

DEVELOPMENT AND EVALUATION OF A MATHEMATICAL
MODEL TO PREDICT FORAGE INTAKE AND ACCOUNT
FOR SUPPLEMENTATION EFFECTS FOR
GROWING CATTLE

By

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TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.....	1
II. REVIEW OF LITERATURE.....	3
Regulation of Feed Intake.....	3
General Mechanisms.....	3
Physical Regulation.....	4
Rate of Passage.....	5
Salivation Effects on Intake.....	7
Energy Supplementation.Effects on Forage Intake.....	8
Modeling Theory.....	9
Model Development.....	10
Types of Models.....	12
Model Application.....	13
Food Intake Models.....	15
III. DEVELOPMENT OF A MODEL TO PREDICT FORAGE INTAKE OF GROWING CATTLE.....	25
Abstract.....	25
Introduction.....	26
Materials and Methods.....	27
Results and Discussion.....	39
IV. EVALUATION OF A FORAGE INTAKE MODEL FOR GROWING CATTLE.....	53
Abstract.....	53
Introduction.....	54
Materials and Methods.....	55
Results and Discussion.....	57
LITERATURE CITED.....	86
APPENDIX.....	92

LIST OF TABLES

Table	Page
Chapter II	
1. Steps in modeling.....	11
Chapter III	
1. State variables in the model of France et al., 1982.....	29
2. Description of the reference sheep	30
3. Composition of the reference Italian ryegrass forage.....	31
4. Fractions flowing with the particulate and liquid phase.....	32
5. Reference forages for beef cattle (DM basis).....	43
6. Rank of model sensitivity to parameter changes...	45
Chapter IV	
1. Description of nutrient composition (%) 42 forages.....	56
2. Description of data points used for evaluation (DM basis).....	58
3. Rank of model sensitivity to parameter changes for the reference Italian ryegrass forage.....	63

LIST OF FIGURES

Figure	Page
Chapter III	
1. The relationship of observed forage intake and steer body weight for the reference data set.....	46
2. The effect of varying the particulate passage slope coefficient BK1 on error sum of squares, reference BK1= .550.....	47
3. The effect of varying the liquid passage slope coefficient BK11 on error sum of squares, reference BK11= .479.....	48
4. The effect of varying microbial use rate constants for fiber (KBH=.460), starch (KAH=.407) and protein (KPROT=.262) on error sum of squares.....	49
5. The effect of varying KU and LM (microbial growth parameters) on error sum of squares.....	50
6. The effect of varying microbial constants KC, and KCN on error sum of squares, where reference KC=.516 and KCN=0.....	51
7. The effect of varying microbial composition parameters for nitrogen (MN=.38) and carbohydrate (MC=.30) on error sum of squares....	52
Chapter IV	
1. Model predicted versus observed forage intake for the reference data set.....	65

Figure	Page
2. The effect of dietary non-degradable fiber on residual intake (model predicted - observed).....	66
3. Error sum of squares for the 42 reference forages when mean values from the reference data set are input as constant nutrient fractions for all forages.....	67
4. The effect of dietary non-degradable beta-hexose for four forages on model predicted intake.....	68
5. The effect of varying microbial use rate constants for fiber (KBH, reference value=.460), starch (KAH, reference value =.407) and protein (KPROT, reference value=.262) on model predicted forage intake.....	69
6. The effect of varying the slope coefficients for particulate (BK1, reference value=.55) and liquid (BKL1, reference value=.479) passage rates on model predicted intake.....	70
7. The effect of changes in dietary degradable beta-hexose of the reference forage on model predicted intake.....	71
8. The effect of changes in dietary alpha-hexose of the reference forage on model predicted intake.....	72
9. The effect of changes in dietary non-protein nitrogen of the reference forage on model predicted intake.....	73
10. The effect of changes in dietary degradable protein of the reference forage on model predicted intake.....	74
11. The effect of changes in dietary non-degradable protein of the reference forage on model predicted intake.....	75
12. The effect of changes in water soluble carbohydrate of the reference forage on model predicted intake.....	76
13. The effect of changes in microbial growth rate constants (KC, reference value= .516) and (KCN, reference value= 0) on model predicted intake.	77

Figure	Page
14. The effect of changes in specific microbial growth rate (UM, reference value= 5) for the reference forage on model predicted intake.....	78
15. The effect of changes in microbial composition parameters for carbohydrate (MC, reference value=.30) and nitrogen (CP equivalent), (MN, reference value=.38) for the reference forage on model predicted intake.....	79
16. The effect of changes in the proportion of microbial mass flowing with the liquid phase (PBUG, reference value=.50) for the reference forage on model predicted intake.....	80
17. The effect of changes in rumen volume (RV, reference value for 350 kg steer=35l) for the reference forage on model predicted intake.....	81
18. Change in model predicted forage intake (substitution ratio, kg forage/kg corn supplement) for forages of different in vitro organic matter digestibility (IVOMD).....	82
19. Change in model predicted forage intake (substitution ratio, kg forage/kg corn supplement) for forages of different degradable protein content.....	83
20. Change in predicted forage and total intake with increasing amounts of a corn grain supplement for the reference forage and a 350 kg beef steer.....	84
21. Change in model predicted forage intake (substitution ratio, kg forage/kg cottonseed meal supplement) for forages of different in vitro organic matter digestibility (IVOMD).....	85

CHAPTER I

INTRODUCTION

Efficiency and productivity of growing cattle eating predominantly forage based diets is directly related to voluntary intake. Thus, the ability to predict performance of grazing cattle hinges on the prediction of forage intake for a variety of forage conditions. When supplementation is added to a forage diet, changes in forage intake occur due to changes in digestion and passage associated with the additional nutrients. Because of the complexity of the relationship between forages and supplements, and the extensive variation associated with forage types and quality, most regression relationships with intake are only applicable to the forage condition for which they are developed. Mechanistic models of intake, which are based on fundamental biological controls, rely less on a fit of a given set of data and thus, can be applied to a more general variety of conditions.

Because of a lack of knowledge regarding plant-animal interactions in the pasture or range environment, there are relatively few models which can be used to predict intake and account for supplementation effects on forage intake. Although much research has been reported regarding forage

intake and the effects of supplements on intake, there is a lack of conceptual models by which intake-supplement relationships can be integrated and equation form developed. Perhaps the integration of knowledge in this manner would enhance our ability to predict forage intake.

The objectives of this research were to: a) adopt a dynamic rumen model, developed for sheep as the fermentation component of a forage intake model, b) reparameterize the forage intake model for growing cattle and c) evaluate the model with respect to parameter and rate constant changes and supplementation programs.

CHAPTER II

REVIEW OF LITERATURE

Regulation of Feed Intake

General Mechanisms

Generally, ruminants will adjust their voluntary intake of feed to meet their energy requirement if the amount of feed available and the energy content of the feed is not limiting (Baile and Forbes, 1974). This adjustment in feed intake is necessary for long term regulation of energy balance. Several reviews have been written which discuss the proposed mechanisms that control feed intake of ruminants (Balch and Campling, 1962; Baumgardt, 1970; Bines, 1971; Allison, 1985; Baile and McLaughlin, 1987). Proposed theories of control involve chemostatic, lipostatic and thermostatic mechanisms associated with neural and hormonal control, and a physical regulation mechanism integrating ruminal fill, rate of passage and rate of digestion. Although prediction of feed intake requires an understanding of control mechanisms, at present most of this knowledge cannot be utilized in a predictive manner because it has not been assembled into animal systems similar to those used for energy and protein (Jarrige et al., 1986). However, several

models have attempted to integrate the factors which influence forage intake. Therefore, the voluntary feed intake segment of this review will focus on physical regulation or control factors, their subsequent effects on intake and how they have been integrated into various feed intake models.

Physical Regulation

In the range or pasture environment, efficiency and productivity of ruminants is directly related to voluntary intake (Allison, 1985). Unlike other animals, the fibrous nature and relatively low energy density of the ruminant diet dictate that physical factors (i.e. ruminal fill) are important considerations in the regulation of feed intake. Considerable evidence indicates that for roughage diets, voluntary intake is limited by the capacity of the reticulo-rumen and by the rate of clearance from this organ (Campling et al., 1961; Van Soest, 1982; Allison, 1985). The rate of disappearance of digesta from the reticulo-rumen depends on the interaction between rate of digestion and rate of passage, which are inversely related to particle size (Ellis, 1978).

Ruminal fill can be defined as the contents of feed, microbial mass and products of digestion within the rumen. The amount of fill is a function of the volume of the reticulo-rumen and the potential of this volume to expand. There are several studies which indicate that feed intake on

roughage diets is limited by a constant level of distension in the reticulo-rumen. Blaxter et al. (1961) found that sheep given diets of poor, medium and good quality hay would eat to a constant fill (100 g/kg body weight^{.75}) of dry matter in the digestive tract. More recently, Grovum (1987) suggested that distension of the reticulum and cranial sac may be involved in feed intake control rather than the rumen and reticulum as was previously hypothesized.

Passage of undigested residues and absorption of digested nutrients are mechanisms by which ruminal fill is decreased. Van Soest (1982) concluded that rate of passage is considerably more important than digestion rate in accounting for intake differences among animals with similar appetites. Hence, rumination and particle breakdown are the primary action to increase rate of passage and decrease ruminal fill, consequently affecting feed intake.

Rate of Passage

Rate of passage refers to the flow of undigested residues through the digestive tract (Van Soest, 1982). The contents of the rumen can be separated into a fluid and particulate pool. Each of these pools are influenced by different factors. Liquid rate of passage is primarily determined by fluid and salivary inflow. Particulate passage rate is influenced by particle size, shape, and density (Van Soest, 1982). Increased intake is associated with faster rates of passage for a variety of forage diets;

however, the slope of this relationship is not consistent. This may be due to compositional differences among forages which are not consistently measured.

McCollum and Galyean (1985) reported that liquid and particulate passage rates in grazing beef steers decreased with increasing maturity of blue gramma pasture. Their results indicated that as in-vitro organic matter digestibility of the forage decreased from 64.9 to 51.4%, fluid passage rate declined from 14.9 to 11.1 %/h and particulate passage rate decreased from 4.6 to 3.7 %/h.

Varga and Prigge (1982) fed wether lambs alfalfa and orchardgrass at a high and low level (60% of high) of intake. Average liquid turnover rate was two-fold higher (7.6 vs. 3.3 %/h) at the high level of intake on both diets. There was a tendency to have higher solid turnover (6.6 vs. 5.3 %/h) on the high level of intake.

Adams and Kartchner (1984) found that liquid dilution rates linearly increased .6 % unit with each .25 % unit increase in feed intake per unit of body weight. Their relationships were determined by feeding Hereford steers a chopped alfalfa hay diet.

The data in the literature indicate that liquid and solid fractions flow at distinctly different rates of passage. Although particulate passage rate is much slower than liquid dilution rate, the rate at which the liquid passes from the tract may influence the particulate flow rate.

Salivation Effects on Intake

Saliva serves as an aid in mastication and swallowing in ruminants. In addition, it contains salts, minerals and nitrogen which aid in the fermentation process. Estimates of daily saliva production are varied and range from 30 to 300 liters per day (Pond et al., 1987). Salivary output is greater when animals are eating than when they are not. The type of diet and moisture content of the feed have the greatest effect on salivary production. Balch (1958) observed the highest saliva output for cattle eating hay, intermediate were fresh grass diets and concentrate diets resulted in the lowest salivary output.

Putnam et al. (1966) fed a pelleted 89% roughage ration to 350 kg steers at .8, 1.4, 2.0 and 2.6% of body weight. Salivary production per day was estimated to be 33.5, 45.2, 52.0 and 54.1 liters per day (l/d), respectively. Yarns et al. (1965) estimated flows of 56.6 and 41.8 l/d for 688 kg steers eating a bermudagrass-corn ration and a pelleted alfalfa diet. Bailey (1961) reported much higher estimates ranging from 124 to 226 l/d for cattle eating various diets. Bartley (1976) reported that the 24 hour salivary production of a 700 kg cow consuming hay and grain would equal 190 kg. The nitrogen content would range from 30 to 80 grams.

Energy Supplementation Effects on
Forage Intake

Supplementation programs for grazing cattle are utilized as a management tool to enhance performance of livestock when either forage quality or quantity is limiting. Under most grazed forage circumstances, when grain based (energy) supplements are added to the forage diet, declines in forage intake are observed (Hennessey and Williamson, 1983). Hence, energy supplements can be used to extend the existing forage or simply increase total energy intake and performance of grazing cattle.

Horn and McCollum (1987), in a review on energy supplementation for grazing ruminants, calculated substitution ratios (change in forage intake per unit increase in concentrate intake) for various types of forages. Negative substitution ratios were observed when forage digestibility was above 40% for sheep and 55% for cattle. As higher quality forages were fed, greater substitution of concentrates for the forage occurred. Their summary indicates that sheep exhibit a greater substitution effect than do cattle, that is, the negative slope of the regression of forage intake on concentrate intake is steeper for sheep than for cattle.

Lusby and Wagner (1987) suggested that although energy supplements reduce forage intake, consideration of the protein content of the forage and supplement and the protein

to digestible energy ratio may be important in interpreting the magnitude of substitution ratios.

There are many theories which have been proposed to explain the effect of readily fermentable energy supplements on forage intake. These include ruminal pH, competition between cellulolytic and noncellulolytic bacteria for nutrients, use of alternative energy sources and metabolic influences (Horn and McCollum, 1987).

Modeling Theory

"There is increasing support for the view that further significant progress is unlikely to result from traditional empirical investigations at the whole-animal level alone, and what is now needed is research which identifies and defines the key processes of digestion and metabolism, and then integrates this knowledge in a conceptual framework which may, in the fullness of time, provide both predictive tools and a sound understanding of whole animal performance" (Thornley and France, 1984). The conceptual framework described is referred to as a mathematical model. More recently, Demment and co-workers (1987) suggested that developing a conceptual framework or model serves several functions in a research program. First, it organizes an approach to a complex problem. Second, it identifies characteristics between the phenomenon being explained and once important relationships have been identified they can be tested against real data. If functions are inadequate to

describe behavior, then future efforts can be directed at elucidating the determinants of the function.

Forrester (1971) suggested that the development of models combines the power of the mind with that of computers. That is: the human mind formulates the concepts and the computer is used to analyze and predict the output or behavior.

A mathematical model can be described as a set of equations that are developed to represent the behavior of a specific system. In this context, a system can represent the functions of the entire beef production system in the United States (Miller et al., 1980) or of the digestive system for a single ruminant (Baldwin et al., 1977). Although each of the previous examples are distinctly different in regard to their application, a characteristic of both is that the interrelationships between the components of the modeled system preclude studying each component separately.

Model Development

Approaches to modeling have been proposed by many workers (Baldwin, 1976; Innis, 1975; France and Thornley, 1984). Perhaps the most important criteria is that procedures should be systematic in model development. Baldwin (1976) proposed steps in modeling animal systems (Table 1).

Table 1. Steps in modeling.^A

-
1. Define problem -- set modeling objective.
 2. Prepare block diagram representing central elements of system and interactions among them.
 3. Convert concepts represented in block diagram to mathematical statements.
 4. Formulate required numerical inputs based on literature data, experimental data or statistical estimation.
 5. Evaluate solutions and/or validate model. Return to steps 2,3 or 4 if evaluation indicates inadequacies.
-

^AFrom Baldwin (1976).

Often when developing a new model much effort is expended in data collection and analysis to determine numerical relationships which can be integrated into equations.

Types of Models

Model form can be classified as either dynamic or static, deterministic or stochastic, and empirical or mechanistic (Thornley and France, 1984). Typically, static models are not time dependent and can be as simple as a linear regression equation. Whereas, a dynamic model is time dependent and usually contains differential equations which describe changes that occur within a system over time. For example:

$$\frac{dw}{dt} = g$$

where w is weight, t represents time and g is some function describing weight gain that is related to weight or other variables.

A deterministic model gives one particular output for a given set of inputs. Empirical, deterministic models are often used to predict relationships between two variables that are at the same level of aggregation. For example, at the whole animal level (i), the relationship between weight and energy intake could be considered as empirical and deterministic (Oltjen, 1987). In contrast, a stochastic

model contains random variables which allow prediction of the expected value of a specific output and its associated variation. This type of approach has been employed in many range models for those factors which are highly variable such as rainfall.

Mechanistic models are of interest in many research situations because they provide both description and understanding (France and Thornley, 1984). These models attempt to explain causal relationships or behavior at different levels of aggregation. For example, a model predicting feed intake at the animal level (i) using fermentation in the rumen at the organ level (i-1) or oxidation of the tissues at the cell level (i-2) is an example of a mechanistic model (Thornley and France, 1984). Thus they are generally more complex than empirical models.

Model Application

Model application should reflect the objectives for which the model is developed. There are differences between research models and models which are used for management or extension purposes (Thornley and France, 1984). Management models are often more empirical in nature due to the necessity of faster, more accurate predictions. However, with many empirically constructed management models, their use is limited to the boundaries of the data with which they were developed (Baldwin, 1976).

Most research models are mechanistic, therefore they are often used as an aid in understanding the system being studied (Oltjen, 1987; Demment et al., 1987). With a research model, a conceptual framework is developed based on the current knowledge of the process of interest. This is accomplished by developing equations which represent the underlying biology of the system. France and Thornley (1984) suggest that when mechanistic models are wrong they may actually help increase our understanding of the system by identifying some misrepresentation of the underlying biology. In contrast, when an empirical relationship fails, it simply suggests that the equation form is inappropriate for the process of interest. Consequently, the mechanistic approach should be more useful than the empirical method for assisting in discovery of knowledge of a system.

Management or applied models which are used for prediction are typically used in practical situations. A prerequisite for their use is that they must be better than procedures which are currently being used (Thornley and France, 1984).

There are many uses of mechanistic models in agriculture; however, because these models are often complex in nature, their use in practical situations is limited because of the expense incurred in model simulation. Some suggestions concerning the potential use of mechanistic models have been proposed by Thornley and France (1984):

1. Hypothesis expressed in mathematics can provide a greater understanding of biological problems.
2. The requirement of mathematical equations to describe the system may help provide the framework to pinpoint areas where knowledge is needed and might stimulate new ideas and experimental approaches.
3. In a system with several linked components, modeling provides a way to bring components together in a framework that will give better understanding of the behavior of the whole system.
4. The predictive power of a mechanistic model can be used in research, planning and management to answer questions like 'what if....?'.
5. Modeling can help provide strategic and tactical support to a research program by motivating scientists and encouraging collaboration.

Food Intake Models

Several models have been developed to predict feed intake of ruminants. These models span the scale from simple empirical relationships relating feed quality and intake to more complex models which predict intake of a dairy cow over an entire lactation integrating both physical and metabolic controls (Forbes, 1977a; Monteiirro, 1972). The major differences observed concerning the complexity of equations and level of aggregation in models is directly related to the objective or scope for which the model was developed (Oltjen, 1983). In more complex models, differential equations that describe a dynamic function, process or biological response are often integrated to develop causal relationships which describe the underlying biology of the animal system.

Some models simulate the production processes of an entire system; for example, range models often account for weather effects, herbage growth, feed intake, body weight gain and economic consequences of different management strategies. Many of these considerations are beyond the scope of this review, thus, emphasis will be placed on the intake component of these models.

In order to predict intake of forage for grazing ruminants, it is imperative that relationships between forage quality and animal intake be characterized. Equations identifying the relationship between intake and digestibility have been developed (Conrad, 1966). The proposed equations postulate that in a low digestibility range (52.1-66.7%) intake is regulated by physical factors such as rate of passage, and therefore, is positively related to digestibility. However, with feeds of high digestibility (66.7-80.0%) intake is regulated by energy requirements; thus, intake and digestibility are negatively related. Modifications of these equations are the basis by which the intake segments of several models have been developed (Brorsen et al., 1983; Kahn and Spedding, 1984). While many models use these equations as a foundation for the prediction of intake, there are numerous other models which account for various factors that have a role in intake regulation. The following is a description of some forage intake models.

A general simulation model of ruminants grazing range situations was developed by Rice et al. (1974). This model has the advantage of being more general in nature than the previous models that have been discussed. The model is mechanistic in its approach, however, empirical equations are used to estimate some parameters such as rumen fill. A model of digestion is used to predict nutrient absorption, passage and subsequent rumen fill and forage intake. To compute forage intake, the workers utilized forage availability and plant height factors with the maximum capacity of the ruminants digestive tract as a limit to intake. Maximum intake (computed each day) is determined by subtracting remaining rumen dry matter from the previous day from the current maximum rumen capacity. Rumen capacity is calculated as a function of body weight. Forage intake each day is partitioned into an indigestible and digestible fraction and digestion is simulated based on the microbial mass and the amount of organic matter fermented in the rumen. This has a direct effect on the amount of food that an animal can consume during the next day via passage, digestion and rumen fill. The microbial growth equations are a driving force in the calculation of forage intake. Microbial growth is a function of the amount of organic matter digested in the rumen and the nitrogen availability. The model accounts for nitrogen transactions based on the concentration of nitrogen in the rumen. Recycling of nitrogen is allowed because the model is sensitive to low

nitrogen diets. In a model of this type, the effects of supplementation can easily be quantified if the supplement composition is known. This is due to the mechanistic nature of the model.

Arnold et al. (1977) described a model of food intake, liveweight change and wool production in grazing sheep. In the model intake is initially determined as a function of fleece-free liveweight. A mature size modification is included in the equation to decrease intake values as sheep approach their maximum liveweight. A unique feature of the model is that the prediction of intake is based on the available green and dry matter content of the pastures. Intake of dry and green material is predicted separately. Equations relating percent green in the pasture to the percent green in the diet are utilized, however, different curves are derived for varying pasture availabilities. Relative intake proportions are also related to dry matter that is available in a pasture. Separate curves for grasses and clovers are used. From these equations, a different group of curves for different grass/clover combinations can be deduced. An adjustment of organic matter intake is made based on the digestibility of the green and dry portions of the diet. Validation of the model indicates that the model is very sensitive to the digestibility value of the diet.

A model of forage intake has been developed which represents both physical and metabolic controls of intake (Forbes, 1977b). The iterative model estimates the weight

of food necessary to supply the animal energy requirement and compares this to a gut capacity constraint. Inputs for the model are target tissue deposition rates, feed dry matter digestibility and metabolizable energy concentrations. The energy needs of the animal are met by partitioning of the food between maintenance needs and protein and fat deposition. Any change in animal fat levels are calculated and added to abdominal fat to cause decreases in the weight of gut contents. The gut capacity constraint is based on relationships between hay intake and rumen volume measurements. Metabolizable energy intake is calculated as the weight of the food necessary to meet maintenance energy requirements plus a target rate of tissue deposition. In the model the two intake values are compared and the lower of the values is used for an actual intake value. The model iterates daily and simulation can be made for fattening or pregnant and lactating mature sheep.

Sibbald et al. (1979) described a conceptual approach to the modeling of forage intake of sheep. Potential intake in the model is first assumed to be related to the digestibility of the forage in a linear manner. The model is driven by empirical equations relating numerous constraints to potential forage intake. Intake of mature sheep has been shown to decrease when they reach a certain level of body fat; therefore, intake in the model is constrained by a relationship between body condition and percent of potential intake. Intake is also restricted by

forage availability by assuming a smaller bite size during a limited grazing day. The most unique feature of the model is a forage selection procedure whereby composite bites are allocated to different ranges of forage digestibility classes available in the pasture. This allows the model to allocate more bites via selection indexes to the higher digestibility classes within a pasture. Grazing pressure is used to determine selection indexes. As grazing pressure increases, the selection index decreases toward zero indicating less selective grazing. If forages are above 60% digestibility, complete removal of forage can occur; however, if forages are below 50% digestibility removal cannot exceed 40% removal. The relationship between rate of removal and digestibility is linear between 50 and 60% digestibility. This is referred to as the vertical distribution. Also, a horizontal distribution of digestibility classes is developed relating the ratio of quantity of dry herbage matter to total dry matter available in a class. This selection approach attempts to simulate sheep that are grazing layer by layer. The procedure used in the model is iterative and the initial forage digestibility value is adjusted according to selection pressure. The model outputs total herbage mass, its mean digestibility, ingested herbage mean digestibility and mean body weight of wethers on a weekly basis and runs for a complete calendar year.

France et al. (1981) developed a model of wether sheep grazing perennial ryegrass. The forage intake portion of the model accounts for selective grazing patterns by grouping the forage into subswards and within each subsward are three quality classes based on digestibility. The sheep then select the subswards which have the highest proportion of high digestibility forage. A pasture density constraint is included in the model limiting intake below a critical level. However, if the critical density level is not reached then the sheep will select the subsward where density is the highest. Therefore, intake is calculated based on a linear relationship with ingested herbage digestibility. This can be reduced according to the herbage mass constraint and a body condition relationship similar to those described in the model by Sibbald et al. (1979).

Black (1984) developed a mechanistic model whereby feed intake is limited by the capacity of the animal to utilize nutrients, by the rate of removal of materials from the rumen or by the time available for the consumption of adequate amount of forage. An upper limit to intake is calculated in the model based on the amount of feed needed to fully satisfy the potential needs of all body processes. A unique feature of the model is that the calculated amount of amino acid nitrogen needed for body functions is compared to that available; if insufficient amino acids are available, protein deposition into tissues and other products is reduced. Fat deposition is also reduced when

protein deposition falls below 85 percent of its potential. Limits due to rumen fill or physical factors are determined by a curvilinear relationship with empty bodyweight. If sheep have an empty bodyweight greater than 50 kg, then maximum organic matter accumulation in the rumen is assumed to be related to a deficit of energy. Rumen fill decreases linearly from 500 to 110 grams as the metabolizable energy falls from 100 to 30 percent of the total requirement. The model does not account for different packing densities of various forages due to a lack of available information in the literature. An additional constraint in the model is grazing and rumination time. This is used to simulate situations when severe pasture shortages limit animal consumption. The model has been developed for sheep and considers the effects of dietary, animal and environmental effects simultaneously over time.

A highly detailed model of food intake in the lactating cow was developed (Bywater, 1984) utilizing some of the principles described in previous work with dairy cows (Monteiro, 1972). The model is similar to the model described by Forbes (1977b) as it assumes intake is regulated by both physical and metabolic controls. Physical regulation is controlled by a rumen fill factor which is a function of body size and the cell wall content of the diet. Digestion and passage relationships are quantified using a model of rumen function. The metabolic portion of the model accommodates declines in feed intake as the metabolizable

energy concentration in the diet is increased above set levels. The model is driven by the fate of the cell wall constituents and therefore is sensitive to these values.

Spreen et al. (1985) developed a microcomputer program for stocker cattle enterprises. The two components are a growth simulation model and a cost accounting model. As part of the growth model, daily forage intake of the animal is determined. Total daily nutrient consumption is predicted as a function of both body weight and forage quality. The body weight component accounts for maintenance intake, and total forage intake is represented as a multiple of the maintenance requirement, which is a function of forage quality. To quantify the effects of supplementation on a forage diet, a linear substitution equation is included in the model. Complete substitution occurs on high quality diets; very little substitution occurs on low quality forages. The forage quality indexes range from .8 (no substitution) to 2.2 (complete substitution). An additional parameter that affects intake is a user specified stocking rate. Stocking rate specifications may reduce intake below the theoretical intakes derived as a function of body weight and forage quality. The model is developed based on empirical relationships and predicts intake and weight changes on a daily basis given a specific forage and supplemental feeding level. A recursive procedure updates animal body weight each day.

Olson et al. (1986) developed a model to predict ingestive behavior of cattle grazing crested wheatgrass. In the model forage intake is a function of ingestion rate and grazing time. Ingestion rate is assumed to be related to available forage biomass by a Michaelis-Menton relationship (Alden and Whittaker, 1970). Above a forage biomass of 550 kg/ha, intake is limited in the model by the crude protein content of the forage. This represents both a quality and quantity constraint. Increases in grazing time are accounted for in the model when forage biomass levels fall below 275 kg/ha.

This review is an attempt to outline some of the important concepts which are currently being used in models to predict feed intake. There are many models which were not mentioned (Guerrero et al., 1984; Smith and Williams, 1973; Freer and Christian, 1983). However, many of the concepts in other models are similar to those that have been discussed.

CHAPTER III

DEVELOPMENT OF A MODEL TO PREDICT FORAGE INTAKE OF GROWING CATTLE

Abstract

A mathematical model to predict daily forage intake and account for energy supplementation effects on forage intake has been developed in several stages. A previously evaluated dynamic rumen model for sheep (France et al., 1982) was adopted as the fermentation component of the intake model. Intake is adjusted to reach a given level of fill, which is the sum of the concentrations of each of the dietary fractions within the rumen. Differential equations describe the rate of change of each nutrient fraction. Genetic size scaling rules based on mature body size relationships were utilized to adjust rate and fill parameters of the intake model from sheep to beef cattle. Nutrient fractions were partitioned into those that flow at the particulate passage rate and at the liquid passage rate. Forty-two data points representing perennial ryegrass, wheat pasture and range grasses were used to parameterize and evaluate the model. The model is relatively sensitive to the coefficient relating dry matter intake to particulate rate of passage, the rate constant for the use of the

degradable fiber fraction of the forage and to the composition constants for the amount of carbohydrate and nitrogen in the microbial mass. Relative insensitivity was observed for starch and protein nutrient use rate constants, the coefficient relating dry matter intake to liquid passage rate and constants relating to the growth of the microbial mass in the rumen.

Introduction

Considerable evidence exists which suggests that feed intake of cattle grazing or cattle fed forage-based diets is limited by the capacity of the reticulo-rumen and the rate of clearance from this organ (Conrad, 1966; Ellis, 1978). This implies that rate of digestion, passage and ruminal fill are important factors regulating feed intake for grazing cattle. When supplements are added to a forage-based diet, changes in forage intake occur due to changes in digestion and passage associated with the additional nutrients. Because of the complexity of the interaction between the supplement and forage, simple regression relationships are inadequate to predict forage intake except for that observed in similar situations from which the regression relationship was developed.

Previously, a dynamic rumen model (France et al., 1982) was evaluated to determine its potential use in predicting intake of grazing ruminants and accounting for supplementation effects on forage intake (Hyer and Oltjen,

1987). The model responded appropriately with regard to energy supplementation. Therefore, the structure of the rumen model has been adopted as the fermentation component of a forage intake model. Genetic size scaling rules (Taylor, 1980) were utilized to adjust rate and fill parameters of the intake model from sheep to beef cattle. Nutrient fractions were partitioned into those that flow at the particulate passage rate and at the liquid passage rate. A reference data set containing forty-two data points representing perennial ryegrass, wheat pasture and range grasses was used to parameterize and evaluate the model. The work presented here is based on the hypothesis that rumen fill governs intake for cattle consuming forage based diets. This mechanistic approach to control of forage intake should be adaptable to various types of supplements and different forage types (Thornley and France, 1984). Differential equations, rate constants for nutrient use, microbial composition and growth constants and coefficients relating dry matter intake to liquid and particulate passage rates are described.

Materials and Methods

Mathematical equations from a dynamic model of rumen function (France et al., 1982) were utilized as the fermentation component for a feed intake model. The rumen model is of intermediate complexity, containing nine state variables. Each state variable (pool) in the model

represents either a nutrient fraction, the microbial mass in the animal or the effective volume of the rumen (Table 1). Differential equations are used to describe the rate of change of each state variable over time. Particulate (PPR, %/hour) and liquid passage rate (LPR, %/hour) estimates were added to model equations to adjust for different rates of passage of forage components.

Initially, the rumen model simulated a reference wether sheep (Table 2) eating a reference Italian ryegrass forage diet (Table 3) at 2.0% of body weight. Genetic size scaling rules (Taylor, 1980) based on mature body size relationships were utilized to adjust the rate and state variables of this intake model to beef cattle. At similar degrees of maturity (proportion of mature body weight), rates of functions in different animals are proportional to their mature weight to the .73 power. Therefore, it was assumed that the mature wether (75 kg) and medium framed mature steer (750 kg) represent mature animal size differences between sheep and cattle, and various functions can be related by an animal size factor (ASF) of 10 (750/75) to the .73 power.

To simulate the processes of digestion and passage as they occur within the rumen, nutrient fractions are partitioned into those that flow from the rumen according to the PPR and the LPR (Table 4). Those components that are assumed to be rapidly solubilized flow with the faster LPR

Table 1. State variables in model of France et al., 1982.

Symbol	Description
AH	alpha-hexose pool (starch)
BH	degradable beta-hexose pool (digestible cellulose)
BUG	pool of microbial matter (microbial mass)
NBH	non-degradable rumen beta- hexose (indigestible cellulose)
NPN	non-protein nitrogen pool (crude protein equivalent)
NPROT	rumen non-degradable protein pool (bypass protein)
PROT	rumen degradable protein pool (degraded protein)
RV	rumen metabolic volume
WSC	water soluble carbohydrate pool (soluble carbohydrate)

Table 2. Description of the reference sheep.

Dry matter intake, g	1000.0
Body weight, kg	50.0
Mature body weight, kg	75.0
Rumen volume, l	5.00
Mature rumen volume, l	7.50
Rumen fill, g DM/l	56.97
LPR ¹ , %/hr.	10.0
PPR, %/hr.	4.0
PBUG, %	50.0
Salivary flow, l/d	8.91
Dietary water intake, l/d	3.09
AH pool, g DM/l	.56
BH pool, g DM/l	9.33
BUG pool, g DM/l	20.90
NBH pool, g DM/l	14.02
NPN pool, g DM/l	4.12
NPROT pool, g DM/l	5.06
PROT pool, g DM/l	2.54
WSC pool, g DM/l	.42

¹For description of symbols see text.

Table 3. Composition of the reference Italian ryegrass forage.¹

Component	Composition, % DM
Alpha-hexose	2.66
Degradable beta-hexose	49.37
Non-degradable beta-hexose	6.73
Water soluble carbohydrates	21.50
Degradable protein	7.29
Non-degradable protein	2.43
Non-protein nitrogen	4.22

¹From France et al., 1982.

Table 4. Fractions flowing with the particulate and liquid phase.

Liquid	Particulate
NPN ¹	NBH
WSC	BH
BUG ²	BUG ²
	PROT
	NPROT

¹For explanation of symbols see Table I.

²50% of the microbial mass flows with each phase.

and the fibrous fractions of the feed pass out with the PPR. It was assumed that 50 percent (PBUG) of the microbial population flows with the liquid, and 50% with the particulate phase.

It was assumed that forage intake is limited by a level of fill in the rumen. Rumen fill (RF) is the sum of the nutrient pools within the rumen. For the reference sheep (Table 2) RF was 56.97 grams of dry matter (DM) per liter of rumen volume. Once RF is determined, an iterative procedure is used to adjust dry matter intake so that a given level of RF is reached at steady state conditions. Three days are required for the dynamic model to achieve steady state using Euler's method of numerical integration, at an interval (DT) of .002 d.

A differential equation is used to describe the change of each nutrient pool. Rumen volume (RV, l) is the metabolic volume of the rumen and is defined as the effective volume where various reactions occur within the rumen (France et al., 1982):

$$RV = 75 * (BW/MBW)$$

here BW is empty body weight (kg) and MBW is mature BW (kg). Hence, RV for a mature medium frame steer (MBW= 750 kg, Oltjen, 1985) is 75 l. The ratio of BW to MBW adjusts rumen volume by mature body size. Thus, mature RV increases by a factor of 10 across species, sheep to cattle, and increases in proportion to BW within a specie.

Initial passage rate constants for sheep were determined to be 4 and 10 %/hour for PPR and LPR (M.L. Galyean, personal communication). Passage was related to dry matter intake (DMI, g/d) by a linear relationship:

$$\text{PPR (\%/h)} = .04 * (\text{BK0} + \text{BK1} * (\text{DMI}/\text{DMI}_{\text{ref}}))$$

$$\text{LPR (\%/h)} = .10 * (\text{BKLO} + \text{BKL1} * (\text{DMI}/\text{DMI}_{\text{ref}}))$$

and DMI_{ref} , (g/d) = $(\text{BW}/\text{MBW} * 8055)$. The reference DMI was determined assuming that a mature sheep would consume 1500 grams intake. This intake was then adjusted across species by the animal size factor of 10 to the .73 power. The intercepts (BK0, BKLO) were calculated as one minus the slope so that initial rate constants were estimated at DMI_{ref} .

Over time, steady state conditions occur within the rumen:

$$dRV/dt = DV + SV - V$$

where DV and SV are rates of fluid inflow from dietary and salivary sources, respectively and V is the rate of outflow of fluid from the rumen. Steady state conditions occur when the differential equation for RV equals zero.

Total liquid flow for the reference sheep (V) is 12 l/d.

$$\text{Liquid flow (V)} = \text{LPR} * 24 * \text{RV}$$

Salivary and dietary sources are fixed:

$$SV = V * .74233$$

$$= 8.91 \text{ l/d}$$

$$DV = V - SV$$

$$= 3.09 \text{ l/d}$$

For cattle, the corresponding reference values are 47.84 (SV) and 16.61 (DV). Thus, liquid flow can be calculated for any situation and DV and SV estimated.

The non-degradable components of the diet in the rumen (NBH and NPROT, g/l) are undigested and must flow undegraded from the rumen:

$$dNBH/dt = (DNBH - NBH * PPR * 24 * RV) / RV$$

$$dNPROT/dt = (DNPROT - NPROT * PPR * 24 * RV) / RV$$

DNBH and DNPROT represent the dietary proportion (g/d) of NBH and NPROT. The rate at which NBH and NPROT pass from the rumen is a function of the nutrient pool (NPROT, NBH, g/l) and PPR.

The remainder of the nutrient pools and the microbial population within the rumen change according to the following:

$$\text{Substrate pool change} = \text{inflow} - \text{outflow} + \text{synthesis} - \text{utilization}$$

where synthesis occurs due to the degradation of forage components by enzymes and utilization is the rate at which

the microbial populations utilize nutrients (France et al., 1982). Therefore, the dynamic properties of AH, DBH and DPROT (g/l) are:

$$dAH/dt = (DAH-AH*PPR*24*RV)/RV-KAH*AH*BUG$$

$$dBH/dt = (DBH-BH*PPR*24*RV)/RV-KBH*BH*BUG$$

$$dPROT/dt=(DPROT+SPROT-PROT*PPR*24*RV)/RV-KPROT*PROT*BUG$$

again DAH, DBH, and DPROT are dietary inputs (g/d) of AH, BH and PROT, respectively, and SPROT is the contribution of salivary protein. SPROT is assumed to be .5 kg per liter of saliva (France et al., 1982). The utilization rate of each nutrient is dependent on the quantity of available substrate in the nutrient pool (AH, BH and PROT), the concentration of the microbial population (BUG, g/l) and the rate constants for nutrient use (KAH, KBH, KPROT). Rate constants estimated for sheep using previously described values and passage rate constants given above were .407, .460 and .262 for KAH, KBH and KPROT, respectively. Each rate constant was multiplied by 10 to the $-.27$ power to account for differential rates between a mature wether and a mature steer.

Inputs of NPN on a crude protein equivalent basis into the animal are from the diet (DNPN), the saliva (SNPN), the degradation of degradable protein by the microbial population (DGNPN) and the non-protein nitrogen released by microbial catabolism (MCNPN). Disappearance of NPN is by

outflow from the rumen at the LPR and usage by the microbial population for maintenance and growth (MGNPN):

$$dNPN/dt = (DNPN+SNPN-NPN*LPR*24)/RV+MCNPN-MGNPN+DGNPN$$

$$DGNPN= BUG * KPROT * PROT$$

$$MCNPN= BUG * MN * L$$

$$MGNPN= BUG * MN * U$$

The amount of SNPN is a function of total salivary flow. It was assumed that 1 kg SNPN is obtained per liter of saliva (France et al., 1982). L and U are microbial constants described below. MN represents the protein equivalent in the microbial mass and was determined by solving the NPN equation using the reference sheep described previously (Table II). Mn is fixed in the model as .38, based on the reference sheep diet. Literature estimates range from .35 to .63 (France et al., 1982).

Inflow to the soluble carbohydrate pool (WSC, g/l) can come from four sources: dietary (DWSC), degradation of AH (DGAH) and BH (DGBH) and soluble carbohydrate released by microbial catabolic activity (MCWSC). Outflow is by flow from the rumen (WSC*LPR*24) and microbial growth (MGWSC):

$$dWSC/dt = (DWSC-WSC*LPR*24)/RV+MCWSC-MGWSC+DGAH+DGBH$$

$$DGAH= BUG * KAH * AH$$

$$DGBH= BUG * KBH * BH$$

$$MCWSC = BUG * MC * L$$

$$MGWSC = BUG * MC * U / YM$$

MC again is the amount of carbohydrate in BUG and is set at .3. Literature estimates range from .1 to .43 (France et al., 1982). YM represents BUG use of soluble carbohydrate and is fixed as .1 (France et al., 1982).

Microbial growth (GBUG) is represented:

$$GBUG = U * RV * BUG$$

where:

$$U = U_m * ASF^{-27} * (1 / (1 + K_c / WSC) + K_n / NPN + K_{cn} / (WSC + NPN))$$

is the specific growth rate of the microbial population dependent on the availability of NPN and WSC. U_m (5 d^{-1}) is the maximum value of U as WSC and NPN go to infinity and K_c , K_n and K_{cn} are constants (France et al., 1982).

Microbial catabolism (DBUG) occurs:

$$DBUG = L * RV * BUG$$

$$\text{where: } L = L_m * ASF^{-27} * (1 / (1 + K_u * ASF^{-27} * U))$$

lambda (L) is the specific rate of catabolism per day and is a function of U and a constant (K_u), where L_m is the maximum rate of L obtained when $U=0$. L_m is related to K_u for the reference sheep:

$$\text{where: } L_m = .55 + 1.23 * K_u$$

Hence, the rate of change of the BUG:

$$d\text{BUG}/dt = (U*\text{BUG} + L*\text{BUG} - \text{PBUG}*\text{BUG}*LPR*24) / \text{RV} - (1 - \text{PBUG}) * \text{PPR} * 24 * \text{BUG}$$

where PBUG is equivalent to the portion of the BUG that passes from the rumen at the liquid rate of passage.

Rumen fill (RF) is determined by taking the sum of each of the nutrient and microbial pools within the rumen on a concentration basis:

$$\text{RF} = \text{AH} + \text{BH} + \text{BUG} + \text{NBH} + \text{NPN} + \text{NPROT} + \text{PROT} + \text{WSC}$$

RF was estimated using flow rates from the reference forage diet (Hyer and Oltjen, 1987); it is set at 56.97 g/l for the reference sheep.

Results and Discussion

To test the feed intake model for beef cattle, a reference data set was developed (Table 5). The reference data were developed from the literature and represent range grasses, wheat pasture and perennial ryegrass forages of moderate to high quality. Nutrient inputs were calculated from commonly measured forage fractions (Table 5). Primary characteristics necessary for inclusion of each data point were body weight and ad libitum forage intake measurements for grazing steers and complete partition of forage components. Estimation of each nutrient fraction is described in Table 5. Forty-two data points representing a wide range of body weights were used in the reference data

set. Twenty-four native range grasses, 12 perennial ryegrass and 4 wheat pasture forages characterize the data set. Figure 1 depicts the relationship between FI and BW for each data point.

To estimate the slope coefficients (BK1, BKL1) for the reference data set and determine an optimum level of RF for beef cattle, a nonlinear, derivative free, least squares fitting procedure (Nelder and Mead, 1965) was utilized. Attempts were made to estimate BK1, BKL1, RF and KU (constant used in microbial catabolism equation) by minimizing the sum of squared deviations (SS) from the observed DMI for each of the 42 data points. Various combinations of the parameters resulted in minimizing error SS. Thus, to achieve model identification it was necessary to fix BK1. Literature estimates vary from .6 (Krysl et al., 1987); (McCollum and Galyean, 1985) to .85 (Coleman et al., 1978) and higher 2.41, (Kennedy, 1982) for a limited number of data points. Therefore, BK1 was fixed in the model at .55, hence BKL1, KU and RF were estimated to be .479, .467 and 96.23 g/l, respectively. In a review on the relationship between passage rate and intake, Owens and Goetsch (1987) reported a value of BKL1 around .5.

Sensitivity of the model to the estimated slope coefficients was determined by varying the parameters, holding all others fixed and determining the change in error SS. BK1 was sensitive over the entire range tested (Figure 2). However, lower sensitivity to BK1 is observed between

parameter values of .45 to .60. Error SS for the model as parameterized is 227, where BK1 was equal to the reference value of .55. A fit of BKL1 (Figure 3) resulted in lower sensitivity to parameter changes below the reference value of .479. However, as BKL1 increased above the reference level, error SS decreased slightly.

Sensitivity of fitted SS to changes in each of the nutrient use parameters KAH, KBH and KPROT was accomplished. Very little change in SS was observed over the entire range tested for KAH and KPROT (Figure 4). Changes of similar magnitude for the degradable fiber rate constant, KBH, resulted in much larger changes in SS particularly below the reference value of .46 (Figure 4). This indicates that the model is sensitive to the fiber fraction of the forage and any parameters associated with this component.

The model was evaluated with regard to changes in microbial growth, catabolism and composition parameters. The model is insensitive to K_u where L_m is calculated as a function of K_u (Figure 5). The equation that describes growth of the microbial mass in the rumen was solved to attempt to identify constants K_c , K_{cn} and K_n . K_n and K_{cn} were unidentifiable in the model and set at zero. Figure 6 illustrates low sensitivity of the model to K_c and K_{cn} over a wide range of parameter values. Figure 7 indicates model sensitivity to changes in MN and MC over the range of possible literature values. The model is sensitive to the microbial composition parameters.

To quantitatively compare the sensitivity of each model parameter, the change in error sum of squares was calculated for a constant proportional change in each parameter (Table 6). The model is sensitive to the coefficient relating dry matter intake to particulate rate of passage. High sensitivity was observed for the rate constant for the use of the degradable fiber fraction of the forage and to the composition constant for the amount of carbohydrate in the microbial mass. Moderate sensitivity was observed for the amount of nitrogen in the microbial mass. Relative insensitivity was observed for starch and protein nutrient use rate constants, the coefficient relating dry matter intake to liquid passage rate and constants relating to the growth of the microbial mass in the rumen.

A mathematical model to predict daily forage intake and account for energy supplementation effects on forage intake has been described (see Appendix).

Table 5. Reference forages for beef cattle (DM basis).

	BW ¹ (kg)	FI (kg)	DNBH ²	DBH ³	DNPN ⁴	DNPROT ⁵	DPROT ⁶	DWSC ⁷	DAH ⁷	REFERENCE ⁸	FORAGE TYPE
1	221.0	3.205	18.46	55.37	1.26	1.42	3.70	5.02	5.02	A	blue grama
2	270.0	7.120	16.48	49.46	2.50	2.22	12.06	6.43	2.14	B	blue grama
3	293.0	6.471	16.66	49.99	2.22	2.33	11.43	6.32	2.10	B	blue grama
4	307.0	5.870	15.22	45.66	1.65	2.73	7.11	13.65	4.55	B	blue grama
5	342.0	7.854	13.81	41.43	1.37	3.81	5.46	18.34	6.11	B	blue grama
6	308.0	5.144	17.72	53.15	1.67	3.02	5.89	4.57	4.57	A	blue grama
7	385.0	9.984	17.34	52.10	1.42	2.28	12.80	3.34	1.11	C	blue grama
8	413.0	11.618	17.94	53.80	1.42	1.70	8.81	5.03	1.67	C	blue grama
9	411.0	8.671	16.67	50.03	1.71	2.28	5.69	7.12	7.12	C	blue grama
10	425.0	8.920	17.20	51.60	0.86	2.28	3.13	7.42	7.42	C	blue grama
11	505.0	13.596	18.38	55.15	1.14	2.28	9.67	2.64	0.88	C	blue grama
12	541.0	12.722	16.68	50.03	1.14	2.28	8.54	8.61	2.87	C	blue grama
13	620.0	13.353	15.77	47.32	0.86	1.70	4.83	9.70	9.70	C	blue grama
14	374.0	9.452	15.12	45.35	3.70	1.14	19.62	5.32	1.84	C	blue grama
15	392.0	9.864	16.09	48.28	1.71	1.70	11.95	8.17	2.72	C	blue grama
16	396.0	8.224	17.35	52.05	1.71	2.84	11.38	2.64	2.64	C	blue grama
17	433.0	10.277	15.95	47.87	0.86	3.98	6.54	7.34	7.34	C	blue grama
18	471.0	13.508	17.84	53.51	1.99	2.28	12.22	2.27	.76	C	blue grama
19	512.0	13.953	17.86	53.60	1.42	1.70	9.38	4.81	1.60	C	blue grama
20	585.0	9.964	16.76	50.28	1.14	2.85	5.12	6.99	6.99	C	blue grama
21	232.2	6.353	15.12	45.37	1.72	1.47	7.40	14.66	4.89	D	blue grama
22	248.8	7.245	17.90	53.66	1.03	1.07	5.23	8.36	2.79	D	blue grama
23	271.9	7.738	17.68	53.04	0.94	1.07	4.40	9.62	3.21	D	blue grama
24	296.1	8.752	17.77	53.32	1.28	1.07	7.71	6.83	2.28	D	blue grama
25	315.0	8.190	6.28	35.57	4.38	2.25	15.88	27.99	9.33	E	wheat pasture
26	385.0	10.703	5.93	33.61	9.38	3.06	18.19	28.28	9.43	E	wheat pasture
27	403.4	9.762	6.56	37.19	7.50	2.75	17.25	26.29	8.76	E	wheat pasture
28	410.3	14.442	7.13	40.44	5.63	2.13	13.50	26.93	8.98	E	wheat pasture

Table 5. Continued.

	BW ¹ (kg)	FI(kg)	DNBH ²	DBH ³	DNPN ⁴	DNPROT ⁵	DPROT ⁶	DWSC ⁷	DAH ⁷	REFERENCE ⁸	FORAGE TYPE
29	170.0	3.842	7.83	44.35	2.66	2.13	16.47	13.50	1.47	F	perennial ryegrass
30	174.0	4.141	8.72	49.42	1.88	1.50	11.62	14.30	1.56	F	perennial ryegrass
31	177.0	4.443	7.89	44.70	1.72	1.38	10.66	21.50	1.46	F	perennial ryegrass
32	148.0	2.621	7.55	42.79	2.24	1.79	13.91	18.10	1.62	G	perennial ryegrass
33	146.0	3.226	7.88	44.60	2.38	1.90	14.72	15.00	1.73	G	perennial ryegrass
34	160.0	4.090	7.93	44.95	2.36	1.89	14.63	14.90	1.74	G	perennial ryegrass
35	167.0	4.261	8.25	46.74	2.08	1.66	12.89	17.60	1.79	G	perennial ryegrass
36	185.0	4.632	9.20	52.15	1.54	1.23	9.54	15.80	1.84	G	perennial ryegrass
37	188.0	4.728	8.65	49.01	1.73	1.39	10.76	15.40	1.76	G	perennial ryegrass
38	214.0	5.908	7.83	44.39	2.69	2.15	16.66	10.70	1.68	G	perennial ryegrass
39	273.0	4.989	9.15	51.83	1.89	1.51	11.73	11.80	1.69	H	perennial ryegrass
40	177.0	3.072	8.07	45.73	1.79	1.43	11.09	17.90	1.29	I	perennial ryegrass
41	200.0	4.707	8.81	49.94	1.77	1.42	11.00	15.80	1.46	I	perennial ryegrass
42	245.0	5.779	8.60	48.71	2.15	1.72	13.32	14.50	1.30	I	perennial ryegrass

1See text for explanation of symbols

2(NDF-DNPROT)-DBH

3(NDF-DNPROT)*.75 (assume 75% degradability of beta hexose and hemicellulose)

4(Soluble N*.5)*6.25 (assumes 50% NPN as soluble N)

5ADIN*6.25

6(Total N - (Soluble N*.5) - ADIN) *6.25

7DWSC+DAH = 100 - (DBH+NBH+PROT+NPROT+NPN+2.0% ether extract) where: DWSC= 75% of DWSC+DAH in growing forage and 50% in dormant forage if not reported directly.

8A&E= M. L. Galyean, personal communication.

B= McCollum and Galyean, 1985; C= Krysl et al., 1987; D= Funk et al., 1987.

F= Beever, et al., 1985; G= Beever, et al., 1986; H= Beever, et al., 1987.

I= Beever, et al., 1986.

Table 6. Rank of model sensitivity to parameter changes.

PARAMETER ¹	SENSITIVITY ²
KBH	20.3
MC	13.5
BK1	15.1
MN	7.0
BKL1	3.1
KPROT	2.7
KC	1.3
KAH	.5
KU	0

¹For description of symbols see text.

²Change in error SS for a constant proportional change in the parameter of 25%.

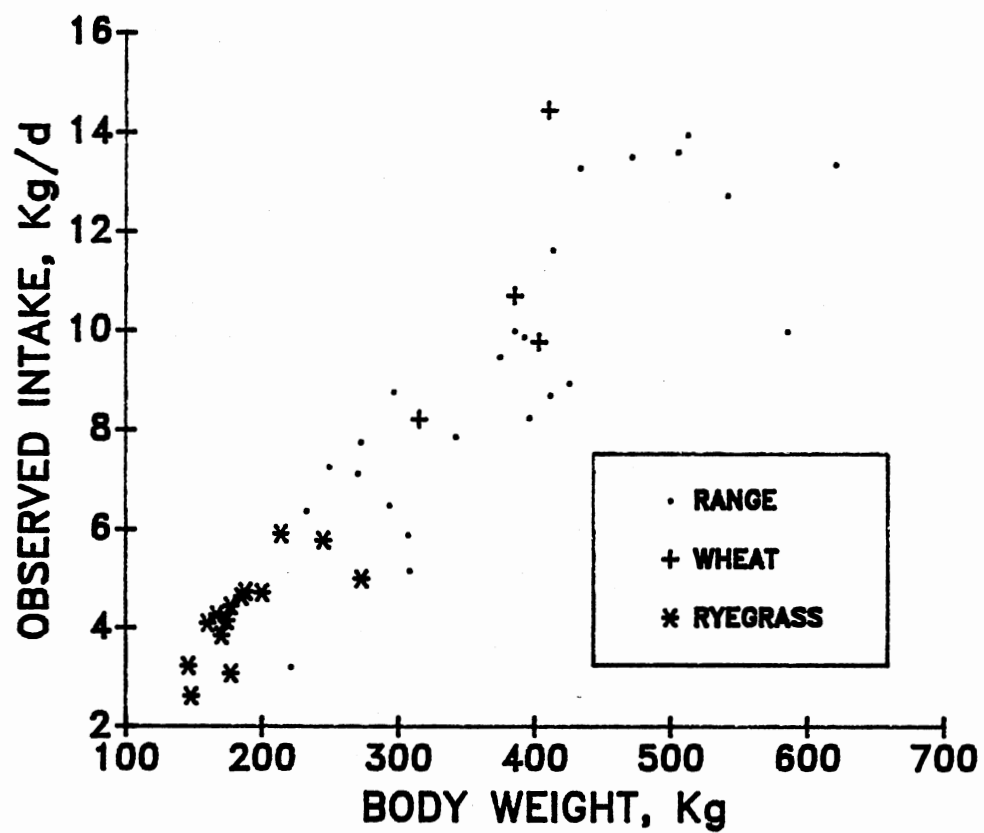


Figure 1. The relationship of observed forage intake and steer body weight for the reference data set.

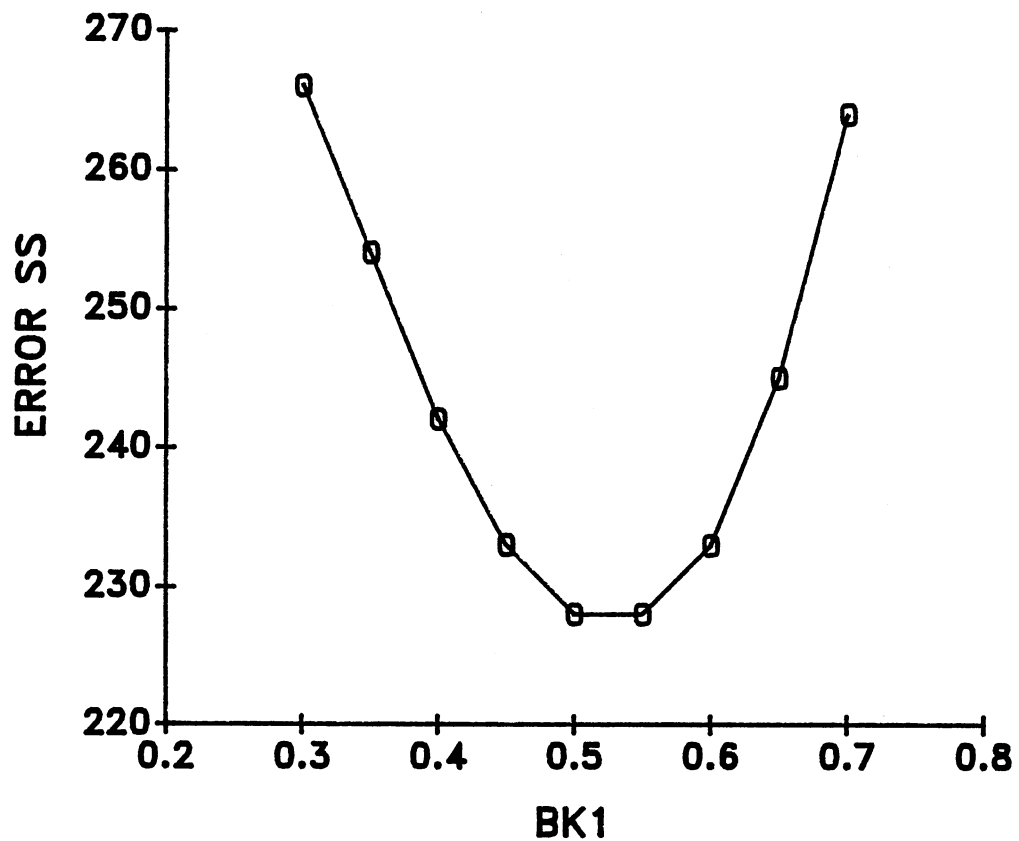


Figure 2. The effect of varying the particulate passage slope coefficient BK1 on error sum of squares, reference BK1= .550.

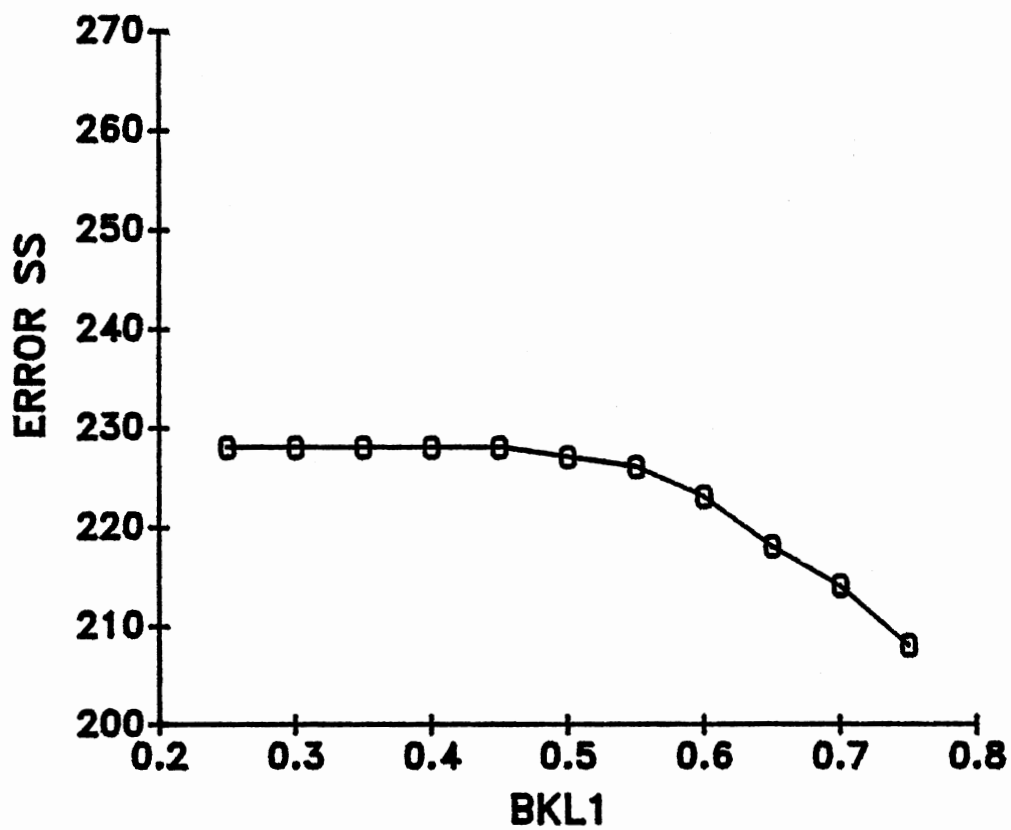


Figure 3. The effect of varying the liquid passage slope coefficient BKL1 on error sum of squares, reference BKL1=.479.

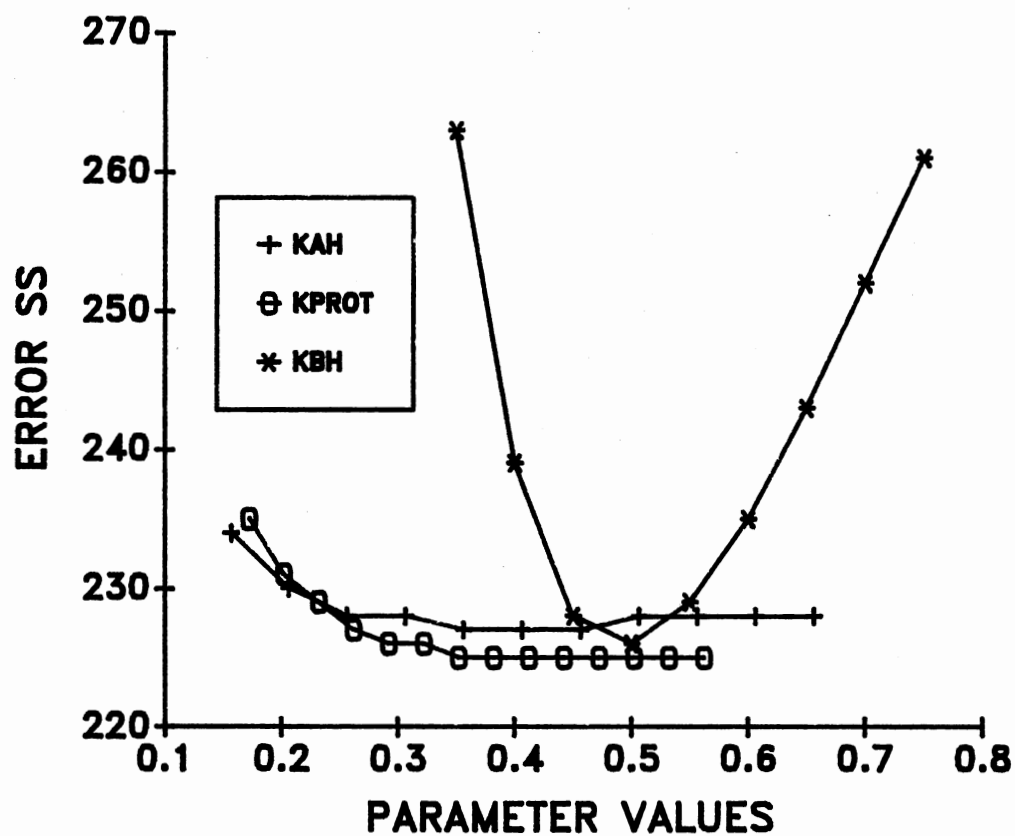


Figure 4. The effect of varying microbial use rate constants for fiber ($KBH=0.460$), starch ($KAH=0.407$) and protein ($KPROT=0.262$) on error sum of squares.

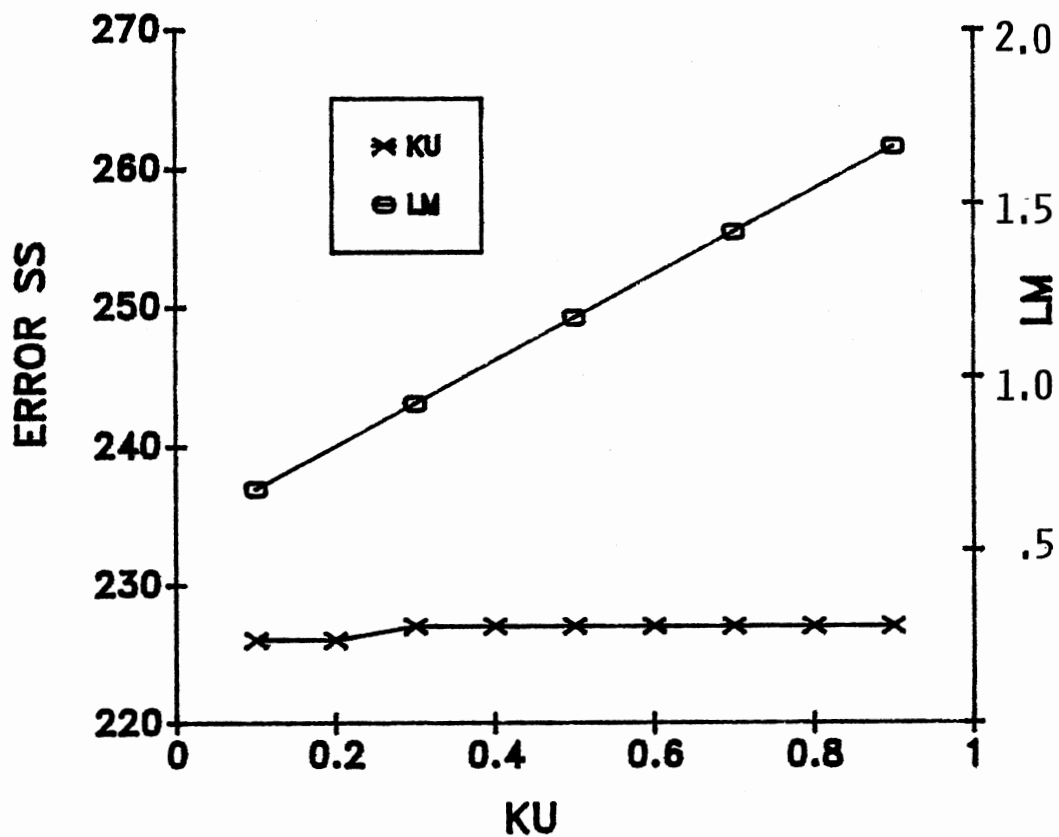


Figure 5. The effect of varying KU and LM (microbial growth parameters) on error sum of squares.

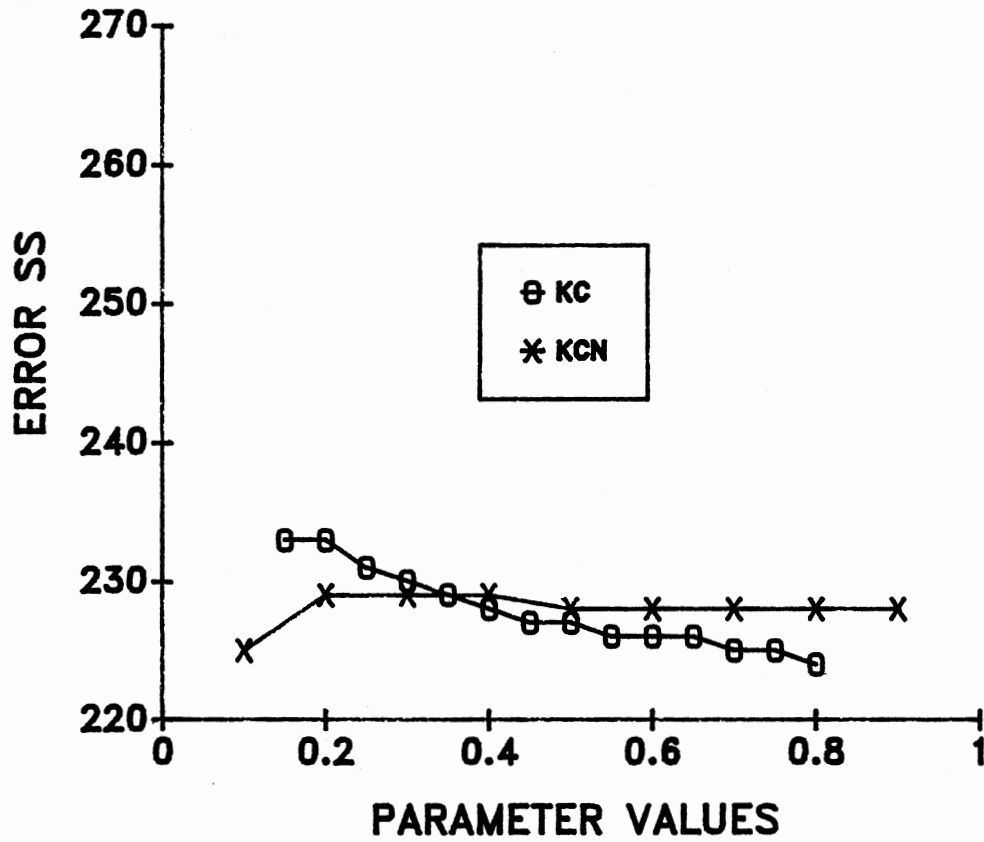


Figure 6. The effect of varying microbial constants KC and KCN on error sum of squares, where reference $KC=0.516$ and $KCN=0$.

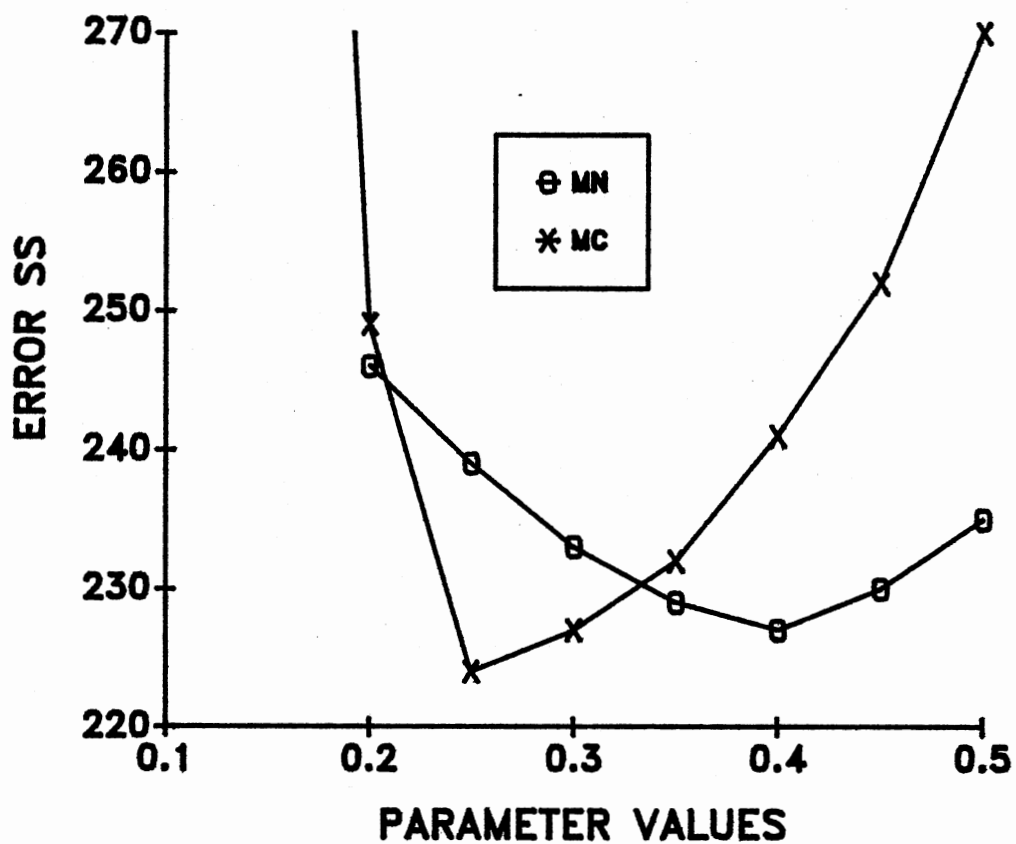


Figure 7. The effect of varying microbial composition constants for nitrogen (MN=.38) and carbohydrate (MC=.30) on error sum of squares.

CHAPTER IV

EVALUATION OF A FEED INTAKE MODEL FOR THE GRAZING BEEF STEER

Abstract

A feed intake model for grazing beef cattle was evaluated with respect to changes in model parameters, forage input values and supplementation programs with energy and protein. Without supplements, systematic underprediction of the model occurs with low quality forages and subsequent overprediction is observed on high quality diets. In general, for a reference diet of Italian ryegrass the model was relatively insensitive to microbial growth parameters, however, high sensitivity was observed for the microbial carbohydrate composition constant and moderate sensitivity for the nitrogen composition constant. Intake prediction was sensitive to changes in the nutrient use parameter for fiber and insensitive to those for protein and starch. Model predictions were highly sensitive to the amount of non-degradable fiber in each of the forages tested. Supplementation effects on forage intake were quantified by supplementing all forage diets with 1 kg of a corn grain and 1 kg cottonseed meal. Supplementation of the forage diet with the concentrate source resulted in

substitution ratios consistent with those previously reported. As forage quality increased, greater substitution of concentrate for the forage occurs. Inadequate effects on intake for protein supplementation suggests that a rumen model alone is insufficient for intake prediction in protein limiting situations. The model correctly predicts the effects of energy supplementation on forage intake.

Introduction

The lack of knowledge of the plant-animal interface has resulted in relatively few models in the literature regarding models which can be used to predict intake of grazing cattle (Hyer and Oltjen, 1987). Several methods to predict feed intake of feedlot cattle have been successfully developed (Plegge and Goodrich, 1987). Most approaches to predict intake of pen fed cattle have used regression relationships based on an empirical fit of a selected set of data and then applied adjustment factors to extend the range of these predictions. For grazing cattle, animal factors such as body weight, physiological state and ruminal fill interact with forage quality and availability to determine forage intake (Allison, 1985). Because of the extensive variation associated with forage type and quality, most regression relationships with intake can only be applied to the forage specie for which they were developed. On the other hand, mechanistic models of intake which are based on fundamental biological controls, rely less on fit of a given

data set, but rather on the appropriate representation of the biology of the process in question. Thus, they can be more generally applied. Previous work by the authors described the conceptual basis, differential equations and parameter estimates of a mechanistic mathematical model to predict forage intake of the grazing beef steer (see Chapter III).

If a mechanistic model is to be used with confidence, it must meet two criteria: it must accurately predict animal response, here feed intake, and appropriately represent the biology of the function being studied, in this case supplementation effects on fermentation in the rumen. The objective of this work was to evaluate the forage intake model for the grazing steer and determine if model behavior is consistent with validated biological concepts which influence intake.

Materials and Methods

Description of model structure, parameter estimation and sensitivity of model prediction to parameter changes for the reference data set has been previously discussed (see Chapter III). Mean values, ranges and variation associated with a reference data set containing 42 forage points is described (Table 1). Sensitivity analysis to forage input values was accomplished using the simplex fitting procedure described by Nelder and Mead (1965).

Table 1. Description of nutrient composition (%) of 42 forages.

Item	AH ¹	BH	NBH	NPROT	PROT	NPN	WSC
Mean:	3.6	48.0	13.0	2.0	10.6	2.2	11.9
Standard deviation:	2.8	5.2	4.6	.7	4.2	1.7	7.1
Minimum:	.8	33.6	5.9	1.1	3.1	.9	2.3
Maximum:	9.7	55.4	18.5	3.9	19.6	9.4	28.3

¹AH is alpha hexose, BH is degradable beta hexose, NBH is non-degradable beta hexose, NPROT is non degradable protein, PROT is degradable protein, NPN is non-protein nitrogen, WSC is water soluble carbohydrate.

To evaluate model behavior with different forages, 4 data points were selected which represent the reference Italian ryegrass forage (France et al., 1982), the average of the native grasses (24 observations), wheat pasture (4 observations) and perennial ryegrass (12 observations) (Table II). Supplementation of each of the reference data points was accomplished using rolled corn (1 kg) as an energy supplement and cottonseed meal (1 kg) as a protein supplement.

Results and Discussion

A plot of the predicted versus observed intake by forage type and the fitted regression line is illustrated in Figure 1. The relationship between residual intake (predicted-observed) and the dietary non-degradable fiber, DNBH, indicates that systematic underprediction occurs on lower quality diets (DNBH: 13-20%) and overprediction is apparent with higher quality forages (DNBH: 6-10%, Figure 2).

To evaluate the sensitivity of the model to the nutrient fractions in the forage, the mean value for each forage component in the reference data set were input, one at a time, as the dietary value of each point and error sum of squares for intake determined. For example, the average value for non-degradable fiber (DNBH) of the reference data set is 13.00%. This value was substituted as a constant to

Table 2. Description of data points used for evaluation.
(DM basis)

AH ¹	NBH	BH	NPN	NPROT	PROT	WSC
A _{1.60}	8.31	47.09	2.06	1.65	12.79	15.49
B _{9.13}	6.48	36.70	6.72	2.55	16.21	27.37
C _{3.85}	16.82	50.48	1.53	2.15	8.34	7.31
D _{2.66}	6.73	49.37	4.22	2.43	7.29	21.50

¹See table I for description of symbols.

A perennial ryegrass

B wheat pasture

C native range grasses

D reference Italian ryegrass

represent the DNBH fraction of each of the 42 forages. Resulting error sum of squares for a constant DNBH value was 416. Error SS for the model with no changes (227) and with each nutrient fraction held constant is illustrated in Figure 3. The model is insensitive to changes in dietary AH (233), WSC (225), NPN (222), NPROT (225) and BH (240). Moderate sensitivity was observed when DPROT was fixed as a constant (270) and high sensitivity was observed for DNBH (416), as previously mentioned, indicating that model predictions are most influenced by the fiber (non-degradable) and protein fractions in the forage. Further evaluation using each of the protein variables as constants, simultaneously, resulted in higher error SS (352); however, when constant ratios of the three fractions were utilized, but their sums equalled actual crude protein, error SS changed very little (235). Error SS decreased (185) when the average ratio of NBH/BH was input for all 42 points and BH plus NBH were equal to total beta-hexose in each individual forage.

Previously, 4 forages were described (Table 2) that represent averages for wheat pasture, native grasses, perennial ryegrass and the reference Italian ryegrass forage. A 350 kg steer was used as a reference steer and intake of each of the forages was simulated. Forage intake was highest for the reference forage (13.43 kg), lowest for the native grasses (7.05) and intermediate for the wheat pasture (8.93) and perennial ryegrass forages (11.36). The

model was then evaluated by varying the NBH fraction of each forage and observing changes in intake (Figure 4).

Reference intakes of each forage correspond with the amount of dietary NBH in the respective forages (Table II).

Similar decreases in intake were observed with increasing NBH; however, wheat pasture intake was consistently lower than the other forages.

To fully evaluate sensitivity of the model for each of the parameter values and rate constants, the reference Italian ryegrass forage was utilized. Figure 5 demonstrates the sensitivity of the microbial nutrient use rate constants for starch (KAH), fiber (KBH) and protein (KPROT).

Parameter estimates used in the model were .407, .460 and .262, respectively. Intake is insensitive to changes in KAH and KPROT over a wide range of parameter values. However, model behavior was highly sensitive to changes in KBH below the reference level of .460, as intake declined notably.

Slope coefficients relating rate of passage to dry matter intake (DMI) have been previously described (see Chapter 3). Figure 6 represents changes in intake associated with varying slope coefficients BK1 (.550, particulate) and BKL1 (.479, liquid) above and below the reference values. Intake declines are noted below the reference value for BK1 and above the reference BKL1.

Sensitivity of the model to changes in the dietary fractions for the reference forage was accomplished. As each dietary fraction was changed, the remaining nutrient

fractions were adjusted in proportion to the change associated with the component in question, thus keeping total organic matter constant. Low sensitivity was observed for dietary beta-hexose (BH, Figure 7), alpha-hexose (AH, Figure 8) and non-protein nitrogen (NPN) on a crude protein equivalent basis (Figure 9). The model is highly sensitive to dietary degradable protein (PROT, Figure 10), non-degradable protein (NPROT, Figure 11) and soluble carbohydrate (WSC, Figure 12). High sensitivity to dietary non-degradable fiber (NBH) has been previously described. For the reference diet intake is sensitive to the percent of NBH over the entire range tested (Figure 4).

The model was tested regarding changes in parameters associated with the microbial mass growth in the rumen. Little change in intake is noted for large changes in the constants for nutrient use: K_c , and K_{cn} (Figure 13). K_{cn} and K_n were unidentifiable and set at zero in the model. Figure 14 depicts changes in the maximum microbial specific growth rate constant UM , where the reference value is $5d^{-1}$. Large changes in intake were associated with changes in the microbial composition parameter for carbohydrate (MC), smaller changes were noted for nitrogen (MN, Figure 15). Small changes in intake resulted when the constant (PBUG) representing the proportion of the microbial mass flowing with the liquid and passage rate was changed above and below the reference value of .5 (Figure 16).

Rumen volume for the reference 350 kg steer is calculated as 35 l. Intake predictions were highly sensitive to changes below and above the reference level (Figure 17), consistent with the original hypothesis that rumen fill limits intake.

Table 3 quantitatively ranks the relative sensitivity of the model to changes in nutrient fractions, rumen volume, microbial passage, growth and composition constants, rate constants for nutrient use and coefficients relating intake to passage rate.

Horn and McCollum (1987) found that the substitution effect of energy supplements on forage intake for both cattle and sheep become more pronounced (i.e. ratios of the change in forage intake to change in concentrate intake become more negative) as forage digestibility increases. Supplementation of the 42 forage data points with 1 kg corn resulted in substitution effects consistent with literature values (Figure 18). Substitution ratio is equal to the model predicted intake with 1 kg corn minus the predicted intake without the supplement. As forage in vitro organic matter digestibility (IVOMD) increases above 65%, substitution ratios become more negative. The relationship between substitution effects and degradable protein in the forage (Figure 19) indicates that at higher levels of available protein (12 to 16%) greater substitution of concentrate for higher quality forage occurs. This is likely the result of a positive correlation between protein

Table 3. Rank of model sensitivity to parameter changes for the reference Italian ryegrass forage.¹

PARAMETER ²	SENSITIVITY ³
RV	1.670
DNBH	.348
DWSC	.283
BK1	.336
KBH	.269
MC	.251
UM	.219
MN	.184
DPROT	.171
DNPROT	.107
DBH	.081
DNP	.056
KC	.047
KPROT	.043
BKL1	.026
KAH	.018
DAH	.012
PBUG	.011
KCN	.000

¹From France et al., 1982.

²For description of symbols see text.

³Slope of (change in predicted intake/predicted intake)/(change in parameter/parameter) or slope/nutrient content.

and IVOMD. However, it is interesting to note that, within forage, greater protein content resulted in less substitution. Increasing the amount of energy supplemented per day is illustrated in Figure 20 for the reference 350 kg steer.

Initial results with energy supplementation indicate that the model responds favorably regarding fermentation changes that occur by adding small amounts of concentrate to the forage diet. However, when small amounts of protein (1 kg cottonseed meal) were supplemented for the 42 forages substitution ratio's were negative (Figure 21). As forage quality increased substitution ratio's became more negative. The inadequacy of the model to account for protein supplementation suggests that post ruminal metabolic controls of intake are important in the protein limiting state. The overprediction of intake observed for range grasses and underprediction on higher quality forages with unsupplemented diets may be a reflection of different forage types. Perhaps the hypothesis that rumen fill limits intake is inadequate for highly digestible forages, and some chemostatic regulation is activated, reducing intake below that predicted by our model. On the average the model overpredicted intake of ryegrass by 1.76 kg/d. For range forages, conversely, wide variation in intake was observed for the experimental data. This may be a reflection of the difficulty in obtaining precise estimates of intake under extensive conditions.

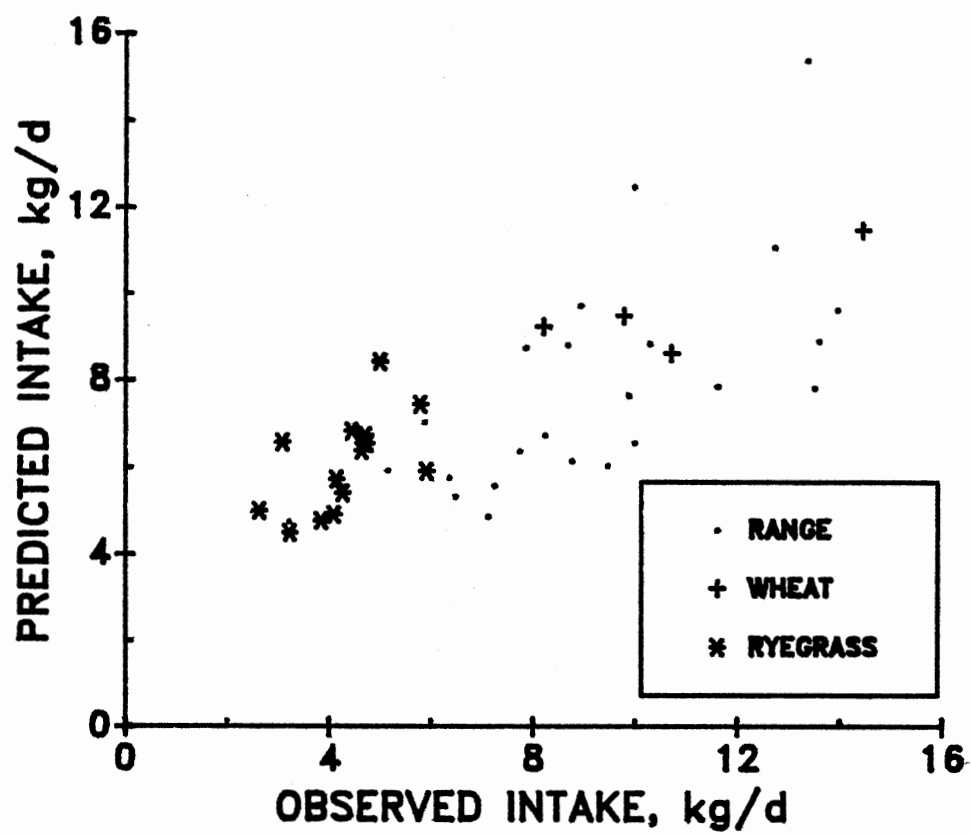


Figure 1. Model predicted versus observed forage intake for the reference data set.

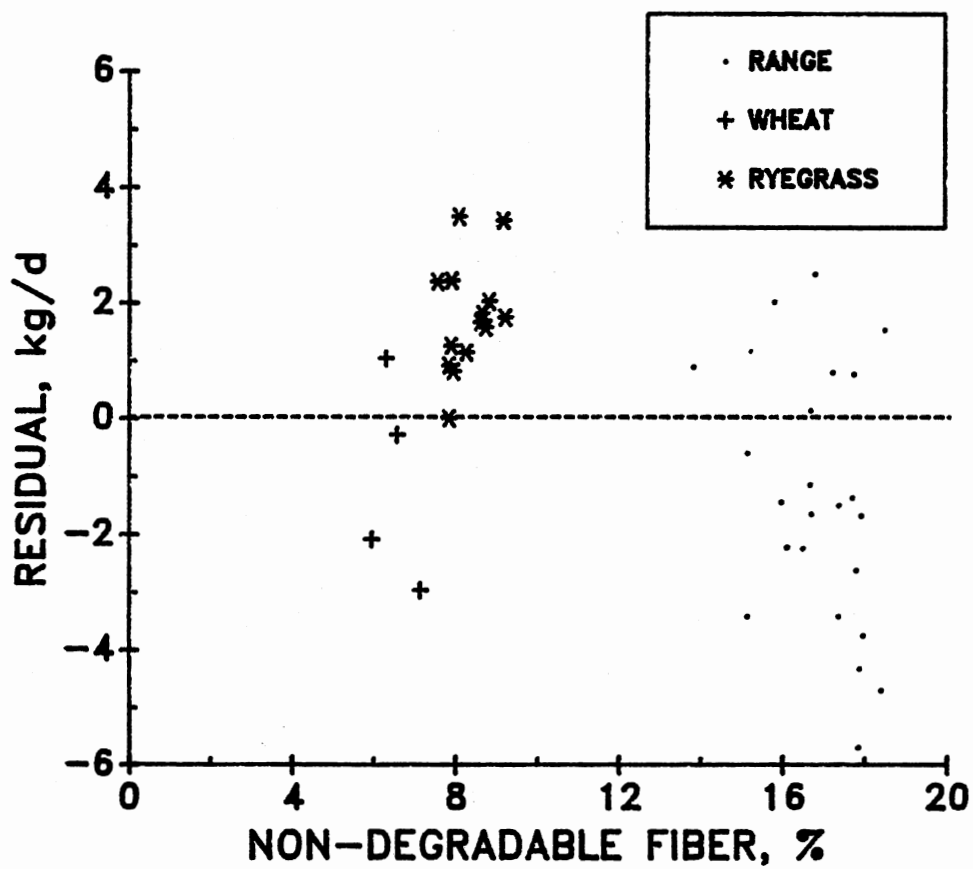


Figure 2. The effect of dietary non-degradable fiber on residual intake (model predicted-observed).

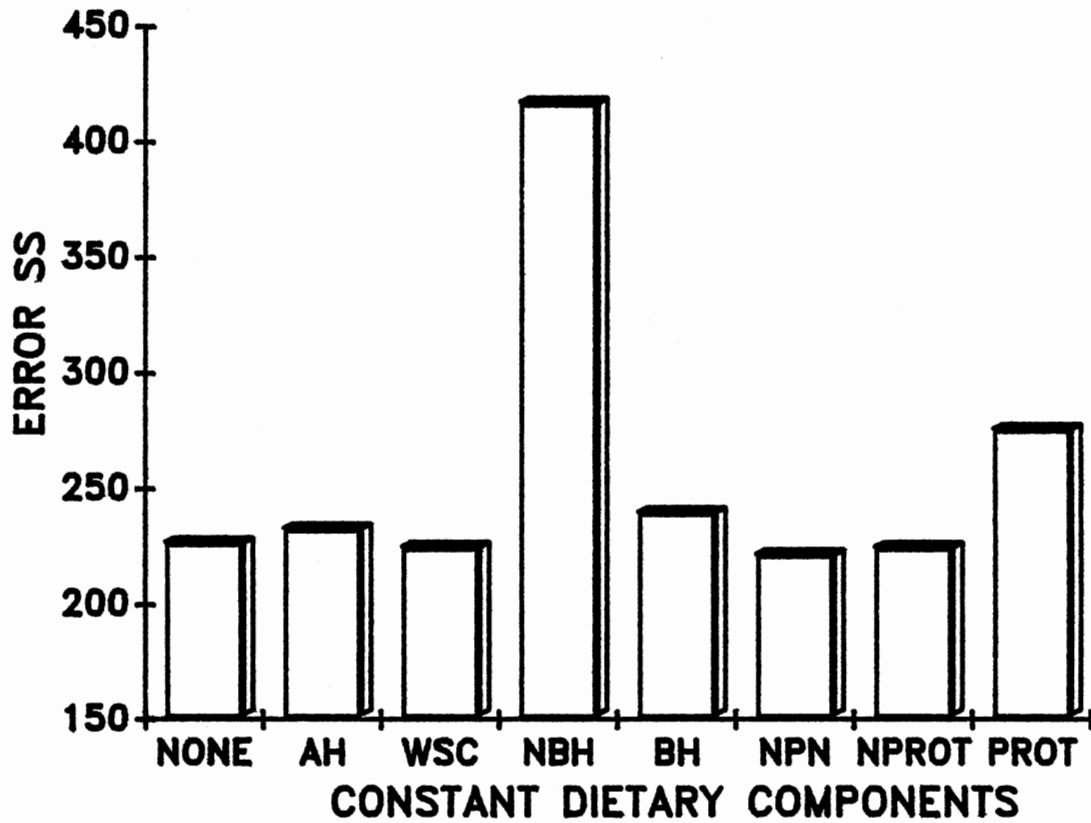


Figure 3. Error sum of squares for the 42 reference forages when mean values from the reference data set are input as constant nutrient fractions for all forages.

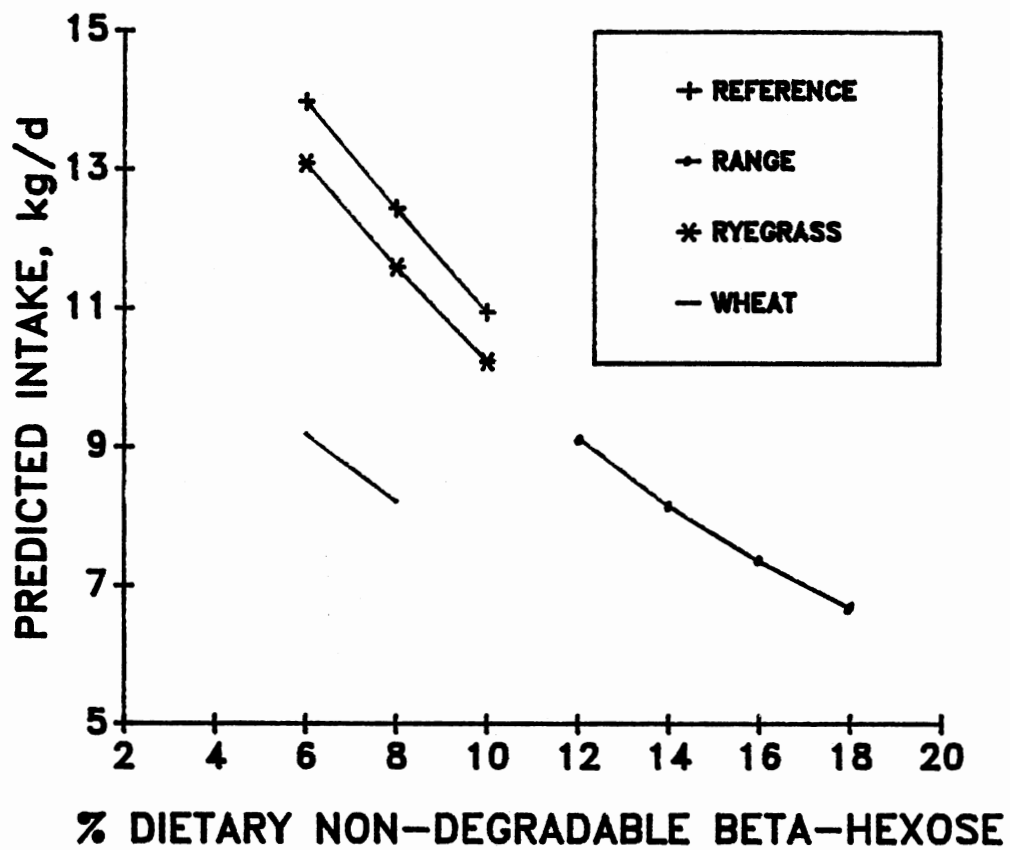


Figure 4. The effect of dietary non-degradable beta-hexose for four forages on model predicted forage intake.

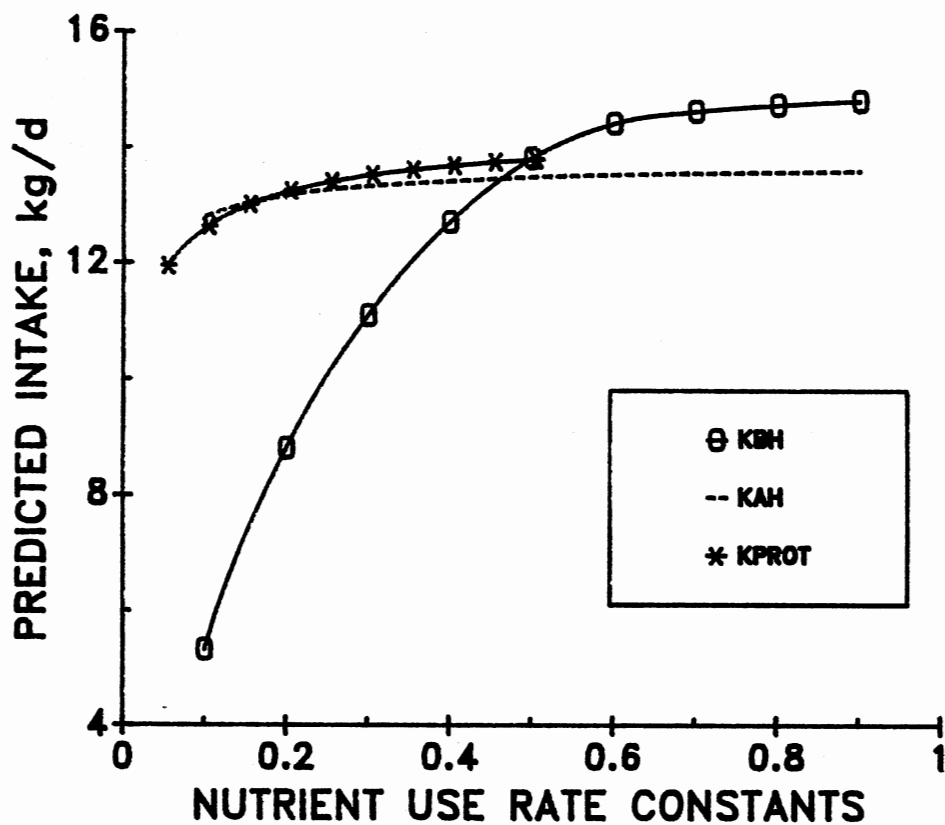


Figure 5. The effect of varying microbial use rate constants for fiber (KBH, reference value=.460), starch (KAH, reference value=.407) and protein (KPROT, reference value=.262) on model predicted forage intake.

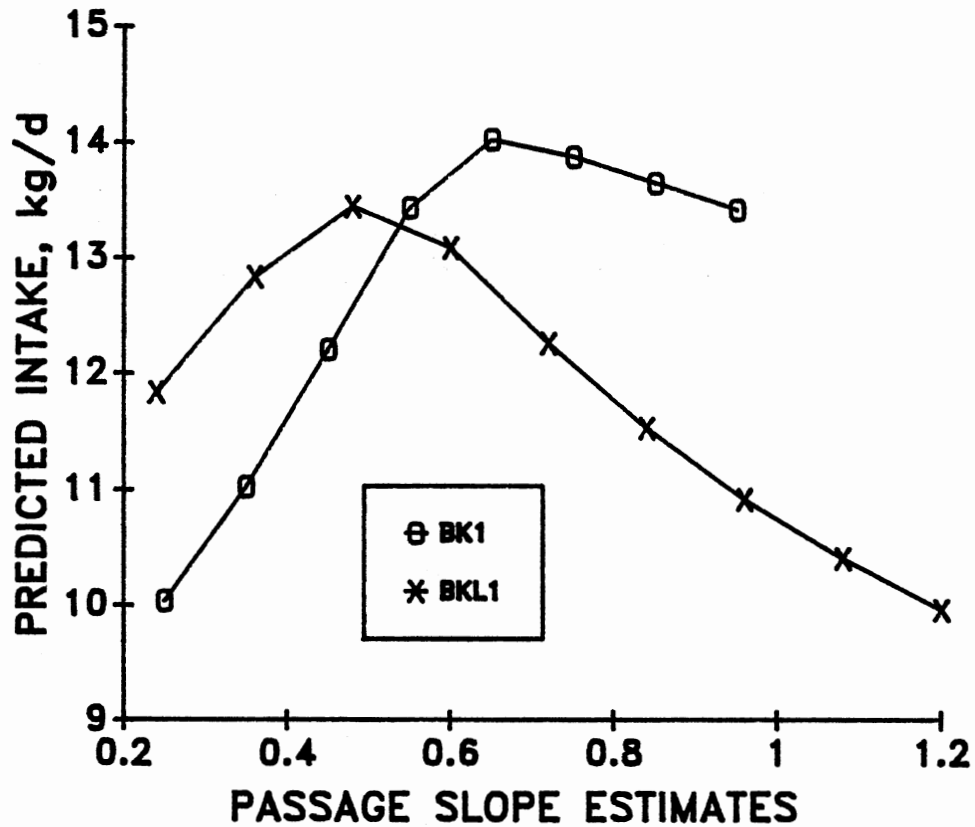


Figure 6. The effect of varying the slope coefficients for particulate (BK1, reference value=.55) and liquid (BKL1, reference value=.479) passage rates on model predicted intake.

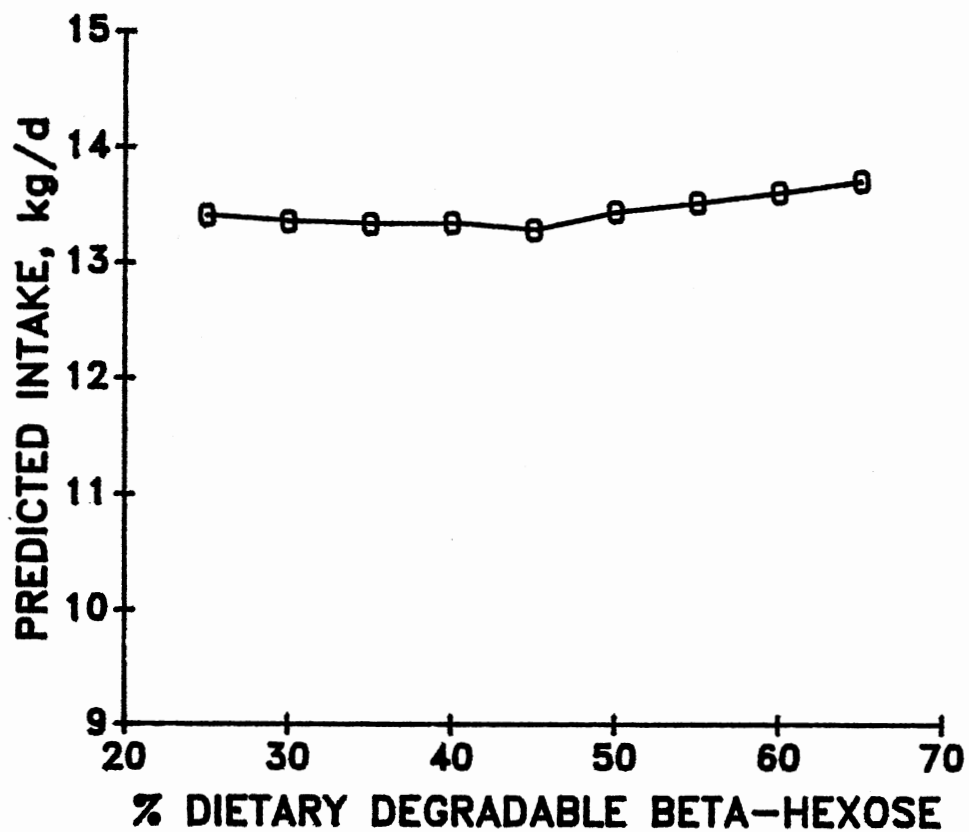


Figure 7. The effect of changes in dietary degradable beta-hexose of the reference forage on model predicted intake.

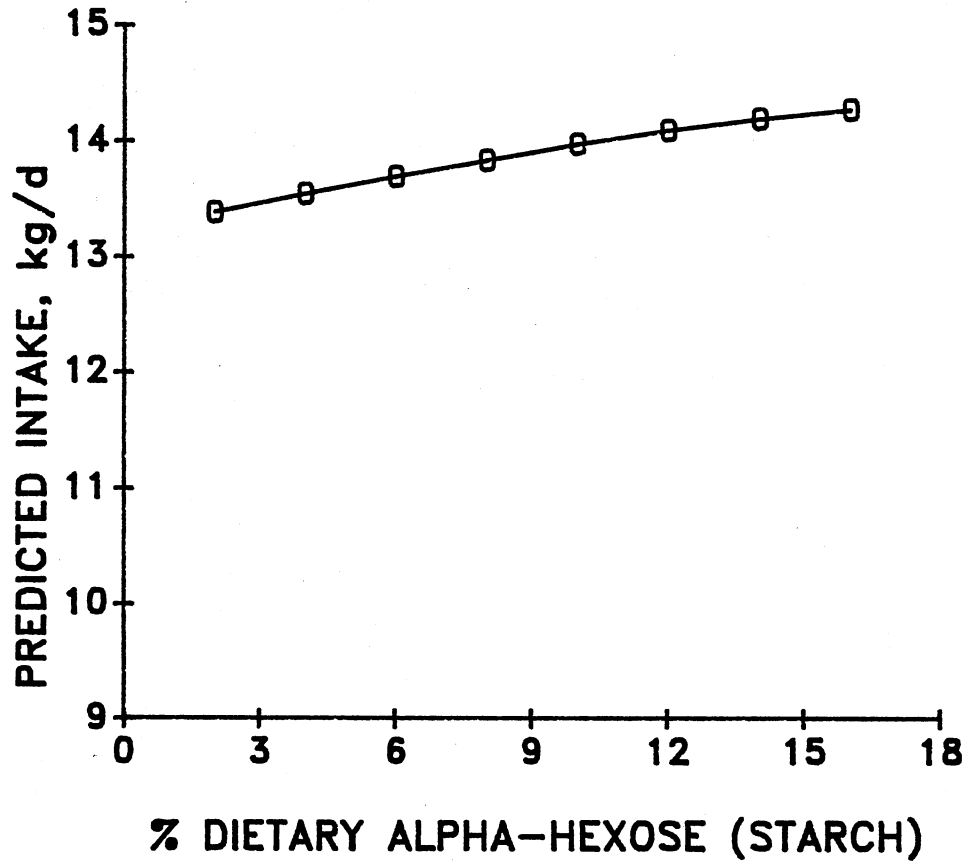


Figure 8. The effect of changes in dietary alpha-hexose of the reference forage on model predicted intake.

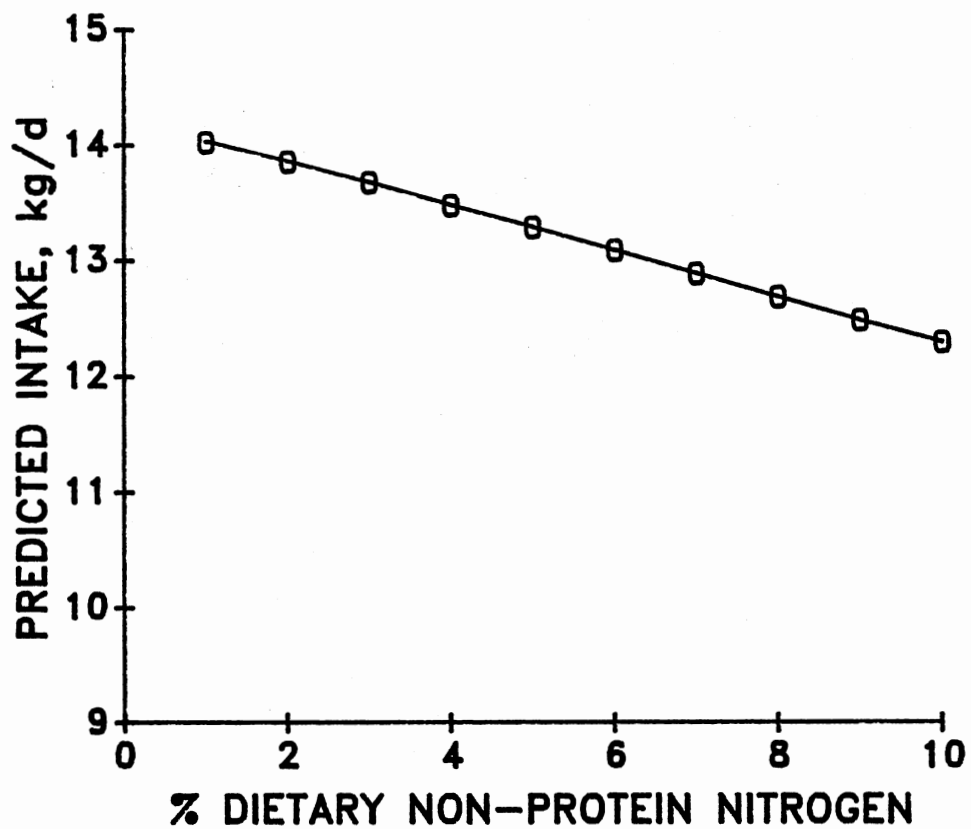


Figure 9. The effect of changes in dietary non-protein nitrogen of the reference forage on model predicted intake.

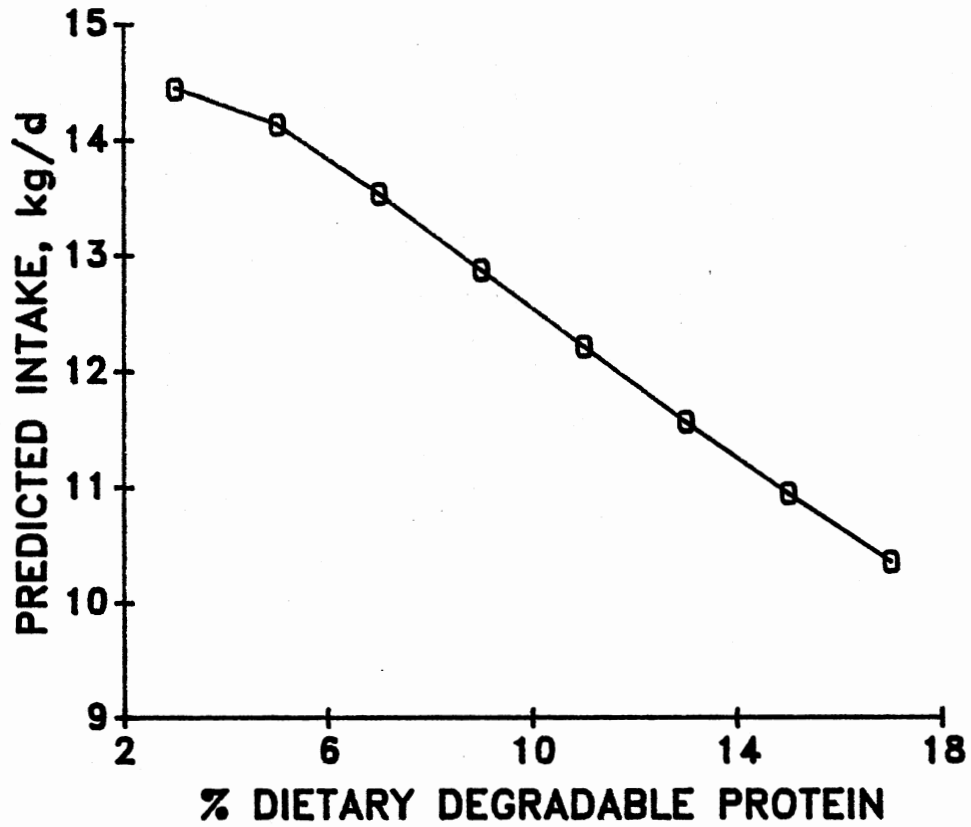


Figure 10. The effect of changes in dietary degradable protein of the reference forage on model predicted intake.

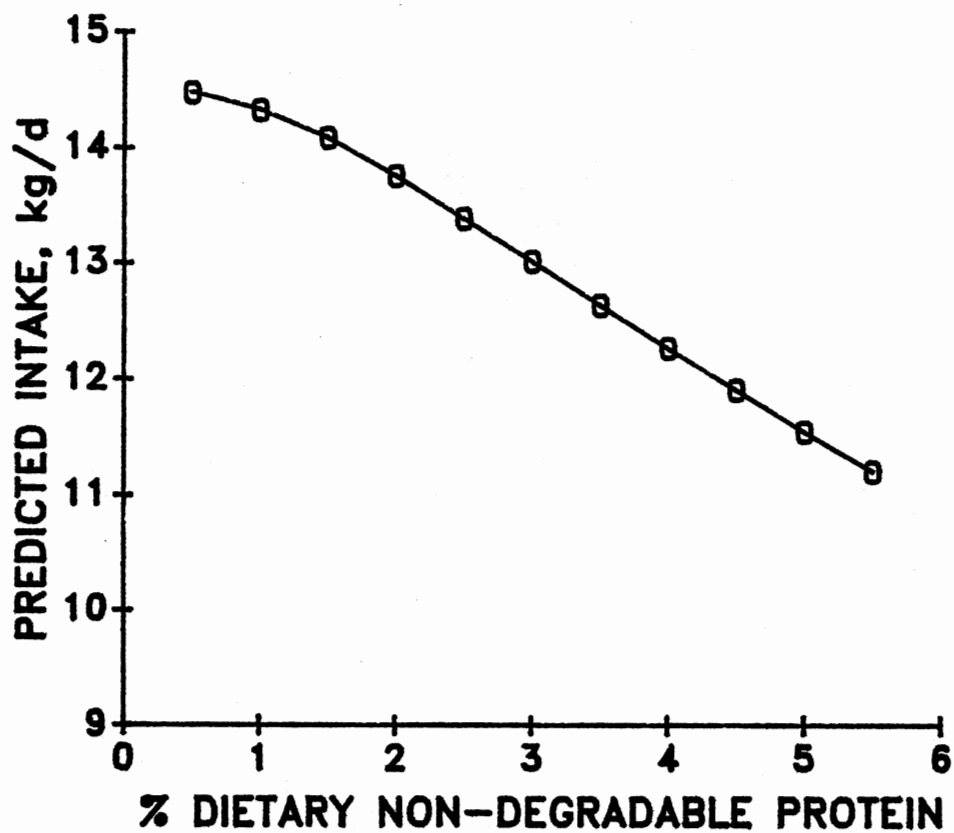


Figure 11. The effect of changes in dietary non-degradable protein of the reference forage on model predicted intake.

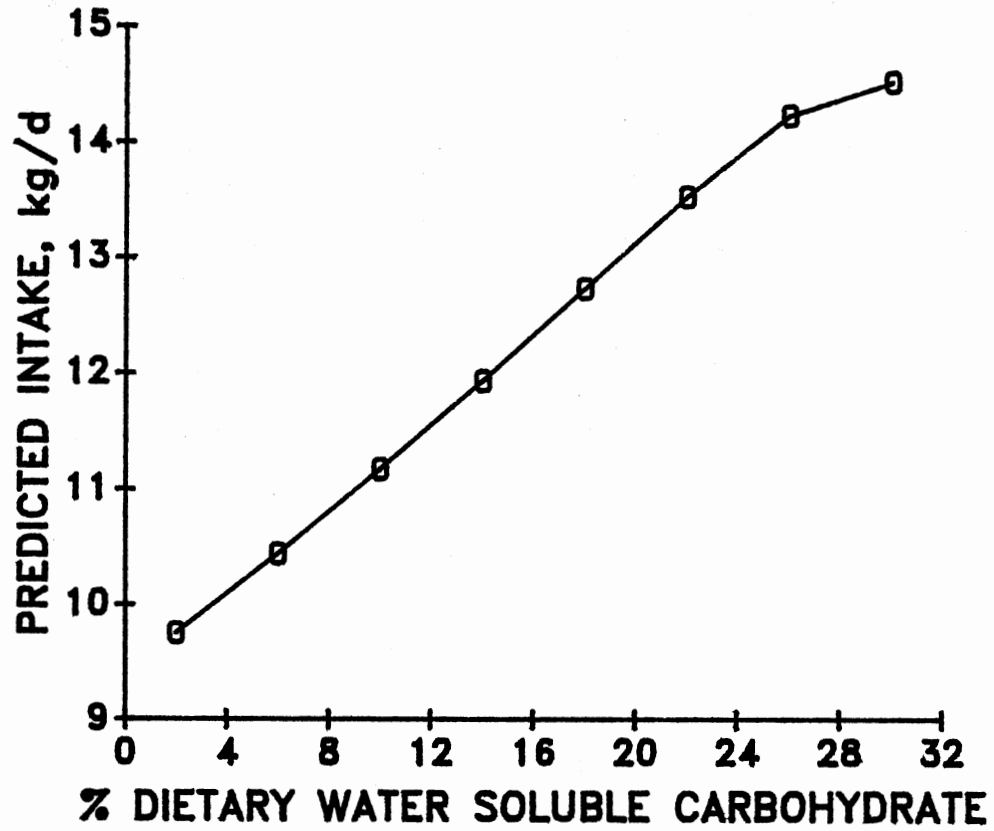


Figure 12. The effect of changes in water soluble carbohydrate of the reference forage on model predicted intake.

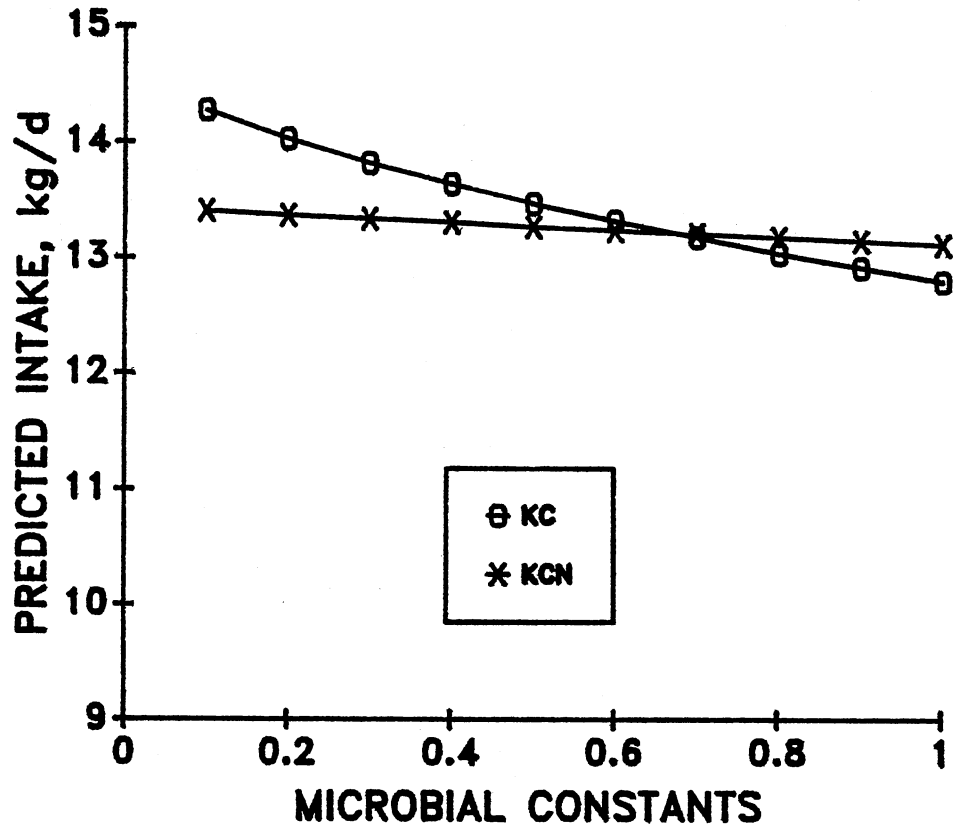


Figure 13. The effect of changes in microbial growth rate constants (KC, reference value=.516) and (KCN, reference value=0) on model predicted intake.

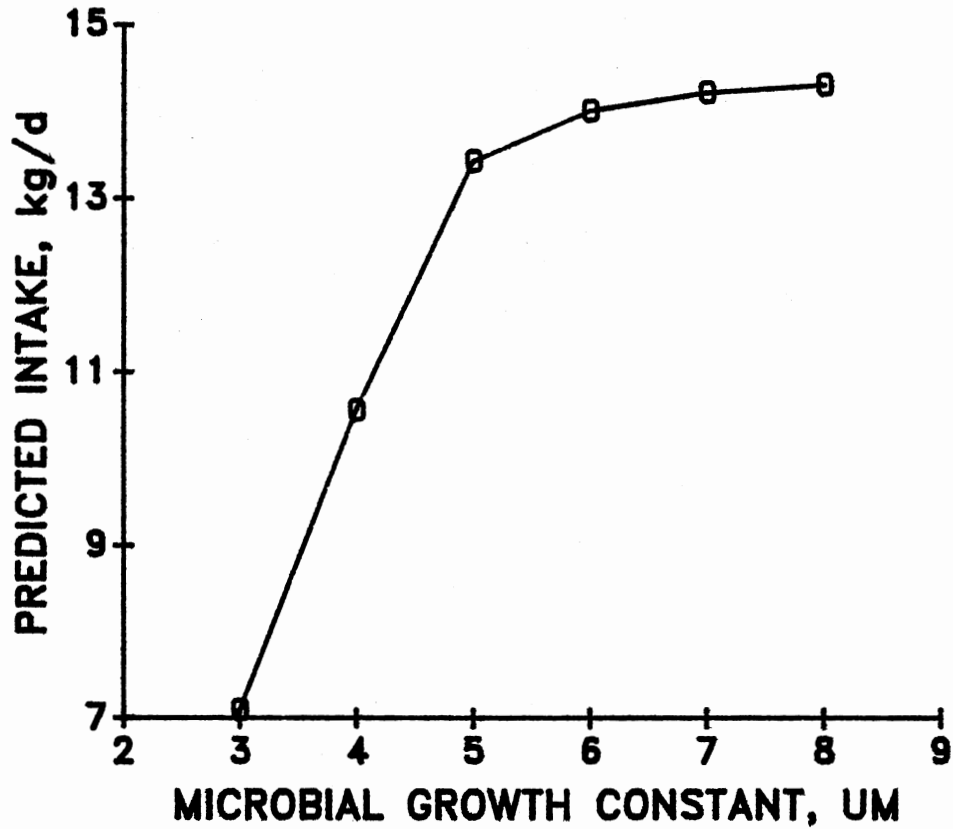


Figure 14. The effect of changes in specific microbial growth rate (UM, reference value=5) for the reference forage on model predicted intake.

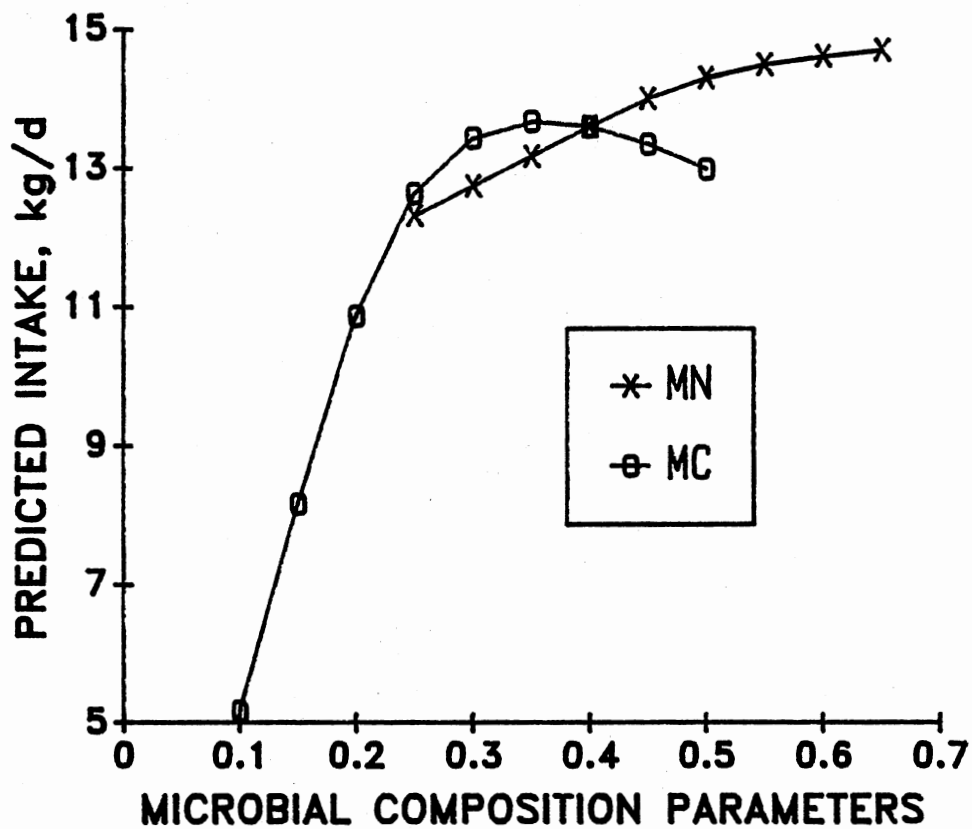


Figure 15. The effect of changes in microbial composition parameters for carbohydrate (MC, reference value=.30) and nitrogen (CP equivalent), (MN, reference value=.38) for the reference forage on model predicted intake.

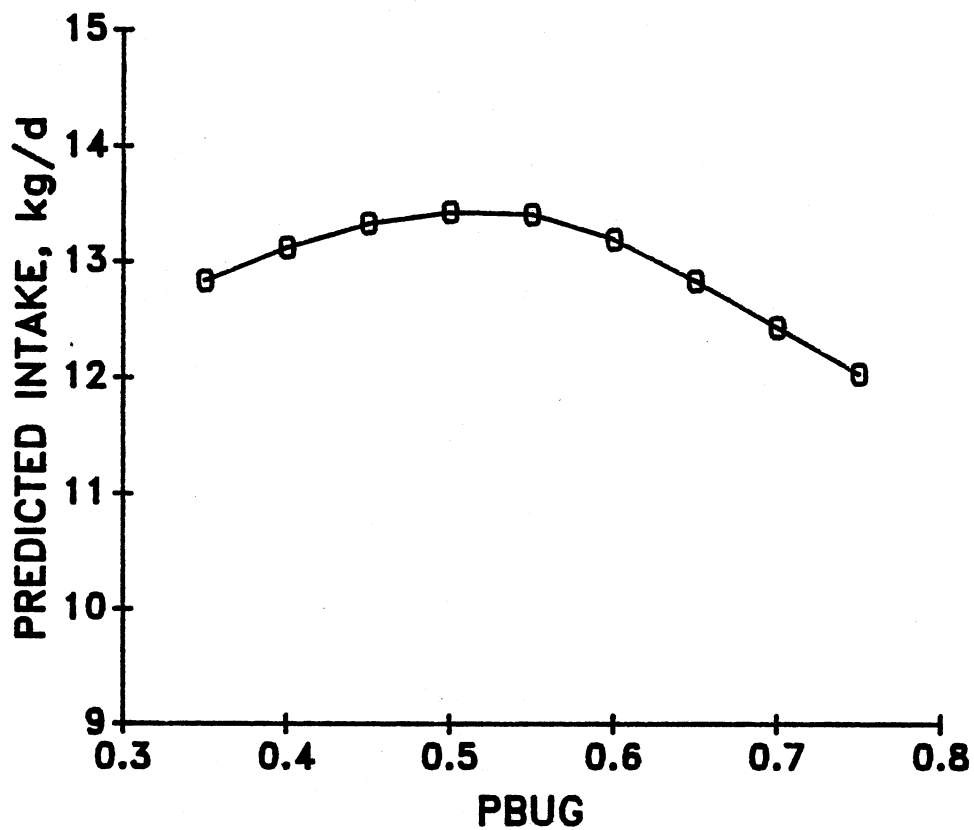


Figure 16. The effect of changes in the proportion of microbial mass flowing with the liquid phase (PBUG, reference value=.50) for the reference forage on model predicted intake.

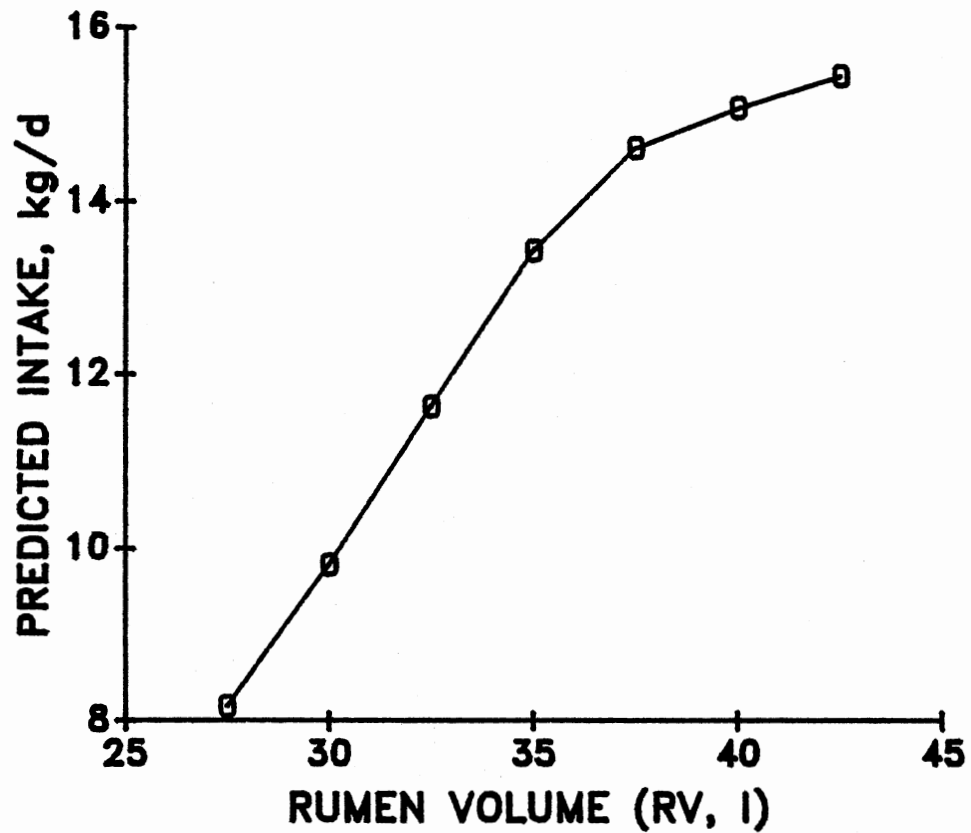


Figure 17. The effect of changes in rumen volume (RV, reference value for 350 kg steer =35l) for the reference forage on model predicted intake.

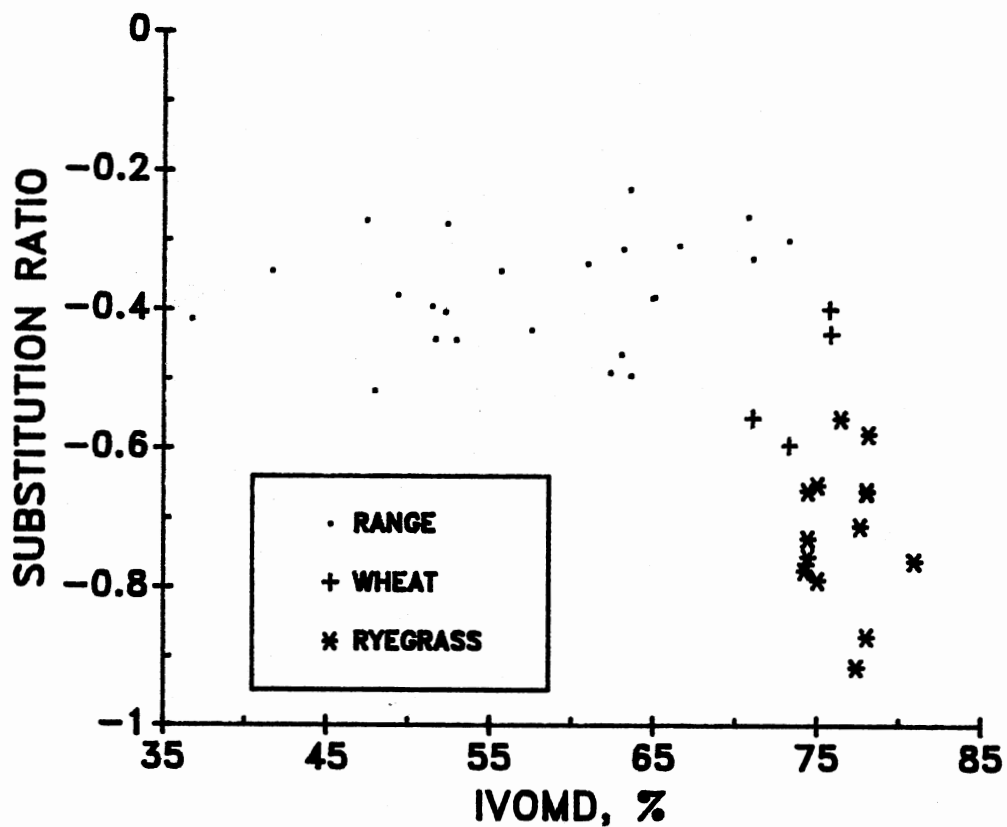


Figure 18. Change in model predicted forage intake (substitution ratio, Δ kg forage/kg corn supplement) for forages of different in vitro organic matter digestibility (IVOMD).

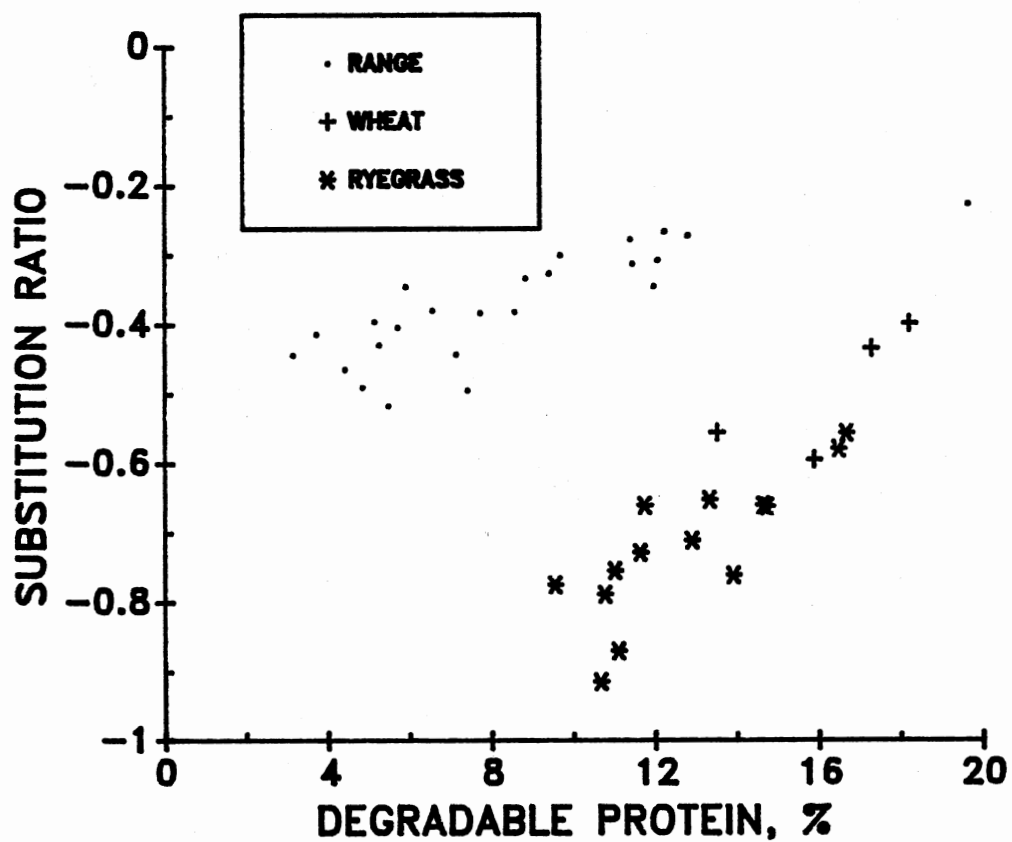


Figure 19. Change in model predicted forage intake (substitution ratio, Δ kg forage/kg corn supplement) for forages of different degradable protein content.

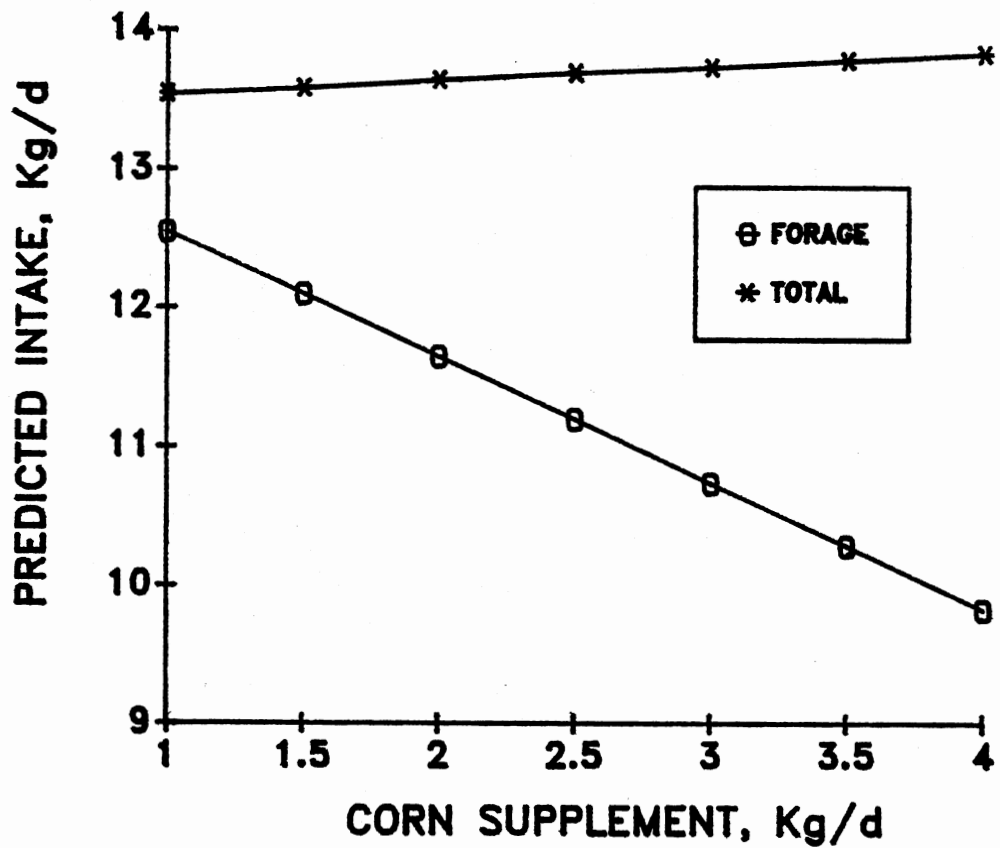


Figure 20. Change in predicted forage and total intake with increasing amounts of a corn grain supplement for the reference forage and a 350 kg beef steer.

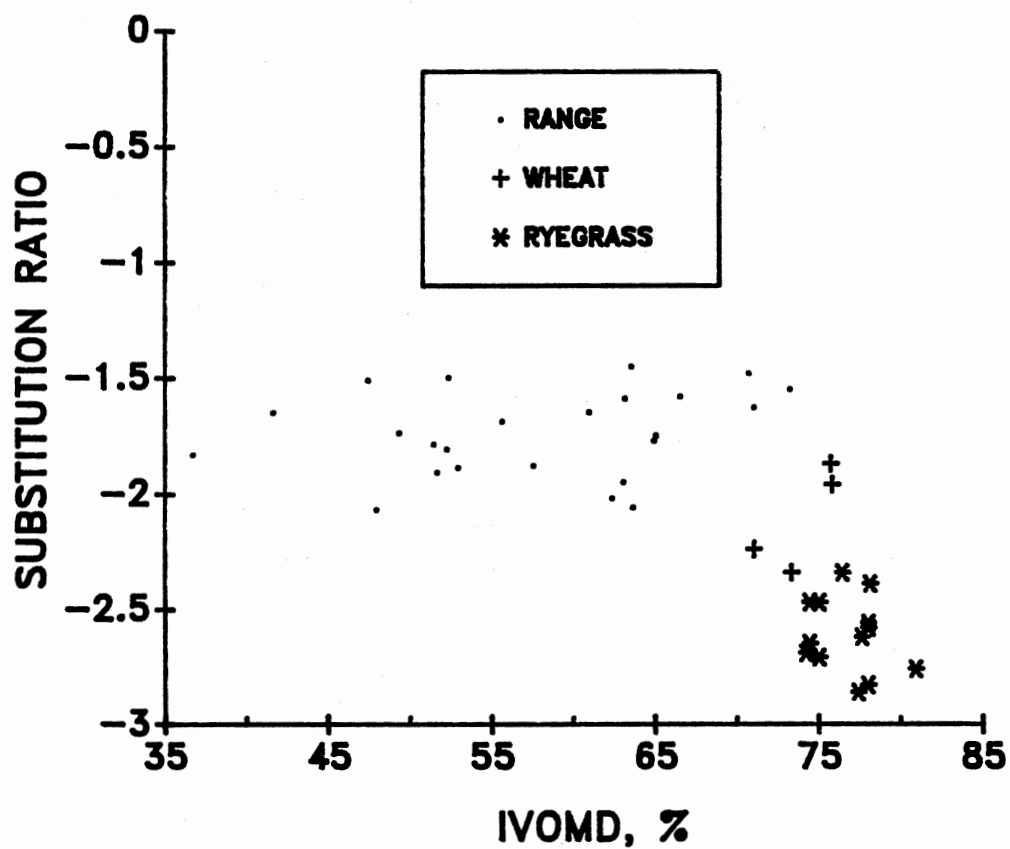


Figure 21. Change in model predicted forage intake (substitution ratio, Δ kg forage/kg cottonseed meal supplement) for forages of different in vitro organic matter digestibility (IVOMD).

LITERATURE CITED

- Adams, D.C. and R.J. Kartchner. 1984. Effect of level of forage intake on rumen ammonia, pH, liquid volume and liquid dilution rate in beef cattle. *J. Anim. Sci.* 58:708.
- Allden, W.G. and I.A.M. Whittaker. 1970. The determinants of herbage intake by grazing sheep: the interrelationships of factors influencing herbage intake and availability. *Aust. J. Agric. Res.* 21:755.
- Allison, C.D. 1985. Factors affecting forage intake by range ruminants: A review. *J. Range Manage.* 38:305.
- Arnold, G.W., N.A. Cambell and K.A. Galbraith. 1977. Mathematical relationships and computer routines for a model of food intake, liveweight change and wool production in grazing sheep. *Agric. Systems* 2:209.
- Baile, C.A. and J.M. Forbes. 1974. Control of feed intake and regulation of energy balance in ruminants. *Physiol. Rev.* 54:160.
- Baile, C.A. and C.L. McLaughlin. 1987. Mechanisms controlling feed intake in ruminants: A review. *J. Anim. Sci.* 64:915.
- Bailey, C.B. 1961. Saliva secretion and its relation to feeding in cattle 3. The rate of secretion of mixed saliva in the cow during eating, with an estimate of the magnitude of the total daily secretion of mixed saliva. *Brit. J. Nutr.* 15:443.
- Balch, C.C. 1958. Observations on the act of eating in cattle. *Brit. J. Nutr.* 12:330.
- Balch, C.C. and R.C. Campling. 1962. Regulation of voluntary food intake of ruminants. *Nutr. Abstr. Rev.*, 32:669.
- Baldwin, R.L. 1976. Principles of modeling animal systems. *Proc. New Zealand Soc. Anim. Prod.* 36:128.
- Baldwin, R.L., L.J. Koong and M. J. Ulyatt. 1977. A dynamic model of ruminant digestion for evaluation of factors affecting nutritive value. *Agric. Systems* 2:255.

- Bartley, E.E. 1976. Bovine saliva: production and functions
In: M.S. Weinberg and A.L. Sheffner (ed.) Buffers in
Ruminant Physiology and Metabolism. pp 61-81. Church
and Dwight Co. Inc., NY.
- Baumgardt, B.R. 1970 Control of feed intake in the
regulation of energy balance. In: A.T. Phillipson (Ed)
Proc. Third Int. Symp., Physiology of Digestion and
Metabolism in the Ruminant. pp.235-253. Oriel Press,
Newcastle, England.
- Beever, D.E., H.R. Losada, D.L. Gale, M.C. Spooner and M.S.
Dhanao. 1987. The use of monensin or formaldehyde to
control the digestion of the nitrogenous constituents
of perennial ryegrass (*Lolium perenne* cv. Melle) and
white clover (*Trifolium repens* cv. Blanca) in the rumen
of cattle. *Brit. J. Nutr.* 57:57.
- Beever, D.E., D.J. Johnson, M.J. Ulyatt, S.B. Cammell and
M.C. Spooner. 1985. The digestion of fresh perennial
ryegrass (*Lolium perenne* L. cv. Melle) and white clover
(*Trifolium repens* L. cv. Blanca) by growing cattle fed
indoors. *Brit. J. Nutr.* 54:763.
- Beever, D.E., M.S. Dhanoa, H.R. Losada, R.T. Evans, S.B.
Cammell and J. France. 1986. The effect of forage
species and stage of harvest on the processes of
digestion occurring in the rumen of cattle. *Brit. J.
Nutr.* 56:439.
- Beever, D.E., H.R. Losada, S.B. Cammell, R.T. Evans and M.J.
Haines. 1986. Effect of forage species on nutrient
digestion and supply in grazing cattle. *Brit. J. Nutr.*
56:209.
- Bines, J.A. 1971. Metabolic and physical control of food
intake in ruminants. *Proc. Nutr. Soc.* 30:116.
- Black, J.L. 1984. The integration of data for prediction of
feed intake, nutrient requirements and animal
performance. In: F.M.C. Gilchrist and R.I. Mackie (Ed.)
Herbivore Nutrition. pp. 649-671. Science Press,
Craighall.
- Blaxter, K.L., F.W. Wainman, and R.S. Wilson. 1961. The
regulation of food intake by sheep. *Anim. Prod.* 3:51.
- Brorsen, B.W., O.L. Walker, G. W. Horn and T. R. Nelson.
1983. A stocker cattle growth simulation model. *S. J.
Agric. Econ.* 15:115.
- Bywater, A.C. 1984. A generalized model of feed intake and
digestion in lactating cows. *Agric. Systems* 13:167.

- Campling, R.C., M. Freer, and C.C. Balch. 1961. Factors affecting the voluntary intake of cows. 2. The relationship between voluntary intake of roughages, the amount of digesta in the reticulo-rumen and the rate of disappearance of digesta from the alimentary tract. *British J. Nutr.* 15:531.
- Coleman, S.W., O. Neri-Flores, R.J. Allen Jr. and J.E. Moore. 1978. Effect of pelleting and of forage maturity on quality of two sub-tropical forage grasses. *J. Anim. Sci.* 46:1103.
- Conrad, H.R. 1966. Symposium on factors influencing the voluntary intake of herbage by ruminants: Physiological and physical factors limiting feed intake. *J. Anim. Sci.* 25:227.
- Demment, M.W., E.A. Laca, and G.B. Greenwood. 1987. Intake of grazing ruminants: A conceptual framework. In: F.N. Owens (Ed.) *Symposium Proceedings: Feed Intake by Beef Cattle.* pp 138-142. Oklahoma State University, Stillwater.
- Ellis, W.C. 1978. Determinants of grazed forage intake and digestibility. *J. Dairy Sci.* 61:1828.
- Forbes, J.M. 1977a. Development of a model of voluntary food intake and energy balance in lactating cows. *Anim. Prod.* 24:203.
- Forbes, J.M. 1977b. Interrelationships between physical and metabolic control of voluntary food intake in fattening, pregnant and lactating mature sheep: a model. *Anim. Prod.* 24:91.
- Forrester, J.W. 1971. In: *World Dynamics.* Wright Allen Press, Cambridge, Mass.
- France, J. and J.H.M. Thornley. 1984. *Mathematical Models in Agriculture.* Butterworths, London.
- France, J., J.H.M. Thornley and D.E. Beever. 1982. A mathematical model of the rumen. *J. Agric. Sci., Camb.* 99:343.
- France, J., N.R. Brockington and J. E. Newton. 1981. Modeling grazed grassland systems: wether sheep grazing perennial ryegrass. *App. Geography* 133.
- Freer, M. and K.R. Christian. 1983. Application of feeding standards to grazing ruminants. In: G.E. Robards and R.J. Packham (Ed.) *Feed information and animal production.* Commonwealth Agric. Bureau, UK.

- Funk, M.A., M.L. Galyean, M.E. Branine and L.J. Krysl. 1987. Steers grazing blue grama rangeland throughout the growing season. I. Dietary composition, intake, digesta kinetics and ruminal fermentation. *J. Anim. Sci.* 65:1342.
- Grovum, W.L. 1987. A new look at what is controlling feed intake. In: F.N. Owens (Ed.) *Symposium Proceedings: Feed Intake by Beef Cattle*. pp 1-39. Oklahoma State University, Stillwater.
- Guerrero, J.N., H. Wu, E.C. Holt and L.M. Schake. 1984. Kleingrass growth and utilization by growing steers. *Agric. Systems* 13:227.
- Hennessy, D.W. and P.J. Williamson. 1983. The roles of energy or protein rich supplements in the sub tropics for young cattle consuming basal diets that are low in digestible energy and protein. *J. Agric. Sci. (Camb.)* 100:657.
- Horn, G.W. and F.T. McCollum. 1987. Energy supplementation of grazing ruminants. *Symposium Proceedings, Grazing Livestock Nutrition Conference*, pp 125-136. Jackson, Wyoming.
- Hyer, J.C. and J.W. Oltjen. 1987. Evaluation of a dynamic rumen model for prediction of forage intake of grazing ruminants. *Okla. Agr. Exp. Sta. MP-119:243*.
- Hyer, J.C., J.W. Oltjen and M.L. Galyean. 1988. Conceptual basis and description of a mathematical model of feed intake of grazing beef steers. *Proc. West. Sect. Soc. Anim. Sci.* 39:339.
- Innis, G.S. 1975. The use of a systems approach in biological research. In: *Study of Agricultural Systems*. pp 369-391. Ed. G.E. Dalton, Applied Science Publishers Ltd., London.
- Jarrige, R., C. Demarquilly, J.P. Dulphy, A. Hoden, J. Robelin, C. Beranger, Y. Geay, M. Journet, C. Malterre, D. Micol and M. Petit. 1986. The INRA "fill unit" system for predicting the voluntary intake of forage based diets in ruminants: a review. *J. Anim. Sci.* 63:1737.
- Kahn, H.E. and C.R.W. Spedding. 1984. A dynamic model for the simulation of cattle herd production systems:2 An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. *Agric. Systems* 13:63.

- Kennedy, P.M. 1982. Ruminant and intestinal digestion in Brahman crossbred and Hereford cattle fed alfalfa or tropical pasture hay. *J. Anim. Sci.* 55:1190.
- Krysl, L.J., M.L. Galyean, M.B. Judkins, M.E. Branine and R.E. Estell. 1987. Digestive physiology of steers grazing fertilized and non-fertilized blue grama rangeland. *J. Range Manage.* 40:493.
- Lusby, K.S. and D.G. Wagner. 1987. Effects of supplements on feed intake. In: F.N. Owens (Ed.) Symposium Proceedings: Feed Intake by Beef Cattle. pp 173-181, Oklahoma State University, Stillwater.
- McCollum, F.T. and M.L. Galyean. 1985. Cattle grazing blue grama rangeland. II. Seasonal forage intake and digesta kinetics. *J. Range Manage.* 38:543.
- McCollum, F.T., M.L. Galyean, L.J. Krysl and J.D. Wallace. 1985. Cattle grazing blue grama rangeland. I. Seasonal diets and rumen fermentation. *J. Range Manage.* 38:539.
- Miller, W.C., G.M. Ward, T.P. Yorks, D.L. Rossiter and J.J. Combs. 1980. A mathematical model of the United States Beef Production System. *Agric. Systems* 3:147.
- Monteiro, L.S. 1972. The control of appetite in lactating cows. *Anim. Prod.* 14:263.
- Nelder, J. A. and R. Mead. 1965. A simplex method for function minimization. *Comp. J.* 7:308.
- Olson, K.C., R.L. Senft and J.C. Malechek. 1986. A predictive model of cattle ingestive behavior in response to sward characteristics. *Proc. West. Soc. Anim. Sci.* 37:259.
- Oltjen, J.W. 1987. Estimating feed intake of beef cattle: mechanistic model development. In: F.N. Owens (Ed.) Symposium Proceedings: Feed Intake by Beef Cattle. pp 138-142. Oklahoma State University, Stillwater.
- Oltjen, J.W. 1983. A model of beef cattle growth and composition. Ph.D. Dissertation. University of California, Davis.
- Owens, F.N. and A.L. Goetsch. 1986. Digesta passage and microbial protein synthesis. In: L.P. Milligan, W.L. Grovum and A. Dobson (Eds.) Control of Digestion and Metabolism of Ruminants. pp 196-223. Prentice Hall, New Jersey.

- Plegge, S.D. and R.D. Goodrich. 1987. Intake equations for feedlot cattle. In: F.N. Owens (Ed.) Symposium Proceedings: Feed Intake by Beef Cattle. pp 232-237. Oklahoma State University, Stillwater.
- Pond, K.R., J.M. Luginbuhl and J.C. Burns. 1987. Salivation, mastication and rumination--Limits to intake by beef cattle. In: F.N. Owens (Ed.) Symposium Proceedings: Feed Intake by Beef Cattle. pp 160-172. Oklahoma State University, Stillwater.
- Putnam, P.A., R. Lehmann and R.E Davis. 1966. Feed intake and salivary secretion by steers. J. Anim. Sci. 25:817.
- Rice, R.W., J. G. Morris, B.T. Maeda and R. L. Baldwin. 1974. Simulation of animal functions in models of production systems: ruminants on the range. Fed. Proc.33:188.
- Sibbald, A.R., T.J. Maxwell and J. Eadie. 1979. A conceptual approach to the modeling of herbage intake by hill sheep. Agric Systems 4:119.
- Smith, R.C. and W.A. Williams. 1973. Model development for a deferred-grazing system. J. Range Manage. 26:454.
- Spreen, T.H., J.A. Ross, J.W. Pheasant, J.E. Moore and W.E. Kunkle. 1985. A simulation model for backgrounding feeder cattle in Florida. Tech. Bulletin 850. Agric Experiment Station, University of Florida, Gainesville.
- Taylor, St. C.S. 1980. Genetic size-scaling rules in animal growth. Anim. Prod. 30:161.
- Thornley, J.H.M. and J. France. 1984. Role of modeling in animal production research and extension work. In Modeling Ruminant Digestion and Metabolism Ed. R.L. Baldwin and A.C. Bywater, pp 4-9. University of California, Davis.
- Van Soest, P.J. 1982. Nutritional Ecology of the Ruminant. O and B Books, Corvallis Oregon.
- Varga, G.A. and E.C. Prigge. 1982. Influence of forage species and level of intake on ruminal turnover rates. J. Anim. Sci. 55:1498.
- Yarns, D.A., P.A. Putnam and E.C. Leffel. 1965a. Daily salivary secretion by beef steers. J. Anim. Sci. 24:173.

APPENDIX

C THIS IS THE USER PART OF THE PROGRAM
 C THE MODEL OR EQUATION TO BE FIT MUST BE SPECIFIED HERE
 C AIN(1) - AIN(9) ARE INPUTS DESCRIBING THE SIZE OF THE
 C ANIMAL AND THE COMPOSITION OF THE FORAGE.
 C SUPP=SUPPLEMENT, AK(41-47)=ARE INPUTS DESCRIBING THE
 C COMPOSITION OF THE SUPPLEMENT.
 C PP(1-9) ARE PARAMETERS TO FIND (MAY BE FIXED)
 C Y(1)=RUMEN FILL; 96.225.
 C FLAG =-1 WHEN ON LAST ITERATION TO PLOT FILE
 C MODEL

C*****

DMIA=PP(1)
 SUPP=PP(2)
 BW=AIN(1)
 DMIA=AIN(2)
 DMI=DMIA + SUPP
 DAH=AIN(3)/100.0
 DNBH=AIN(4)/100.0
 DBH=AIN(5)/100.0
 DNPB=AIN(6)/100.0
 DNPROT=AIN(7)/100.0
 DPROT=AIN(8)/100.0
 DWSC=AIN(9)/100.0
 DAH=DMIA*DAH + SUPP*AK(41)
 DNBH =DMIA*DNBH + SUPP*AK(42)
 DBH=DMIA*DBH + SUPP*AK(43)
 DNPB=DMIA*DNPB + SUPP*AK(44)
 DNPROT=DMIA*DNPROT + SUPP*AK(45)
 DPROT=DMIA*DPROT + SUPP*AK(46)
 DWSC=DMIA*DWSC + SUPP*AK(47)
 IFT=3.0
 DT=.02
 ASF=10.0
 NPROT=5.0625
 NBH=14.02084
 WSC=.41667
 BH=9.33333
 AH=.56250
 PROT=2.54167
 NPB=4.1250
 BUG=20.90477
 KAH=(ASF**(-.27))* .40650
 KBH=(ASF**(-.27))* .46015
 KC=.26388
 KCN=0
 KN=0
 KC=.5164037 - .1010099*KN
 KPROT=(ASF**(-.27))* .26201
 KU=.46675
 LM=.552772 + 1.234215*KU
 MC=.30
 MN=.38019
 UM=(ASF**(-.27))*5.0
 YM=.10

```

RV=ASF*7.5*(BW/(75.0*ASF))
BK1=.550
BKL1=.47952
BK0=1.0-BK1
BKL0=1.0-BKL1
KP=.04
PPR=.04*ASF**(-.27)*(BK0+BK1*DMI/((BW/(ASF*75.0))
!      *1500.0*ASF**.73))
KL=.10
LPR=.10*ASF**(-.27)*(BKL0+BKL1*DMI/((BW/(ASF*
!      75.0))*1500.0*ASF**.73))
V=LPR*24*RV
SV=V*.74233
DV=V-SV
SNPN=SV*.50
SPROT=SV*1.0
PBUG=.50
IEND=1/DT
DO 870 IT=1,IFT
DO 870 ITT=1,IEND
U=UM/(1+KC/WSC+KN/NPN+KCN/(WSC*NPN))
L=LM*ASF**(-.27)/(1+KU*U*ASF**(.27))
XRV=DV+SV-V
XNBH=(DNBH-NBH*PPR*24*RV)/RV
XNPROT=(DNPROT-NPROT*PPR*24*RV)/RV
XBUG=BUG*U-BUG*L-PBUG*BUG*(DV+SV)/RV-(1-
!      PBUG)*PPR*24*BUG*RV/RV
XAH=(DAH-AH*PPR*24*RV)/RV-KAH*AH*BUG
XBH=(DBH-BH*PPR*24*RV)/RV-KBH*BH*BUG
XPROT=(DPROT+SPROT-PROT*PPR*24*RV)/RV-KPROT*PROT*BUG
XNPN=((DNPN+SNPN-NPN*DV-NPN*SV)/RV)+(MN*BUG*L)-
!      (MN*BUG*U)+(KPROT*PROT*BUG)
XWSC=(DWSC-WSC*DV-WSC*SV)/RV+MC*BUG*L-
!      MC*BUG*U/YM+BUG*KAH*AH+BUG*KBH*BH
RV=RV+DT*XRV
NBH=NBH+DT*XNBH
NPROT=NPROT+DT*XNPROT
BUG=BUG+DT*XBUG
AH=AH+DT*XAH
BH=BH+DT*XBH
PROT=PROT+DT*XPROT
NPN=NPN+DT*XNPN
WSC=WSC+DT*XWSC
870      CONTINUE
OTBH=RV*PPR*24*NBH+RV*PPR*24*BH
OTPROT=RV*PPR*24*PROT+RV*PPR*24*DPROT
OBUG=V*BUG*PBUG+(1-PBUG)*PPR*24*RV*BUG
OAH=PPR*24*RV*AH
ONPN=V*NPN
OWSC=V*WSC
DOM=DAH+DBH+DNBH+DWSC+(SPROT+DPROT+DNPROT)
OOM=OAH+OBCHO+OTPROT+OWSC
OMTFR=(DOM-OOM)
EFF=(OBUG*.08/OMTFR)*1000

```

```
      BYPASS=(OTPROT*100)/(DPROT+DNPROT)
      RF=(NBH+NPROT+BUG+AH+BH+PROT+NPN+WSC)
      FLOW=(OBCHO+OTPROT+OBUG+ONPN+OWSC+OAH)
      IF (FLAG.GT.-.5) GOTO 900
      WRITE(1,897)
      WRITE(1,898)
897  FORMAT(' NBH,BH,PROT,NPROT,NPN,WSC,AH,BUG,DMIA')
898  FORMAT(' OTBH,OTPROT,OBUG,ONPN,OWSC,OAH,V,RV,LPR,PPR')
      WRITE(1,*)NBH,BH,PROT,NPROT,NPN,WSC,AH,BUG,DMIA,
      !      OTBH,OTPROT,OBUG,ONPN,OWSC,OAH,V,RV,LPR,PPR
900  CONTINUE
      Y(1)=RF
C*****
C      END OF MODEL
      RETURN
      END
```

VITA

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Master of Science

Thesis: DEVELOPMENT AND EVALUATION OF A MATHEMATICAL MODEL
TO PREDICT FORAGE INTAKE AND ACCOUNT FOR
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