Anderson, V.J. and D.D. Briske. 1990. Root and shoot responses of *Schizachyrium scoparium* to defoliation in the presence of competition from lower seral species. Proc. Society for Range Management, Reno NV.

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- Aizpuru-Garcia, Eduardo. 1989. Kleingrass growth and utilization under early-season grazing. PhD Dissertation. Texas A&M University, College Station.
- Anderson, V.J. 1989. Species replacement in response to herbivory: Influence of grazing history, competitive interactions and population structure. Ph.D. Dissertation. Texas A&M University, College Station.
- Cohen, D. 1990. The influence of early season grazing deferment on the production of herbaceous pasture. PhD. Thesis. Hebrew University, Jerusalem.

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- Kothmann, M.M., R.T. Hinnant, and Jose Casco. 1987. Production and utilization of oats for grazing. pp 55-65, *In* McGregor Field Day Report-1987. Tex. Agric. Exp. Sta., Research Center Technical Report No. 87-1.
- Aizpuru-Garcia, E., and M.M. Kothmann. 1987. Growth of Kleingrass under early season grazing. pp. 66-67, *In* McGregor Field Day Report-1987. Tex. Agric. Exp. Sta., Research Center Technical Report No. 87-1.

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