TISSUE PROTEIN AND ENERGY DEPOSITION IN STEERS FED
DIETS WITH DIFFERENT UREA FERMENTATION POTENTIALS (UFP)

BY

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with thee i have lingered once again,
asked and begged and pleaded, cried and wept
for what i have and can not have.
you must think me, an open-hearted fool,
settling for the comfort and confusion in your smile.
so thee i love, before long i die.

thee

innocence
jeanne
joseph
andrew
jeffrey

dying
jill
anita

inquisitive
jamey
jan
jane
john
joanne
robert
susan

independence
david

athletic
o. william
james
kathleen dawn
catherine

disconcertive
melanie lynn
alice
kathleen pinckney
paul
steven

probing
candace
guiomar

cultural
humberto
ligia

artistic
clarita

pragmatic
elizabeth
maria ines
polixsene

commencement
stacy

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Abstract of Dissertation Presented to the Graduate Council
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DIETS WITH DIFFERENT UREA FERMENTATION POTENTIALS (UFP)

By

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A 5 x 5 Latin square metabolism trial and a comparative slaughter feedlot trial were conducted with 85 British type steers to evaluate diets with various urea fermentation potentials (UFP). With increasing dietary nitrogen, UFP values were calculated to be +3.8, +1.2, -1.4, -3.9 and -6.9 g urea per kg diet. The dietary metabolizable protein (MP) levels were determined to be 69.2, 76.6, 80.1, 80.8 and 80.0 g per kg diet, respectively. Crude protein digestibility increased with decreasing UFP values ($P < .005$), but TDN, DE and ME showed no significant relationship to variation in UFP. While NE_m was not significantly related to UFP, feed efficiency improved and NE_g increased logarithmically ($P < .05$) with decreasing dietary UFP levels. Average daily gain, DM intake, ME intake and energy balance were parabolically related ($P < .005$) to dietary UFP levels. Optimal feedlot performance

and energy utilization were observed at -1.4 to -3.9 UFP, which corresponded to maximum dietary MP concentration. Carcass specific gravity was utilized to determine empty body fat and protein. Daily gains in empty body weight, fat and energy were parabolically related ($P < .001$) to dietary UFP levels. Optimal empty body gains were also observed to occur between -1.4 and -3.9 UFP levels. Empty body protein gain per day increased logarithmically ($P < .05$) with decreasing dietary UFP levels. Carcass characteristics followed similar parabolic patterns with changes in dietary UFP. Their respective maxima and minima suggested that an increased degree of carcass finish occurred with increased dietary MP concentration. While the MP system has merit with respect to predicting animal performance, it overestimated NP_g available for protein gained in tissues over the 119-126 day feedlot trial. While predicted NP_g ranged from 196 to 283 g per day, observed tissue protein gains ranged from 62 to 109. This suggested that only about one third of the predicted NP_g was actually deposited in tissues.

CHAPTER ONE INTRODUCTION

While Florida is a high inventory state in total beef cattle population, the number of animals finished within the state is much less than the demands of the consumer. Over 80% of the beef consumed in Florida is finished out of state. The successful establishment of an adequate Florida feedlot industry will depend on development of efficient marketing, slaughter and feedlot facilities. An efficient feedlot operation is contingent on proper evaluation of local feed ingredients. Typical feedlot rations are rich in energy with the proper balance of nitrogen to optimize utilization. While the grains of Northern Florida are productive, due to lower digestibility they may not have the nutritive quality of midwestern grains. Nutrient levels in common feedstuffs given for meeting the requirements of beef cattle (NRC, 1976; Church, 1980) may led to underestimation when Florida grown feedstuffs are fed. Studies by Maxson et al. (1973) and Brommelsiek et al. (1979) demonstrated that typical Florida grains do not have the nutrient availability suggested by comparable feedstuffs listed by the NRC (1971a).

Energy and nitrogen are principle nutrients in feedlot diets. Understanding the nitrogen to energy relationship is essential for optimal ration formulation. Microbial fermentation in ruminants, which precedes mammalian digestion and metabolism, complicates the

nitrogen to energy relationship. Understanding the nitrogen to energy balance should enhance maximum substitution of dietary non-protein-nitrogen sources for more expensive natural protein ingredients.

The feedlot industry has accepted the California net energy system (Lofgreen and Garrett, 1968) to predict liveweight gains. However, net protein as a dietary guideline has been evaluated in a very limited manner. Burroughs et al. (1975b) proposed the metabolizable protein (MP) system to predict the net protein available for maintenance and production. The quantity of MP available to the animal is a function of the amount of rumen microbial protein synthesis from ammonia and energy and the amount of natural protein that resists rumen degradation and bypasses to the abomasum. Under the MP system, corn grain has approximately 72 g MP per kg when fed to cattle. Corn grain also has sufficient excess energy for rumen bacteria to generate an additional 26 g MP, if 12 g urea per kg corn are added to the diet. To evaluate this addition of non-protein-nitrogen to the diet, Burroughs et al. (1975b) developed the urea fermentation potential (UFP). UFP is expressed as the grams of urea equivalent in terms of excess energy (positive) or excess nitrogen (negative) per kg dry matter. Positive UFP values represent dietary energy excesses from which additional MP may be synthesized if urea or other nitrogen sources are added to the diet. Burroughs et al. (1975b) determined UFP values for approximately 90 common feedstuffs. UFP values are determined from the total digestible nutrients and crude protein composition of the ration. The MP system and UFP values have not been evaluated with regard to net protein tissue gains using feedlot cattle nor with respect to the proper nitrogen to energy balance using Florida feedstuffs.

The present study was designed to test the nitrogen to energy balance in feedlot diets using the UFP and MP system. A metabolism trial and comparative slaughter feedlot trial were utilized to test feedlot performance and carcass characteristics for isocaloric rations. Rations varying in UFP and MP were fed to steers to determine if MP generated by excess energy plus additional urea could be detected by increased carcass protein using specific gravity determinations. The addition of urea to high energy feedlot rations was observed for its effect on net energies for maintenance (NE_m) and gain (NE_g). Data were also obtained for the dietary nitrogen to energy relationship with regard to feedlot performance, quality of edible meat and empty body tissue gains.

CHAPTER TWO LITERATURE REVIEW

Energy

Energy, the principal dietary constituent, generally represents between 70 and 90% of the daily dry matter intake. Historically, energy nutrition and general animal nutrition developed concurrently. About 1777, the first animal calorimeter was constructed by the French chemist, Antoine Lavoisier (Maynard and Loosli, 1969). The work of the German physician, Julius Mayer, and the English brewer, James Joule, led to the formulation of the First Law of Thermodynamics, that energy is neither created or destroyed. Mayer reportedly (Moore, 1972) conceived the idea of the conservation of energy and matter from the observation that oxidation of nutrients in the animal body produced heat and work. While the proportions of heat and work might differ for the same quantity of food combusted in the animal body, their sum should be constant. An alternative approach, made by the French engineer, Sadi Carnot (Moore, 1972; Brody, 1974), arrived at the theoretical maximum efficiency of an ideal engine. Carnot devised a cycle, in complete accordance with the First Law of Thermodynamics, which gave a precise model for the conversion of heat into work with the system returning to an isothermal state through a series of reversible steps.

While the First Law of Thermodynamics could express a theoretical maximum efficiency for the conversion of heat into work, it was obvious that theoretical perpetual motion, consistent with the principle of conservation of energy and matter, had never been observed. The subsequent development of the concept of entropy and its relation to free energy, were directly related to the formulation of the Second Law of Thermodynamics, that there is an energy loss in the transformation of heat to work. The initial expressions of the Second Law of Thermodynamics dealt with the impossibility of constructing the theoretically ideal engine, as described by Carnot in 1924 (Moore, 1972). Thomson used the Second Law to define a thermodynamic temperature scale (Kelvin). Clausius introduced the concept of entropy (S), which gives the directional nature to the physical and chemical changes that are unaccounted for by the First Law of Thermodynamics (Lehninger, 1971). Summarizing, the First Law confirms that, although energy must be conserved, it can be transformed into work. The Second Law further stipulates that this total energy can be divided into two fractions, that which is available for work (free energy) and that which gives direction to physical and biological processes (entropy).

A consequence of the Laws of Thermodynamics is that the change in energy in a system is dependent upon the initial and final stages, independent of the energy path between these states (Brody, 1974; Moore, 1972). For isothermal conditions, J. Willard Gibbs derived his classical relation associating free energy (G), free enthalpy (H), and entropy (S), for a process changing from one state to another

(Moore, 1972):

$$\Delta G = \Delta H - T \Delta S.$$

ΔG [or ΔF , which is conventionally used for biochemical reactions, (Lehninger, 1971)] is the maximal free energy which is theoretically capable of being transformed into work under conditions of constant pressure and temperature. ΔH represents the change in enthalpy or heat content of the process and is the total energy available for a biochemical process. T is the constant temperature in degrees Kelvin, and ΔS , or change in entropy, is that portion of the total energy (ΔH) which directs biochemical processes towards randomness and is thus unavailable for work.

Brody (1974) and Blaxter (1962) pointed out similarities between the concepts of thermodynamics and net energy. Since animals are homeothermic and conform to the Laws of Conservation of Energy and Matter, then it is not surprising that the concept of net energy (Armsby, 1910) adheres to the principle of Gibbs free energy. In this comparison, metabolizable energy (ME) represents the total energy available to animals. In nutritional terms, ME is analogous to the ΔH of biochemical reactions. Given this premise, that portion of the total energy not convertible to work ($T\Delta S$) is nutritionally analogous to heat increment or specific dynamic action (SDA). Finally, it is seen that the portion of the total available energy which is capable of doing work (ΔG) may nutritionally be considered to be the net energy (NE). Thus, the Gibbs free energy equation,

$$\Delta G = \Delta H - T \Delta S$$

is seen to be analogous to

$$NE = ME - SDA.$$

This analogue is made with the realization that it is dependent upon the initial and final states of the process. While these states may be readily definable for a series of biochemical reactions, the numerous metabolic processes of even the simplest organism make it possible to estimate only the initial and final states. The NE represents maximum utilizable energy, but no reference is given to level of production or to factors which can affect the efficiency of this partitioning.

Rubner (Kriss, 1943) postulated that the SDA was a composite, waste energy effect derived from numerous oxidations and side reactions occurring in intermediate metabolism. Since the evolved heat of biochemical processes is a function of the initial and final states and is independent of the path between these states, Swift and French (1954) concluded that the potential energy of ingested food must be conserved in the potential energies of the excreta, stored body tissues and heat production. The term heat increment (HI) has become synonymous with SDA. However, SDA, as it was originally derived from Rubner's theory of isodynamic replacement (Armsby, 1910), refers only to the heat of nutrient metabolism (HNM). Isodynamic replacement was probably the first systematic attempt to address the problems of animal nutrition to the Laws of Thermodynamics. Derived from Rubner's work with dogs, it postulated, below maintenance, that nutrients replaced each other in a ration inversely proportional to their ME values. As Armsby (1910) and later Kromann (1973) pointed out, HI, as it can be experimentally determined, is a combination of HNM and

the heat of fermentation (HF). Although, in a true energy scheme, HF would be considered a digestion loss, it is impossible to experimentally separate HF from HNM. Thus, the commonly determined HI, as does ME, contains not only the SDA but the HF, as well.

Even though Armsby (1910) pointed out this discrepancy in Rubner's isodynamic replacement theory, he continued to determine NE values below maintenance. To Armsby (1917) the NE of a feed or nutrient was a measure of the feedstuff's ability to diminish the observed energy loss caused by feeding below maintenance. Developing the first large animal calorimeter, Armsby and Fries (1915, 1918) derived the first NE feeding system for cattle. Basically their approach was to determine basal catabolism and NE values for maintenance by comparing the heat production (HP) at two different, sequential submaintenance levels of intake. This procedure is based on the logic that, above the lower critical temperature, the consumption of feed increases HP proportional to intake (Armsby 1910, 1917). Assuming that the animal is above the lower critical temperature, the HP, in addition to HI, includes the heat produced in the various metabolic processes necessary to maintain life. This is that portion of the NE required for maintenance (NE_m). With this general concept of HP, the NE values of Armsby were based on the assumption that the utilization of ME was of equal efficiency (linear) above and below maintenance (Forbes et al., 1927). Earlier, Forbes et al. (1926a) showed that the computing of HP with above maintenance levels of feed intake consistently lead to lower estimates of fasting catabolism than with submaintenance intake levels. With dairy cows, Forbes et al. (1926b) demonstrated that the greatest efficiency

of utilization of feed energy was for maintenance, followed by milk production and body weight gain, respectively. Instead of proposing that HP be estimated by extrapolating above maintenance levels of intake, Forbes et al. (1927) concluded that HP should be estimated from observed HP during fasting. This HP estimate was less variable and significantly lower than that determined with above maintenance feed intake levels. This observation led Forbes et al. (1928) to conclude that the relation between HP and intake was not linear and that energy was more efficiently utilized for maintenance than for gain.

This conclusion gave impetus to the division of NE into values for maintenance (NE_m) and for production (NE_p). Summarizing the data of Forbes et al. (1928, 1930) and his own, Marston (1948) demonstrated that when HP and available energy intake were reduced by the parameter of weight in kilograms raised to the 0.73 power (Brody, 1974), the relation between them was essentially linear for above maintenance levels of intake. If the relation between HP and ME intake (MEI) is linear above maintenance and animals conform to the Law of Conservation of Energy (Blaxter, 1962; Brody, 1974; Kleiber, 1961), then the observation, that beef cattle have a linear relation between energy gain and available energy intake above maintenance, is in agreement with thermodynamic principles (Garrett et al., 1964). Due to these observations, Lofgreen and Garrett (1968) concluded that NE_g of cattle is linear and independent of level of feeding above maintenance (Garrett et al., 1959a, b).

Below maintenance there is general agreement that HP is not linearly related to MEI (Armsby, 1910; Forbes et al., 1928, 1930;

Garrett et al., 1959b; Garrett, 1971; Moe et al., 1971, 1972).

Marston (1948) found this discrepancy consistent with the principles of thermodynamics. Forbes et al. (1926a) observed that a linear extrapolation of HP versus intake always resulted in a lower HP intercept than experimentally determined HP values. Marston (1948) postulated that such an extrapolation would represent the animal's true basal energy requirement, which would be equivalent to the true NE_m . The difference between this true basal energy requirement and the observed basal energy requirement would be accounted for by sub-maintenance catabolism of animal tissue. Accordingly Marston (1948) reasoned that the augmentation of HP, at below maintenance feed intake, is due to heat of catabolism of animal tissue and should not be included in the true basal energy requirement. The distinction, between using a linear or a curvilinear model to describe the relation between HP and MEI, is more dependent upon the interpretation of the definition of maintenance than upon the interpretation of experimental results (Flatt et al., 1965; Moe and Tyrrell, 1973). In the NE system proposed for dairy cows (NRC, 1971b, 1978; Moe et al., 1972), the maintenance and production requirement are expressed in an equivalent linear relation.

Blaxter (1962, 1969) developed a ME system in accordance with the postulation that the efficiency of energy utilization for maintenance exceeds that for production with beef cattle (Forbes et al., 1926b; Kleiber, 1961). In this ME system (ARC, 1965), ME has different partial efficiencies for maintenance (K_m) and for fattening (K_f). The ME for maintenance (ME_m) needs are based on fasting meta-

bolism. This is equivalent to using the observed HP for determining the maintenance requirement. K_m , the efficiency of ME utilization for maintenance, is expressed as:

$$K_m = 54.6 + 0.30 Q_m.$$

Q_m represents the percent of dietary MEI of the gross energy intake (GEI) at maintenance. The daily fasting energy expenditure (E) is calculated from the expression:

$$E = 0.077 \text{ Mcal/W}_{\text{kg}}^{0.75}.$$

Thus, the ME_m is a measure of the fasting energy required and efficiency of ME for maintenance:

$$ME_m = E/K_m.$$

The efficiency of ME for fattening (K_f) is also expressed as a function of Q_m :

$$K_f = 0.81 Q_m + 3.0.$$

From the average daily gain (ADG), K_f and ME_g , the proportion of ME for gain per amount of dietary energy can be determined:

$$\frac{\text{Mcal ME}}{\text{kg diet}} = \frac{K_f (ME_g)}{\text{ADG}}.$$

The NE system for beef cattle, recommended by the NRC (1970, 1976), was presented in its definitive form by Lofgreen and Garrett (1968). This system has commonly been referred to as the California net energy system (CNES), due to the extensive work done at the University of California at Davis (Garrett et al., 1959b, 1964; Lofgreen et al., 1962, 1963; Lofgreen, 1965a, b; Lofgreen and Garrett, 1968; Lofgreen and Otagaki, 1960). It was demonstrated by Garrett et al. (1959b, 1964) and Lofgreen et al. (1963) that the partial effi-

ciency of net energy for body weight gain (NE_g) was linearly related to intake when cattle were fed between maintenance and ad libitum levels. In the CNES, NE requirement is dependent upon two main factors: animal size and animal production (or level of intake). Using these factors, NE is expressed separately as the partial net energy for maintenance (NE_m) and the partial net energy for gain (NE_g). NE_m and NE_g are expressed separately, because they are more accurate and less variable, particularly with varying levels of intake, than a combined NE_{m+g} term.

The determination of NE_m and NE_g involves two experimental phases: a metabolism trial and a feedlot trial. The metabolism trial is used to determine metabolizable energy (ME) by

$$ME = GE - (\text{energy lost in feces, urine, fermentation}).$$

In practice, these values are obtained using bomb calorimetric values of the feed (GE), feces and urine. The energy lost in fermentation, as CH_4 gas, is usually estimated from the equation of Bratzler and Forbes (1940);

$$E = 4.012\chi + 17.68.$$

In this equation, χ represents 10^{-2} times the grams of carbohydrate digested, which yields E grams of methane (CH_4) produced. Each gram of CH_4 represents a loss of 13.2 kcal.

In a feedlot trial, a comparative slaughter technique (Lofgreen and Otagaki, 1960) is used to determine the amount of energy accumulated as fat and protein during the feeding period. Lofgreen and Otagaki (1960) demonstrated that NE_m is constant with respect to metabolic body weight ($W_{kg}^{0.75}$) and that the fat and protein deposited by

the animal represents the energy retained for calculation of NE_g . Reviewing methods of estimating HP, Blaxter (1962) concluded that the comparative slaughter technique was the only acceptable alternative to the costly and laborious methods of direct and indirect large animal calorimetry.

The accuracy of the comparative slaughter technique is primarily dependent upon the estimate of carcass composition. While ideally a complete carcass dissection and composition analysis would be a definitive measure, the laborious nature of this task places it out of the realm of practicality. Therefore, alternative carcass composition methods have been used. Initially, Lofgreen and Garrett (1968) utilized equations from Kraybill et al. (1952) and Reid et al. (1955) to estimate fat and protein composition by carcass specific gravity and body water by an antipyrine dilution technique (Garrett et al., 1959; Whiting et al., 1960). However, serious objections were raised concerning the accuracy of this technique (Reid and Robb, 1971). In 1969, Garrett and Hinman developed regression equations from actual chemical determinations of ether extract, water, nitrogen and energy in the carcass and empty body in relation to carcass specific gravity. These equations, utilizing carcass specific gravity, enable the direct estimation of fat (ether extract), protein (nitrogen) and energy. Although criticism has been raised of the methods used to estimate empty body composition by the CNES (Reid and Robb, 1971; Knox and Handley, 1973), it is not imperative to the NE concept that any particular method be used to estimate composition. Other procedures have also been used. Hankins and Howe (1946) developed a 9-10-11

rib estimation technique for determining carcass composition. Powell et al. (1971) proposed the use of multiple regression equations, using fat thickness over the 12th rib, ribeye area, percent kidney-heart fat and hot carcass weight, to estimate energy gain. These two techniques are based on physical separation of the lean and fat in the carcass, while Garrett and Hinman (1969) actually analyzed the entire carcass for ether extract and nitrogen and based their equations on this more sound basis.

Using the comparative slaughter feedlot trial and the metabolism trial to determine MEI and energy accumulation in the tissue, Lofgreen and Garrett (1968) have estimated HP from the expression:

$$HP = MEI - EB.$$

EB is the energy balance in accordance with the conservation of energy. If this is compared with the equation:

$$NE = ME - SDA,$$

it is seen that at maintenance ($EB = 0$), HP is equal to MEI, and

$$MEI = NE_m + SDA.$$

It is surprising from these concepts, that Lofgreen and Garrett (1968) arrived at a curvilinear model to express the relation between HP and MEI. While it is true that the curvilinear model better fits their data (Garrett et al., 1959b; Lofgreen and Garrett, 1968), this may be due to the curvilinear nature of the relation between HP and MEI below maintenance (Armsby, 1910; Forbes et al., 1928, 1930; Marston, 1948). One of the primary criticisms of the CNES is that the slight advantage in data fit gained by the curvilinear model is unjustified (Knox and Handley, 1973; Reid and Robb, 1971). Nevertheless, Lofgreen and

Garrett (1968) chose a curvilinear model to explain the relation between HP and MEI:

$$\log \text{HP} = 1.8851 + 0.00166 \text{ MEI}.$$

The HP and MEI are expressed in kcal per kg metabolic body weight ($W_{\text{kg}}^{0.75}$). The value 1.8851 represents the log HP of a fasting animal (MEI = 0) and corresponds to a basal HP of 77 kcal/ $W_{\text{kg}}^{0.75}$. Blaxter (1962) utilized the same basic value for his ME system.

Lofgreen and Garrett (1968) used both maintenance and ad libitum intake levels from which the basal HP is derived by extrapolation to zero MEI. This value would represent the HP for the NE_m and would logically be constant per unit metabolic weight (Marston, 1948). Numerous studies have been conducted in which the basal HP fell within the narrow range of 70 to 82 kcal/ $W_{\text{kg}}^{0.75}$ (Brommelsiek, 1977; Harris, 1981; Kleiber, 1961; Knox and Handley, 1973; Lofgreen et al., 1963; Maxson, 1973; Richter, 1977). The NRC (1970, 1976) has accepted the value of 77 kcal/ $W_{\text{kg}}^{0.75}$ for NE_m determinations.

The mean daily MEI is determined experimentally by the CNES. Then from the relation between log HP and MEI, an equilibrium point is obtained. This is the point where MEI is equal to HP. It is at this point that energy balance is equal to zero and the value of MEI represents the energy necessary for maintenance of physical activity and basal metabolic activity. By means of the ration's ME, the DMI necessary for energy equilibrium may be determined:

$$\text{DMI} = \text{MEI} / \text{ME of ration}.$$

And the NE_m may be determined for the ration:

$$\text{NE}_m = 77 / \text{DMI}.$$

The NE_g is calculated from the energy retained (EB above maintenance) and the DMI above that which is required for maintenance of energy equilibrium:

$$NE_g = \frac{EB \text{ (above maintenance)}}{\text{Total DMI} - \text{DMI at energy equilibrium}} .$$

Nitrogen and Energy

Ammonia, amino acids and peptides represent the extracellular nitrogenous sources available for microbial protein synthesis. Of these, ammonia is the primary nitrogenous substrate for microbial cells (Bryant and Robinson, 1962; Nolan, 1975). Ammonia is of such importance that in 1963 Hendericks and Martin (Hungate, 1966) observed a correlation between protein solubility and the extent of protein digestion in the rumen. However, as pointed out by Satter (1978) and MacGregor et al. (1978), this correlation is misleading because it suggests that solubility and digestion are synonymous. Nevertheless, rumen ammonia levels function as an important regulator in the incorporation of dietary nitrogenous sources into microbial protein (Hungate, 1966; Bryant, 1977). In 1963, Bloomfield et al. observed that some rumen bacteria will utilize ammonia as the sole nitrogen source, and other strains require ammonia for growth. Ammonia is the key metabolic intermediate in rumen fermentation through which dietary protein and non-protein-nitrogen (NPN) sources serve as microbial nitrogen sources. Stangel (1967) reported that in the the early 1900's Morgan and coworkers demonstrated that up to 40% of the dietary protein in sheep could be replaced by urea. Satisfactory gains by heifers consuming dietary urea supple-

mentation were reported by Hart et al. (1939). In a classical study, Loosli et al. (1949) demonstrated that sheep could maintain a positive nitrogen balance on purified diets containing urea as the sole nitrogen source. These authors found that all essential amino acids were synthesized in the rumen of the sheep.

It is well established that ruminants are capable of utilizing urea as a dietary nitrogenous source. Urea is synthesized from ammonia in the liver of ureotelic animals via the urea cycle (Lehninger, 1975). The ammonia arises from the digestive tract and enters the liver by way of the hepatic portal vein. The urea, formed in the liver, is either excreted through the renal system, or recycled to the alimentary canal. Recycling has been shown to occur either through the rumen epithelium (Houpt, 1959; Houpt and Houpt, 1968) or in the saliva (Houpt, 1959; Somers, 1961a, b, c, d). Houpt (1959) found that roughly half the urea injected into sheep, fed a low protein diet, was not recovered in the urine nor found in other body fluids. It was concluded that the urea served as a microbial protein source and that urea was recycled primarily through the rumen wall. Bloomfield et al. (196)) observed that urea was readily hydrolyzed by bacterial urease. The urease is found in close association with the rumen epithelium. The rapid rate of urea hydrolysis, to ammonia and carbon dioxide, has been implicated as a major problem in the efficiency of urea utilization for microbial protein synthesis (Chalupa, 1968). Bloomfield et al. (1960) found that urea was hydrolyzed at a rate of 80 mg urea nitrogen per 100 ml rumen fluid per hour. Under low dietary energy conditions, this could represent

a four-fold greater rate of ammonia production than rate utilization by rumen microbes. This is consistent with the knowledge that it is essentially the nitrogen to energy balance in the rumen which controls the growth rate of microorganisms.

The readily hydrolyzable nature of urea may account for its toxicity problem and its effect on feed intake reduction. Urea toxicity has been studied by Repp et al. (1955) and Word et al. (1969). These authors concluded that toxicity generally resulted from ingestion of large quantities of urea during a short period to time. Diets which are low in natural protein and high in available energy, benefit most from urea addition. If the dietary nitrogen to energy balance is properly considered and unadjusted animals are gradually adapted to urea over a period of two or three weeks, then problems with urea toxicity are avoided (Davis and Roberts, 1959). Even if the urea is properly balanced, it has been demonstrated to have a depressing effect upon feed intake (Bowstead et al., 1948; Byers et al., 1955; Loosli et al., 1958). Van Horn et al. (1967) observed that as little as 1.9% urea added to concentrates depressed the intake of these concentrates in dairy cows. The nitrogen to energy balance was not maintained in their urea substitution.

Since ammonia absorbed from the rumen is dependent both upon its concentration and rumen pH (Bloomfield et al., 1963; Hogan, 1961), it follows that dietary energy content and frequency of feeding have important roles in regulating microbial growth rate. Knight and Owens (1973) observed that slow release of ammonia improved its utilization. The release of ammonia from urea is dependent upon the

quantity of urea in the diet. Caffrey et al. (1967) observed that the rate of urea hydrolysis was more rapid in rumen fluid from sheep receiving a diet without urea than in rumen fluid from sheep adapted to a diet containing urea. These authors concluded that adaptation to diets containing urea was more a matter of adjustment to urea ammonia utilization than an adaptation to detrimental effects of urea.

One of the earliest attempts to quantify the biological value of protein was the protein efficiency measure proposed by Osborne et al. (1919). Their protein efficiency value was the body weight gain per unit of protein intake. Though this measure had some relative merit, it was criticized both practically and theoretically. Practically, Hegsted and Worcester (1947) demonstrated that protein efficiency was directly correlated to body weight gain and was no real improvement over body weight gain as an indicatory protein value. Theoretically, Mitchell (1924, 1943) criticized protein efficiency evaluation on the basis that the composition of body weight gain is too highly variable and that no consideration is given to maintenance protein requirements. When considering diets of similar composition in rats, Harte et al. (1948) concluded that body weight gain was essentially a function of caloric intake.

Bosshardt et al. (1946) observed that restriction of caloric intake resulted in an increased excretion of urinary nitrogen. Lusk (1928) reported that increasing carbohydrate intake gave a sparing effect on urinary nitrogen excretion. This effect was probably due to increased protein nitrogen utilization in the presence

of higher caloric intake. Bosshardt et al. (1946), studying mice and rats, observed that the level of maximum protein utilization corresponded to the level of maximum caloric intake per unit body surface area. These authors observed that, when percentage of absorbed protein utilized for body gain was plotted against grams protein absorbed, and when daily caloric intake per gram body weight raised to the two-thirds power was plotted against grams protein absorbed, the maxima of both curves occurred at the same quantity of absorbed protein. Both protein utilization and caloric intake decreased on either side of the maxima. Sibbald et al. (1956) postulated, there is an optimal DE level for each nitrogen level of a ration. These results indicate that there is an optimal nitrogen to energy balance or that at all levels of protein intake, there is better growth utilization of protein, if the non-protein caloric intake is increased.

In ruminant metabolism, the microbial population serves as a primary source of protein (Purser, 1970). Microbial protein synthesis requires sources of nitrogen, carbon skeletons, minerals, vitamins and energy (Hungate, 1966). The rumen microbial population has the capacity to synthesize the necessary alpha-keto acids to a large extent from carbon dioxide and to synthesize all its essential vitamins. The microbial population can utilize ammonia for its protein nitrogen source (Bryant, 1977).

Rumen anaerobic fermentation of carbohydrates generates chemical energy in the form of adenosine triphosphate (ATP) upon which the microorganisms depend for cell synthesis and growth. Baldwin (1965)

and Hungate (1966) summarized the known metabolic pathways of rumen carbohydrate fermentation (figure 1). Acetate, propionate, butyrate, CO_2 and CH_4 are the general end products of rumen microbial fermentation. Stoichiometrically, Hungate (1966) calculated that from the ratio of end products formed, four to five moles of ATP per mole of hexose fermented would be expected. Owens and Isaacson (1977) determined that, dependent upon the proportional distribution of end products, between 3.6 and 5.6 moles of ATP would be produced per mole of hexose fermented. While the majority of these pathways are fairly well established, the mechanisms of methanogenesis and propionatogenesis have not been completely determined (Wolin, 1975).

Hungate (1966) suggested that rumen methanogenesis was a means of hydrogen disposal, which would increase overall ATP production. Methanogenesis permits other substrates to remain unhydrogenated and thus available for increased ATP production. Wolin (1975) observed that rumen methanogens exist at an extremely low partial pressure of H_2 (about 3×10^{-4} atm.). The low partial pressure would induce the formation of H_2 , particularly from $\text{NADH} + \text{H}^+$. This would in part account for the oxidation of the extensive quantities of reduced nicotinamide produced during fermentation. Acetate, H_2 and CO_2 are produced as end products by fermentative bacteria (Bryant, 1979). The methanogenic bacteria have a very high affinity for H_2 utilization in methane production (Hungate, 1967; Hungate et al., 1970). Although the mechanism of ATP formation has not been determined for methanogens, analysis has indi-

Figure 1. General pathways of rumen carbohydrate fermentation. Underscored compounds are those which accumulate as products. Diagram adapted from Hungate (1966).

cated that they have at least three coenzymes unique to the energy metabolism of methanogenesis (Bryant, 1979).

The formation of propionate from pyruvate occurs by two different metabolic pathways. The proportion of propionate formed by the acrylate pathway, via lactate, increases as the proportion of readily fermentable carbohydrate increases in the diet. If feedlot diets are improperly managed, increasing lactic acid production can lead to acidosis, founder and laminitis (Church, 1976).

Stoichiometrically, the formation of propionate, via acrylate instead of succinate, represents an energy loss to microbial growth. Studying propionate formation by the succinate pathway, Hobson and Summers (1967) observed higher microbial growth yields per mole of ATP generated than would have been anticipated from currently accepted ATP yields. Hobson and Summers (1972) postulated a flavoprotein- and nicotinamide-linked energy transfer which accounted for the generation of an additional ATP in the formation of propionate by the succinate pathway. While this postulate has not been proven, it is consistent with two types of experimental evidence. The additional ATP appears essential to the stoichiometric balance, and the reverse reaction, that of succinate formation from propionate in liver mitochondria, requires ATP (Flavin et al., 1955). It should be recognized that these factors are not conclusive evidence. Frequently biochemical reactions, which require ATP to proceed in one direction, do not generate ATP when they proceed in the reverse direction. Also,

the initial stoichiometry was based on the assumption of a specific upper limitation to microbial growth with respect to energy.

Using Streptococcus faecalis, Bauchop and Elsdon (1960) defined Y_{ATP} as the yield in grams of microbial cell (dry weight) per mole of ATP and established Y_{ATP} to be from 9 to 12. Even though higher Y_{ATP} values have been observed (Hungate, 1963; Hobson and Summers, 1967), a Y_{ATP} value of 10.5 was concluded to be the constant which represented the energetic limitation of microbial growth (Payne, 1970). It was based upon this assumption that Hobson and Summers (1972) and Hungate et al. (1971) postulated the generation of additional moles of ATP to account for higher yields of microbial cells than anticipated. However, there are higher yields which can not be logically explained by postulating greater ATP production (Walker and Nader, 1968; Bucholtz and Bergen, 1973). Stouthamer and Bettenhausen (1973) observed that when Y_{ATP} was measured in an energy limiting chemostat, as the dilution rate (growth rate) increased, there was a corresponding augmentation in Y_{ATP} . These authors concluded that there is a maximum yield of microbial cells obtainable per available ATP. However, what determines the actual Y_{ATP} is the proportioning of the available ATP into energy for maintenance of the microbial population and into energy for growth. In a steady-state system, the specific growth rate is equivalent to the dilution rate or turnover rate.

Using a mixed rumen culture, Isaacson et al. (1975) and Owens and Isaacson (1977) observed that with a constant energy supply,

as the dilution rate increased, the efficiency of microbial cell synthesis increased. That portion of the available energy which contributed to the yield of microbial cells was greater at higher turnover rates. This was in part due to a more rapid turnover of the microbial population which led to a smaller population maintenance requirement. For their mixed rumen culture, Owens and Isaacson (1977) calculated the theoretical maximal Y_{ATP} to be 19.3, if all the available energy could be used for growth. Y_{ATP} increased from 7 at a dilution rate (D) of 0.02 per hour to 17 at $D = 0.12/h$.

Thomson et al. (1975) demonstrated that while the total volatile fatty acid production remains unchanged, as the dilution rate increases, there is an increase in the molar proportion of acetate with a corresponding decrease in propionate production. Wolin (1975) found that increasing the dilution rate shifted the production of propionate away from the succinate pathway towards the acrylate pathway for Selenomas ruminantium but no such shift was observed for Ruminococcus albus.

Cole et al. (1976c) and Kropp et al. (1977a) found that urea could be substituted, isonitrogenously and isocalorically in the diet of cattle, without any significant effect on microbial protein synthesis. While there was a tendency to increase microbial protein synthesis with increasing urea substitution, there was significantly less abomasal nitrogen ($P < .01$) due to a decrease in bypass protein ($P < .01$) with increasing urea substitution. The dilution rate tended to increase with increasing urea

substitution. It was concluded that at a constant dilution rate, urea and soybean meal were isonitrogenously interchangeable with respect to microbial protein synthesis. Soybean meal gave higher organic matter digestion and nitrogen retention than substituted urea. The mean ruminal ammonia-nitrogen ($\text{NH}_3\text{-N}$) concentrations ranged from 12.3 to 13.6 mg per 100 mg rumen fluid. This is well in excess of the 5 mg per 100 ml necessary for bacterial growth (Satter and Slyter, 1974). The urea fermentation potentials of these diets ranged from -40.6 to 6.3 g urea/kg with increasing percentage of urea substitution from zero to 75% of the supplemental soybean meal nitrogen. There were about 10 g microbial protein synthesized per 100 g DM digested. This value is in agreement with results by Hume et al. (1970) and Leibholz and Hartmann (1973). However, this is only about half of the more generally accepted value, 22 to 23 g microbial protein synthesized per 100 g OM digested in the rumen (Hogan and Weston, 1970; Miller, 1973; Thomas, 1973).

Several studies (Hungate, 1966; Smith, 1975; Bryant, 1977) have focused on the ability of rumen bacteria to utilize various nitrogenous sources for protein synthesis. The majority, but not all, of the bacteria can rely on ammonia as a primary source of nitrogen. There are relatively little data concerning the proportional importance of $\text{NH}_3\text{-N}$ compared to proteins and amino acids studied in vivo. Nitrogen metabolism in sheep was investigated, using continuous infusion of ^{15}N -ammonium sulfate, by Pilgrim et al. (1970). These authors found ^{15}N comprised 76-78% of rumen

bacterial nitrogen (64-43% for protozoa) with a low protein diet (12.5 g N/day) and 62-64% for bacteria (41-35% for protozoa) with a high protein diet (22.9 g N/day). The microbes depended upon ammonia to a minimal extent of 65% for the low protein diet and 53-55% for the high protein diet. Using a single injection technique with ^{14}C -urea, ^{15}N -urea and ^{15}N -ammonium sulfate, Nolan and Leng (1972) found that 71% of the microbial protein was formed utilizing ammonia with high protein diets (mean = 23.4 g N/day). Nolan (1975) and Bryant (1977) estimated that between 50 and 70% of the microbial protein is formed through ammonia as the primary nitrogen source.

Using a tungstic acid precipitable N measurement, Satter and Slyter (1972) and Roffler and Satter (1973) demonstrated that, when ammonia was limiting, the close relationship between microbial growth and fermentation (Hungate, 1966) did not exist. They showed that increasing amounts of urea yield a linear increase in microbial protein synthesis up to a concentration of 5 mg $\text{NH}_3\text{-N}$ per 100 ml rumen fluid, which they estimated to be about 110 g/kg dietary crude protein equivalent. Above this level of rumen ammonia concentration, no further effect was noted. Studies by Orskov et al. (1971, 1972, 1974) suggested that maximum rumen microbial growth occurred between 4 and 9 mg $\text{NH}_3\text{-N}$ per 100 ml abomasal fluid, equivalent to about 12% dietary crude protein. Hume et al. (1970) found the point of rumen ammonia accumulated to be between 8.8 and 13.3 mg $\text{NH}_3\text{-N}$ per 100 ml rumen fluid. These authors also observed little difference between rumen and abomasal ammonia concentrations. Although additional work by

Satter and Slyter (1974) found actual values of 1.7, 1.9 and 2.0 mg $\text{NH}_3\text{-N}$ per 100 ml rumen fluid, they chose to use the 5 mg per 100 ml value to allow for a small excess. Figure 2 shows the relationship between $\text{NH}_3\text{-N}$ concentration of continuous-culture fermentor contents (dash line) and output of tungstic acid-precipitable nitrogen (TAPN) (solid line) as averages of several diets used by Satter and Slyter (1974). The crude protein equivalent value corresponds to the estimated dietary CP which would give rise to the corresponding mg $\text{NH}_3\text{-N}$ per 100 ml rumen fluid. For cattle the %CP and mg $\text{NH}_3\text{-N}$ /100 ml rumen fluid are related to each other by the equation:

$$\text{NH}_3\text{-N} = 10.57 - 2.5 \text{ CP} + 0.159 \text{ CP}^2$$

(Satter and Roffler, 1977). This equation had an $r^2 = 0.88$. By the addition of %TPN, the r^2 is raised to 0.92 for the multiple regression equation:

$$\text{NH}_3\text{-N} = 38.73 - 3.04 \text{ CP} + 0.171 \text{ CP}^2 - 0.49 \text{ TDN} + 0.0024 \text{ TDN}^2.$$

TDN as an energy measure was originally selected by Roffler and Satter (1975a) for use with dairy cattle diets. When the model was tested against the data in the literature (Roffler and Satter, 1975b), it was concluded that it would accurately predict growing and lactating responses to NPN supplementation in dairy cows.

Digestible dry matter (DDM) may be used as an energy measure instead of TDN. Moe et al. (1972) have established the energy relationships necessary to convert TDN to DDM.

For the purified diet utilized by Satter and Slyter (1974), the Y_{ATP} was estimated and is presented graphically (figure 3)

Figure 2. Relation between ammonia concentration ($\text{NH}_3\text{-N}$) of continuous-culture fermentor contents (dash line) and output of TAPN (solid line). Adapted from Satter and Slyter (1974).

Figure 3. Microbial growth yields (Y_{ATP}) in continuous-culture fermentors with purified diets containing urea. Data from Satter and Sylter (1974).

with respect to dietary crude protein equivalent. The TAPN measured point of ammonia overflow (figure 2) corresponds to the dietary crude protein level at which Y_{ATP} plateaus (figure 3). The actual dietary %CP at which the point of ammonia overflow occurs would vary with the specific type of diet consumed. Diets high in energy, containing true protein, with protein resistant to rumen degradation and which decrease saliva flow, have an increased dietary crude protein level at which ammonia would accumulate. Conversely, diets low in energy, high in NPN, containing easily degradable protein and inducing high saliva flow, would decrease the dietary crude protein level for the point of ammonia overflow (Satter, 1978).

Satter and Roffler (1975) have summarized their results on ammonia accumulation in a practical system for the determination of nitrogen requirements with respect to energy balance. In this system, nitrogen and energy are considered the dietary determinants of the point of ammonia accumulation. Dietary CP and TDN determine the rumen ammonia concentration, using the multiple regression equation of Satter and Roffler (1977). NPN may be added to the diet to the extent that the CP to TDN balance produces up to 5 mg NH_3 -N per 100 ml rumen fluid. Satter and Roffler (1975) expressed the CP, TDN and NPN relationship in tabular form. Ammonia accumulation at 5 mg per 100 ml rumen fluid represents the point of maximal microbial synthesis. Addition of dietary nitrogen, either CP or NPN, above this level would not contribute to increased microbial protein synthesis.

Metabolizable protein (MP), as introduced by Burroughs et al. (1972, 1973a), is the alpha-amino nitrogen available to the animal for metabolism. The MP is composed of the microbial protein plus the dietary CP which bypasses rumen degradation. While NPN can contribute only to microbial protein (Roffler et al., 1976), dietary CP, both above and below the point of ammonia overflow, can also contribute undegraded protein to MP.

The MP concept was originated by Burroughs et al. (1971b), specifically to deal with the problem of urea addition to cattle rations. Burroughs et al. (1971c) demonstrated the inaccuracy of utilizing N times 6.25 to satisfy protein requirements when NPN feedstuffs are considered in feedlot cattle rations. In order to overcome the inadequacies of the 6.25 multiplication system, Burroughs et al. (1971a) introduced the urea fermentation potential (UFP) to the MP system. The MP and the metabolizable amino acids(MAA) are the quantities of digested protein or absorbed amino acids which are available to the animal for metabolism. This system is the first attempt to express requirements directly at the tissue level. MP is the sum of feed protein, which bypasses rumen degradation, and the microbial protein, which passes from the rumen to the abomasum (Burroughs et al., 1972).

The animal's MP requirements were established by a modification of a method proposed by Mitchell (1929). In this procedure, the maintenance needs for net body protein (grams per animal per day) were derived using the equation of Smuts (1935):

$$\text{Maintenance} = (0.0125)(70.4 w_{\text{kg}}^{0.734}).$$

The W is empty body weight in kilograms. The net protein deposition in tissues was determined from the data of Haecker (1920), Moulton et al. (1922) and Fowler (1968). Additional data by Fowler et al. (1970) and Burroughs et al. (1970a) was in agreement with the previously obtained protein deposition data. In the Iowa State University studies, comparative slaughter feedlot trials were conducted using the 9-10-11th rib procedure of Hankins and Howe (1946) to estimate carcass composition. Once the total net protein needs were determined, the requirement was converted to MP on the basis that 53% of the MP is lost in metabolism for maintenance and 5% is lost in metabolism for milk production, as established by Virtanen (1966), Oltjen et al. (1972) and Burroughs et al. (1973b). MAA requirements were established on the basis of the body amino acid composition data of Block and Bolling (1945), Burroughs et al. (1970b) and the NRC (1964) composition of meat scraps.

Burroughs et al. (1974) summarized the methods of establishing MP values for feedstuffs. This procedure involves the determination of the undegraded dietary protein reaching the abomasum for each feedstuff. The degraded protein is synthesized into microbial protein, in the presence of adequate energy, to the extent of 10.44% of the dietary TDN (Pitzen, 1974). The bypass protein reaching the abomasum was transformed into amino acids using Morrison (1956) and NRC (1964) data. The amino acid composition of rumen microorganisms was calculated using data by Meyer et al. (1967). The MP and MAA were calculated assuming 80% digestion for

microbial protein (Johnson et al., 1944) and 90% digestion for the undegraded or rumen bypassed feed protein (NRC, 1964).

The estimated MP and MAA requirements were published for feedlot cattle by Burroughs et al. (1972), Burroughs and Geasler (1973) and Rouse (1978) and for dairy cows by Burroughs et al. (1975a, b). The total MP requirement needed to maintain a specific ADG decreases slightly with increasing body weight gain for feedlot steers. Since the maintenance requirement for MP increases with increasing body weight, the amount of MP required per unit of body weight gain decreases with increasing body weight. This reflects the differences in carcass composition at different animal weights. As weight increases, there is a decrease in the proportion of protein gain with respect to fat gain (Berg and Butterfield, 1967; Elsley, 1976).

The available MP in a given ration is calculated from the DMI, the proportion of CP degraded in the rumen, the proportion of CP bypassing rumen degradation and the TDN of a ration (Burroughs et al., 1975b).

$$MP = (P_1 \times .90) + [(P_2 - 15.0) \times .80].$$

The P_1 in the equation is the grams of bypass alpha-amino protein per kg feed DM and is considered 90% digestible. The P_2 represents the grams of abomasal microbial protein per kg feed DM and is considered to be 80% digestible. The number 15.0 represents the amount of abomasal protein needed to satisfy the metabolic fecal protein requirement. The P_2 factor represents the metabolic balance between energy and nitrogen. The grams of microbial protein are derived

from either the grams of dietary CP degraded in the rumen or 10.44% of the grams of TDN per kg feed DM. The P_2 is calculated from the CP in the case of an energy excess and from the TDN in the case of a nitrogen excess.

From the amino acid percentages of P_1 and P_2 ,

$$MAA = (.9P_1 \times AA\%P_1)/100 + [(.8P_2 - 12.0) \times AA\%P_2]/100.$$

Logically, if the dietary protein, which is degraded and synthesized into microbial protein, passes through an ammonia intermediate, than NPN should be substitutable into microbial protein on an ammonia equivalence basis. For this purpose, the urea fermentation potential (UFP) was introduced by Burroughs et al. (1971a). UFP reflects the microbial ability to incorporate ammonia, in the case of sufficient energy, into microbial protein. A positive UFP value represents the maximal amounts of urea (g/kg feed DM) which can be fed to obtain maximum formation of microbial protein. The derivation of UFP assumes that only 40 percent of the fed urea is actually converted to microbial protein as,

$$UFP = (1.044 \text{ TDN} - P_3) \div 2.8.$$

The P_3 is the total grams of rumen degraded protein per kg feed DM. This is the protein which contributes ammonia to the rumen ammonia pool. The 2.8 factor converts to an equivalent amount of urea. A positive UFP value times 2.2 gives the grams of microbial protein synthesized from the additional grams of urea added per kg feed DM. The 2.2 factor is derived from the grams of MP synthesized from a kg of urea in the presence of excess energy.

$$MP_{\text{urea}} = (P_1 \times .90) + [(P_2 - 15.0) \times .80].$$

$$MP_{\text{urea}} = [2800(0) \times .90] + ([2800(1.00) - 15.0] \times .80).$$

$$MP_{\text{urea}} = 2228 \text{ g MP/kg urea.}$$

The MP concept has taken protein beyond the digestibility stage. MP is the requirement expressed at the level of absorption in the small intestine after rumen ammonia and digestion losses. The MP system takes into account microbial synthesis and bypass protein to express the MP and MAA values of feedstuffs.

The animal requirements are actually determined on a net protein basis in terms of maintenance protein and tissue protein growth (or production) requirements. The efficiencies of utilization of MP for maintenance and for production have been used to convert animal net protein requirements to animal MP requirements.

Even with all the adjustments and assumptions accounted for by the MP system, a net protein (NP) system has been outlined by Fox et al. (1977) and Fox and Black (1977) to make additional adjustments not accounted for in the MP system.

The basic NP system (Fox et al., 1977; Bergen et al., 1979) is structured like the MP system (Burroughs et al., 1975a, b). The maintenance net protein (NP_m) requirement is also based upon the equation of Smuts (1935):

$$NP_m = (0.0125)(70.4 W_{\text{kg}}^{0.734}).$$

The W is empty body weight in kilograms.

The empty body protein composition (EB_p) of the average framed steer is derived from the equation of Reid (1974):

$$EB_p = 0.235 W - 0.00013 W^2 - 2.418.$$

Adjustments for frame size and sex are made so that animals may be

compared at a standard composition (Brumgardt, 1972; Ayala, 1974; Crickenberger et al., 1976b; Klosterman and Parker, 1976). Fox et al. (1977) have chosen empty body fat at 28.2 to 30.5% as the standard where steers are expected to grade low choice (Fox and Black, 1976; Byers et al., 1977).

The animal NP for gain (NP_g) requirement is the first derivative of the Reid (1974) equation, expressed at various average daily gains (ADG):

$$NP_g = (0.235 + 0.00026 W) \times ADG.$$

The efficiency of the utilization of MP is assumed to be equal for maintenance and for gain (Bergen et al., 1978).

The NP values of feedstuffs were determined by nitrogen balance trials (Bergen et al., 1974; Fox et al., 1976; Crickenberger et al., 1976a). The protein of feedstuffs is measured as a nitrogen retention quotient:

$$\left[\frac{N \text{ retained}}{N \text{ intake}} \right],$$

which can be used to convert CP values to NP values. Only one NP value for feedstuffs is expressed, since the utilization, for maintenance and for gain, is assumed to be at similar efficiencies.

In order to account for the use of NPN supplementation, Bergen et al. (1978, 1979) developed the ammonia utilization potential (AUP). AUP represents the upper limit on microbial protein synthesis:

$$AUP = \text{Rumen ATP yield} \times \text{Efficiency of microbial protein synthesis.}$$

$$AUP = DMI \times DE \times \text{Rumen OMD} \times \text{Efficiency of cell yield.}$$

The DMI is the kg of dry matter intake, and DE is the digestible energy in Mcal per kg feed DM. Rumen OMD represents the extent of

organic matter digestion in the rumen. The efficiency of cell yield is the grams of microbial protein synthesized per Mcal of rumen DE. Rumen DE is the DE of the feed times the percent ruminal digestion. The rumen OMD and the efficiency of cell yield are dependent upon the dilution rate of the ration. Dilution rates for several types of rations have been determined by Cole et al. (1976c) and Kropp et al. (1977b). The efficiency of microbial cell yield, as protein yield per Mcal DE available in the rumen, is determined from the relationship of dilution rate to microbial cell yield (Cole et al., 1976c; Kropp et al., 1977b). The extent of rumen OMD is expressed as apparent rumen OMD as a percent of total apparent OMD. Cole et al. (1976a, b) and Kropp et al. (1977a) determined the extent of rumen OMD for several types of rations. If the rumen OMD and the efficiency of microbial cell yield are known for the ration, then the AUP can be determined from the DMI and DE content of the ration.

In the NP system, NP values for NPN ingredients are determined comparably to true protein feedstuffs. However, in ration calculation NPN is only utilizable to the extent that

$$\text{NPN (NH}_3\text{)} \leq \text{AUP.}$$

The NPN (NH₃) is the ammonia derived from NPN ingredients. To the extent that the NPN (NH₃) exceeds the AUP, the NP value of excess NPN is zero.

CHAPTER THREE MATERIALS AND METHODS

General

The experimental design consisted of two trials. A metabolism trial and a comparative slaughter feedlot trial were conducted simultaneously from September, 1979, to February, 1980, at the Agricultural Research Center of the Institute of Food and Agricultural Sciences located near Jay, Florida. Eighty-five yearling steers were randomly selected. Since some of the steers were purchased at local auction markets, their true ancestry is unknown. Animals utilized in the study were predominantly Angus, Hereford and Angus-Hereford crosses. Through visual examination, the 85 steers were sorted into three breed groups of 58 Angus, 15 Hereford and 12 Angus-Hereford crosses. Further randomizations were made from the breed groups into the experimental groups.

All the animals were slowly adapted to corn silage and corn grain diets during the summer preceding the two trials. Five Angus steers were selected at random, for the metabolism trial, and placed in individual feeding stalls, where they were fed the silage and grain diets. The experimental diets were designed to be isocaloric but to vary in nitrogen to energy balance utilizing the urea fermentation potential system (UFP) of Burroughs et al. (1975a, b). The ingredient composition and proximate analyses of the five experimental diets are shown in tables 1 and 2, respectively.

TABLE 1. INGREDIENT COMPOSITION OF DIETS TO EVALUATE UFP, DRY MATTER BASIS

Ingredient, ^b % DM	Reference no. ^c	UFP ^a				
		+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Corn grain	4-02-935	64.10	62.74	62.25	64.30	66.46
Corn silage	3-08-153	34.76	33.70	32.65	31.40	30.06
Soybean meal	5-04-604	-	2.43	3.87	2.60	1.34
Urea ^d	-	-	-	.10	.56	1.01
Salt ^e	-	.45	.46	.45	.45	.46
Limestone ^f	6-02-632	.69	.68	.67	.68	.67

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis from feedstuffs given by Burroughs et al. (1975b).

^b Added 2200 IU Vitamin A per kg diet DM from 16.8g of Rovimix A-650 (Roche).

^c NRC, 1971a.

^d Contained 281% crude protein equivalent (min).

^e Trace mineralized salt containing $97.0 \pm 2.0\%$ NaCl, 0.35% Zn, 0.34% Fe, 0.20% Mn, 0.033% Cu, 0.007% I and 0.005% Co.

^f Contained 38.8% Ca (min).

TABLE 2. DRY MATTER AND PROXIMATE ANALYSES COMPOSITION OF DIETS TO EVALUATE UFP

Item, %	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Dry matter	58.22	58.85	59.45	60.25	61.12
Dry matter basis					
Ash	2.14	2.24	2.30	2.20	2.09
Crude fiber	7.06	7.00	6.92	6.70	6.48
Crude protein ^b	9.71	10.62	11.42 ^c	12.21 ^d	13.00 ^e
Ether extract	3.25	3.22	3.19	3.20	3.22
Nitrogen-free extract	77.84	76.92	76.17	75.69	75.21

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis from feedstuffs given by Burroughs et al. (1975b).

^b Crude protein difference reflects the change in dietary UFP, since diets were designed to be isocaloric.

^c Includes 0.28% crude protein equivalent from urea.

^d Includes 1.57% crude protein equivalent from urea.

^e Includes 2.84% crude protein equivalent from urea.

Metabolism Trial

A 5 x 5 Latin square design was utilized for the metabolism trial. The five diets (table 1) were rotated through the five periods in the order shown in table 3. The five Angus steers were halter-broken and housed in individual concrete floor stalls. Dietary ingredients were weighed using milk scales and mixed by hand in metal tubs. One of the five steers was removed from the experiment after the second period, due to refusal of feed when placed in the elevated metabolism crate. The limited data of this steer was not included in the statistical analysis.

At the beginning of the first metabolism period, the steers were implanted with 36 mg zeranol. Each metabolism period consisted of 21 days divided into three phases: adjustment to the diet, adjustment to the metabolism crate and fecal and urinary collection phase. The animals were adjusted for 11 days in stalls with concrete floors to the diet fed during that period. The diets were fed ad libitum to the steers in their individual feeding stalls. The steers were weighed before being placed into their metabolism crates and again after being removed. The steers were adjusted for 3 days to living in elevated metal metabolism crates. Feed offered in the crates was initially cut to approximately 80% of ad libitum level, then adjusted so the animals left a minimal amount of orts. During the last 7 days of each period, total urine and feces were collected. Daily samples of feed were taken at the beginning of the last 7 days of each period. The animals were fed twice daily, and orts, when present, were collected once daily

TABLE 3. EXPERIMENTAL DESIGN OF METABOLISM TRIAL USING STEERS TO EVALUATE UFP^a

Period	Steer no.				
	108A	11A	142A	129A	121A ^b
1	-1.4	-6.9	+3.8	+1.2	-3.9
2	+1.2	-3.9	-6.9	+3.8	-1.4
3	-6.9	+1.2	-1.4	-3.9	+3.8
4	+3.8	-1.4	-3.9	-6.9	+1.2
5	-3.9	+3.8	+1.2	-1.4	-6.9

^a Diets listed by urea fermentation potential values determined in the present study.

^b Steer 121A terminated from experiment after period 2; no data from steer 121A used in analysis of results.

at the time of urine and fecal collection. The steers were given water in plastic pails twice daily, and their water consumption was recorded. Two fecal collections were obtained daily. The initial collection was stored in metal trash cans with plastic liners. Following the second collection, the two collections were composited, weighed and mixed thoroughly. An aliquot, representing 1% of the daily fecal material, was stored in plastic bags and frozen for later analysis. Urine was collected in plastic bottles covered with two layers of cheese cloth to minimize contamination. Urine samples were preserved by 10 ml of toluene and 150 ml HCl (diluted 1:4) added to the bottles at the beginning of the collection period. Daily the total urine volume was recorded, and after thorough mixing a 2% aliquot was collected in a nalgene bottle and refrigerated for later analysis. The urine samples were composited from day to day by storage in the same nalgene bottle. At the end of each period, the feed,orts and fecal samples were thawed, thoroughly mixed and composite samples taken. The composite samples were weighed and dried in a forced-air oven at 60°C for approximately 48 hours. The samples were then ground to pass through a one mm screen in a Wiley mill. Proximate analyses were conducted on these samples in accordance with AOAC (1970) methods. The Parr adiabatic bomb calorimeter was utilized for gross energy determinations, as described by Anonymous (1960) and Easley et al. (1965). Urine samples were analyzed for nitrogen and gross energy following the same procedures. Prior to calorimetric analysis the urine was dried on solka floc absorbant.

Metabolizable energy was calculated as the energy in the feed minus the energy losses in feces, urine and methane of digestion. Methane energy was estimated from the equation of Bratzler and Forbes (1940):

$$E = 4.012\chi + 17.68.$$

In the equation, E is the grams of methane produced, and χ represents 10^{-2} times the grams of carbohydrate digested. Digested carbohydrate is the sum of the digested crude fiber and digested nitrogen-free extract. Each gram of methane produced represents a loss of 13.2 kcal of energy.

Digestion coefficients for the various nutrients were determined as the apparent digestibility by the equation:

$$DC = \frac{\text{Nutrient intake} - \text{Nutrient fecal output}}{\text{Nutrient intake}}.$$

The data were analyzed statistically using simple regression models with dietary UFP as a continuous variable and using analysis of variance comparing treatment effects by the probability of difference in values by comparing least square means (Steele and Torrie, 1960). The computer system used the General Linear Models procedure as outlined by Barr et al. (1979).

Feedlot Trial

Ten pens with concrete floors and tin roofs covering dirt areas at one end were used in the feedlot trial. Dicalcium phosphate (Dynafo), trace mineralized salt and sodium chloride were provided free choice in each of the feedlot pens. Ten feedlot groups of eight steers each were randomly selected from the remaining

80 steers. Proportional numbers were allocated to each pen from the various breed groups. One animal from each of the ten feedlot groups was randomly selected to be an initial slaughter group for a comparative basis. The ten groups of eight steers were randomly assigned, two groups per diet, to the five experimental diets. All steers were fed the adjustment ration, shown in table 4, for two weeks. At the end of this adjustment period, the steers were fasted without feed or water for 18 hr prior to being individually weighed. At this time, the 10 steers selected as the initial slaughter group were sent to the University of Florida Meats Laboratory in Gainesville. The remaining 70 animals were each implanted with 36 mg of zeranol and returned to the ten feedlots, where they were fed their respective experimental diets (tables 1 and 2). The diets were fed twice daily utilizing a Davis transit mixer-feed wagon equipped with electronic scales. The steers were gradually adjusted to their respective diets by increasing their allotment of feed from day to day until ad libitum intake was reached in 10 to 14 days. The steers were continued on ad libitum feed consumption for the duration of the feedlot trial. The quantity consumed per group per feeding was recorded. All the ingredients, except corn silage and most of the corn grain, were combined to form a supplement. A small amount of corn grain was added so that all supplements would constitute the same percent (as fed) of each diet. At feeding times, the corn silage and remaining corn grain were weighed directly into the wagon. The supplement was weighed in a plastic pail using milk scales and added to the bulk ingredients in the wagon. Diets were thoroughly mixed and weighed out of the wagon

TABLE 4. INGREDIENT COMPOSITION OF FEEDLOT ADJUSTMENT RATION,
DRY MATTER BASIS

Ingredient ^a	Reference no. ^b	DM, %
Corn grain	4-02-935	61.46
Corn silage	3-08-153	31.49
Soybean meal	5-04-604	5.45
Urea ^c	-	.60
Salt ^d	-	.40
Limestone ^e	6-02-632	.60

^a Added 2200 IU Vitamin A per kg diet DM using 16.8 g of Rovimix A-650 (Roche).

^b NRC, 1971a.

^c Contained 281% crude protein equivalent (min).

^d Trace mineralized salt containing $97.0 \pm 2.0\%$ NaCl, 0.35% Zn, 0.34% Fe, 0.20% Mn, 0.033% Cu, 0.007% I and 0.005% Co.

^e Contained 38.80% Ca (min).

into the feed troughs. There were two feedlot groups each with seven animals for each of the five experimental diets. One group, on each diet, was fed first in the morning, and the other one was fed first in the evening. The diets were fed every day in the same order, from highest to lowest UFP. One of the two feedlot groups, fed an experimental diet, was fed for a 119-day period, and the other group was fed for a 126-day period, as illustrated in table 5. The feeding period began on October 3, 1979 for all groups. Due to limited slaughter facilities, half the steers on each dietary treatment were slaughtered one week later than the others.

At the end of their respective feeding periods, the animals were weighed following an 18 hr fast and shipped to the University of Florida Meats Laboratory in Gainesville and slaughtered. The initial comparative slaughter steers and the steers in the ten feedlot groups were weighed upon their respective arrivals at the Meats Laboratory. All animals were reweighed the next morning just prior to slaughter. Empty body weight was determined by manual emptying of the gastrointestinal tract and by subtracting the weight of its contents from the live animal weight just prior to slaughter. Hot carcass weight was obtained on the kill floor. After cooling for 48 hours, the left sides of the carcasses were evaluated for maturities of the lean and bone, color of the lean, texture of the lean, firmness of the lean, color of the fat, marbling in the ribeye, fat thickness over the 12th rib, ribeye area and percent kidney-heart fat. After evaluation the loin area was removed and frozen for tenderness evaluation using the Warner Bratzler shear. Dressing percentage (DP) was de-

TABLE 5. EXPERIMENTAL DESIGN OF FEEDLOT TRIAL USING STEERS TO EVALUATE UFP^a

Pen	No. of steers ^b	Days on feed	Diet, UFP
1	7	126	+1.2
2	7	119	+1.2
3	7	119	-1.4
4	7	119	-6.9
5	7	126	+3.8
6	7	126	-1.4
7	7	119	+3.8
8	7	119	-3.9
9	7	126	-3.9
10	7	126	-6.9

^a Diets listed by urea fermentation potential values determined in the present study; refer to tables 1 and 2 for diet composition.

^b Does not include the 10 steers in the initial comparative slaughter group.

terminated by the equation:

$$DP = \frac{\text{Hot carcass weight}}{\text{Live animal weight}} \times 100.$$

Overall maturity is the mathematical average of the maturities of the lean and bone. Quality grade was determined from the overall maturity and marbling in accordance with the standards set by the USDA (1975). Yield grade (YG) was calculated from the following USDA (1975) equation:

$$YG = 2.50 + (2.50 \times \text{fat thickness over 12th rib}) + \\ (0.20 \times \text{percent kidney-heart fat}) + (0.0038 \times \\ \text{hot carcass weight}) - (0.32 \times \text{ribeye area}).$$

The right sides of the carcasses were utilized for specific gravity measurements. Specific gravity was determined on both sides for the initial comparative slaughter group. However, the right side was chosen for later specific gravity determinations, since there was no difference between the left and right sides for the initial comparative slaughter group. Also, the equations derived by Garrett and Hinman (1969) were based on the use of the right side of the carcass. Only the right side specific gravity determinations were used in subsequent comparisons. To determine specific gravity, the right side of each carcass was weighed in air and then weighed in water. Both the water and air were at the same temperature (34°C) to which the carcasses had been chilled during the previous 48 hours. Specific gravity of the carcass (SGC) was then determined by the equation:

$$SGC = \frac{\text{Cold carcass weight in air}}{\text{Cold carcass weight in air} - \text{weight in water}}.$$

Using the carcass specific gravity values, carcass and empty body compositions were calculated from the equations of Garrett and Hinman (1969).

Carcass ether extract, % = $587.86 - 530.45$ (SGC).

Carcass water, % = 375.2 (SGC) - 343.8 .

Carcass N, % = 20.0 (SGC) - 18.57 .

Carcass energy, kcal/g = $49.54 - 43.63$ (SGC).

Empty body ether extract, % = $551.38 - 498.5$ (SGC).

Empty body water, % = 378.74 (SGC) - 345.18 .

Empty body N, % = 15.97 (SGC) - 14.17 .

Empty body energy, kcal/g = $47.58 - 41.97$ (SGC).

The protein compositions were determined by multiplying the percent N times 6.25.

Lofgreen and Garrett (1968) reported that the kcal daily heat production (HP) per kg metabolic body weight raised to the three-fourths power is related to the kcal daily metabolizable energy intake (MEI) per kg metabolic body weight raised to the three-fourths power by the equation:

$$\text{Log HP} = 1.885 + 0.00166 \text{ MEI}.$$

The 1.885 factor is the log of the basal metabolic rate (BMR) as

$$\text{Log BMR} = \log (77 \text{ kcal/W}_{\text{kg}}^{0.75}).$$

The equilibrium point is where the kcal of MEI equals the kcal HP. This value determines the grams of the specific diet necessary to maintain the BMR. The ration's net energy for maintenance (NE_m) in kcal per g is calculated as:

$$NE_m = \frac{77 \text{ kcal/W}_{kg}^{0.75}}{\text{grams of intake at equilibrium point}}$$

The grams of intake at the equilibrium point is the daily dry matter feed intake, obtained in the feedlot trial, necessary to give the intake of ME at the equilibrium point.

The net energy for gain (NE_g) is measured using the energy deposition determined from the carcass specific gravity (Garrett and Hinman, 1969). The NE_g in kcal per gram of diet is a measure of the energy retention divided by the diet dry matter intake (DMI) above maintenance (NE_m) as:

$$NE_g = \frac{\text{Energy retained, kcal/W}_{kg}^{0.75}/\text{day}}{(\text{Total g DMI} - \text{g DMI for } NE_m)/W_{kg}^{0.75}/\text{day}}$$

The total daily DMI is the average daily DMI measured in the feedlot trial.

The daily fat and protein deposition was determined from the percent ether extract and percent N ($\times 6.25$) obtained with the equations of Garrett and Hinman (1969). Using these equations and the weights of the empty body and the carcass, the total kg of protein and fat were determined. Using the initial comparative slaughter group's composition for the determination of initial empty body and carcass compositions of the steers in the various dietary treatments, the kg of protein and fat gained with each diet were calculated. Carcass protein gain (CPG) in kg per day, for example, was calculated as:

$$CPG = \frac{\text{Carcass protein, kg} - \text{Adjusted initial carcass protein, kg}}{\text{Days on feed}}$$

The adjusted initial carcass protein is the estimated initial carcass weight and percent protein determined using the initial comparative slaughter group of steers as a representative sample. The daily gains of carcass fat and energy and of empty body fat, energy and protein are derived in the same manner.

Urea fermentation potential (UFP), metabolizable protein (MP) and metabolizable amino acids (MAA) were calculated using the formulae of Burroughs et al. (1975a, b). These equations are outlined in the literature review. Estimations of percentages of protein degraded in the rumen for the various feedstuffs were taken from the data of Burroughs et al. (1975a). Comparative UFP, MP and MAA values were derived using the compositions and values of comparable feedstuffs, as reported by Burroughs et al. (1975a, b).

The point of ammonia accumulation was determined using the equation of Satter and Roffler (1977) with the TDN and CP values determined in the present metabolism trial. This equation is outlined in the literature review. Using the tables presented by Roffler and Satter (1975a) and Satter and Roffler (1975), the upper limit of NPN utilization was evaluated as the percent dietary crude protein equal to the point of ammonia accumulation.

Net protein (NP) and ammonia utilization potential (AUP) were determined using the equations of Fox et al. (1977) and Bergen et al. (1978, 1979). These methods are outlined in the literature review.

The data were analyzed statistically using simple regression models with dietary UFP as a continuous variable. As covariates,

initial metabolic body weight and initial animal age were utilized in an analysis of covariance with UFP. The computer system utilized the General Linear Models procedure as outlined by Barr et al. (1979).

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CHAPTER FOUR RESULTS AND DISCUSSION

Metabolism Trial

The data on digestibilities of proximate analysis constituents and TDN are presented in table 6. The proximate analyses digestibilities and TDN data were analyzed by linear regression analysis for significance related to variation in dietary UFP. The digestibilities of organic matter, ether extract and nitrogen-free extract were not significantly related to dietary UFP levels. Total digestible nutrient values showed no significant relationship with dietary UFP levels when compared by either linear regression analysis ($P=.30$) or least squared means analysis ($P=.73$). Both the crude protein and crude fiber digestibilities showed significant linear relationships to decreasing dietary UFP ($P < .002$ and $P < .04$, respectively). Crude fiber digestibility decreased with decreasing dietary UFP. The diets had a decrease in the percentage of crude fiber with decreasing UFP values (table 2). Much of the overall regression model significance ($P < .002$) was contributed by animal and period significance ($P < .001$ and $P < .007$, respectively). The UFP variable was only slightly significant ($P < .04$) in the linear regression model. Crude protein digestibility increased with decreasing dietary UFP. There was also an increase in the percentage of dietary crude protein with decreasing UFP values (table 2). Since the diets were

TABLE 6. DIGESTIBILITIES OF PROXIMATE ANALYSIS CONSTITUENTS AND TOTAL DIGESTIBLE NUTRIENTS (TDN) OF DIETS DESIGNED TO EVALUATE UFP^a, DRY MATTER BASIS

Item, % DM	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Organic matter	68.4	68.1	68.0	69.9	69.8
Crude fiber*	39.8	38.9	37.7	37.6	33.4
Crude protein**	50.9	53.2	53.9	60.5	62.5
Ether extract	64.8	67.3	65.6	64.1	70.4
Nitrogen-free extract	73.4	72.9	72.9	74.6	74.2
TDN	69.6	69.3	69.0	71.0	71.2

* Means are significantly related to UFP by linear regression analysis (P<.05).

** Means are significantly related to UFP by linear regression analysis (P<.005).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

isocaloric, an increase in dietary crude protein gives a corresponding decrease in UFP value, going from a positive UFP (energy excess) to a negative UFP (nitrogen excess). Protein is considered a nutritive entity (Lucas and Smart, 1959), because it has the same true digestibility independent of its percentage in the diet. However, the apparent crude protein digestibility increases with increasing dietary crude protein concentration due to the metabolic fecal component which represents a constant proportion of dry matter intake. Data in table 7 demonstrate the similarity between the crude protein digestibility obtained in the present study and that predicted utilizing the equations given by Schneider and Flatt (1975) which assume constant true digestibility and constant metabolic fecal component. Although the apparent crude protein digestibility increased linearly with decreasing dietary UFP values, in agreement with Schneider and Flatt (1975), the true crude protein digestibility is probably about 90% (DM basis) and unaffected by variation in dietary UFP. Additional linear regression analyses of crude fiber and crude protein digestibilities related to a logarithmic transformation of UFP values gave similar, but slightly less significant results.

The energy utilization data determined in the metabolism trial are presented in table 8. Gross energy intake increased linearly with decreasing dietary UFP values ($P < .10$). Increasing dietary nitrogen concentration apparently caused a corresponding increase in energy intake. This increased energy intake probably was related to the increased urinary energy loss. Urinary energy output, both in terms of Mcal per day and percent energy intake, increased linearly with de-

TABLE 7. COMPARISON OF CRUDE PROTEIN DIGESTIBILITIES DETERMINED BY METABOLISM TRIAL AND CALCULATED BY DIGESTIBLE PROTEIN REGRESSION EQUATIONS

Crude protein digestibility, %	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Metabolism trial	50.9	53.2	53.9	60.5	62.5
Silage equation ^b	52.0	55.3	57.8	59.9	61.8
Energy feed equation ^c	50.8	54.3	56.9	59.2	61.2

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis from feedstuffs given by Burroughs et al. (1975b).

^b Digestible protein = $0.908 (\text{crude protein}) - 3.77$; Schneider and Flatt (1975) equation for silages.

^c Digestible protein = $0.918 (\text{crude protein}) - 3.98$; Schneider and Flatt (1975) equation for energy feeds.

TABLE 8. METABOLISM TRIAL DATA ON ENERGY UTILIZATION OF DIETS TO EVALUATE UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Energy intake, Mcal/day*	24.14	25.68	26.04	26.68	26.90
Energy output					
Feces, Mcal/day	8.16	8.90	8.95	8.71	8.88
Feces, % intake	33.9	34.5	33.9	32.4	33.0
Urine, Mcal/day***	1.06	1.14	1.24	1.49	1.48
Urine, % intake**	4.2	4.4	5.0	5.6	5.2
Methane, Mcal/day	2.00	2.06	2.07	2.15	2.13
Methane, % intake	8.3	8.1	8.0	8.1	8.0
Digestible energy, Mcal/kg DM	2.87	2.86	2.86	2.92	2.91
Metabolizable energy, Mcal/kg DM	2.32	2.31	2.30	2.33	2.33

* Means are significantly related to UFP by linear regression analysis (P<.10).

** Means are significantly related to UFP by linear regression analysis (P<.01).

*** Means are significantly related to UFP by linear regression analysis (P<.005).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

creasing dietary UFP values ($P < .002$ and $P < .01$, respectively). Since there was no observed relationship of dietary UFP variation with fecal and methane energy losses, the increased dietary energy intake was excreted primarily in the urine. Total urinary excretion accounted for 4.2 to 5.6% of energy intake. Digestible and metabolizable energies showed no significant relationships with dietary UFP levels when compared by either linear regression analysis ($P = .45$ and $P = .77$, respectively) or least squared means analysis ($P = .74$ and $P = .71$, respectively). Additional linear regression analysis of feed energy intake and urinary energy output related to a logarithmic transformation of UFP values gave similar results. While the urinary energy output results were slightly less significant using the logarithmic transformation, the feed energy intake results were slightly more significant (R^2 increased from .80 to .81). This slight increase does not justify the use of the more complex logarithmic regression model.

The nitrogen utilization data determined in the metabolism trial are given in table 9. Nitrogen intake increased linearly with decreasing dietary UFP values ($P < .0002$). This is in agreement with energy utilization data in table 8, which showed increasing energy intake with decreasing UFP values. Both nitrogen and energy intakes increased with decreasing UFP values. While increasing the nitrogen content of isocaloric diets resulted in increased nitrogen and energy intakes, increased nitrogen and urinary excretions were also observed. Urinary nitrogen, both in terms of grams per day and percent of nitrogen intake, increased linearly with decreasing dietary UFP values ($P < .0001$

TABLE 9. METABOLISM TRIAL DATA OBTAINED FOR NITROGEN UTILIZATION IN DIETS TO EVALUATE UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
N intake, g/day ***	86.4	100.2	109.0	120.4	128.8
N excretion					
Feces, g/day	42.5	47.3	50.4	47.3	48.7
Feces, % intake**	49.6	46.5	45.6	40.0	37.5
Urine, g/day***	28.6	34.6	37.6	52.0	55.0
Urine, % intake*	30.6	33.0	36.4	44.9	40.2
N retention, g/day	15.3	18.4	21.1	21.2	25.2
N retention, % intake	18.9	18.6	19.8	18.2	20.5
N retention, % absorbed	34.8	34.7	36.0	29.0	31.4
N digestibility, % diet**	50.9	53.2	53.9	60.5	62.5
Digested N retained, % diet	36.3	35.5	37.7	30.3	31.3

* Means are significantly related to UFP by linear regression analysis (P<.01).

** Means are significantly related to UFP by linear regression analysis (P<.005).

*** Means are significantly related to UFP by linear regression analysis (P<.001).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

and $P < .006$, respectively). The linear decrease ($P < .002$) in fecal nitrogen loss, as a percentage of nitrogen intake, with decreasing dietary UFP values, is the analogue of increasing nitrogen (crude protein) digestibilities. This reflects the nutritive entity relationship between apparent and true digestibilities (table 7). Although nitrogen retention tended to increase with decreasing UFP values ($P < .08$), the significance in the model is due more to differences between animals ($P < .05$) than to variation in dietary UFP ($P < .14$). Additional linear regression analysis of nitrogen intake, nitrogen excretions and nitrogen retention when related to a logarithmic transformation of UFP values gave similar, but slightly less significant, results. Although quadratic UFP variables were not considered due to the experimental design, both nitrogen retention, as a percent of absorbed N, and digested N retention, as a percent of dietary N, appear to have optimal values near zero UFP values. This would imply a maximal efficiency of N retention associated with a value of zero UFP.

Feedlot Trial

The feedlot performance data of steers fed diets varying in UFP is shown in table 10. Simple regression analysis was conducted using UFP values as linear variables (UFP), as linear and quadratic variables ($\text{UFP} + \text{UFP}^2$) and as linear, quadratic and cubic variables ($\text{UFP} + \text{UFP}^2 + \text{UFP}^3$). In addition, a simple logarithmic transformation [$\ln(e^2 - \text{UFP})$] of UFP values was analyzed by linear regression analysis. Those models in which the most complex UFP variable made a significant

TABLE 10. FEEDLOT PERFORMANCE OF STEERS FED DIETS WITH VARYING UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
No. of steers	14	14	14	14	14
Average initial weight, kg	318	318	304	310	313
Average final weight, kg	416	451	447	449	451
Average gains, kg	98	133	143	139	138
Daily dry matter intake, kg**	7.92	8.66	9.17	9.16	8.90
Average daily gain, kg**	.80	1.09	1.16	1.13	1.12
Dry matter/ gain*	9.86	7.94	7.90	8.15	7.92

* Means are significantly related to a logarithmic transformation of UFP by linear regression analysis ($P < .05$); the logarithmic transformation used is $\ln(e^2 - \text{UFP})$.

** Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .005$).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

contribution ($P < .10$) to the model are summarized in table 11. F tests were conducted to compare the model error sums of squares (SSE) for the significance of including quadratic and/or cubic UFP variables in the model (Cornell, 1981). For example, if the SSE of a reduced model (i.e., ... UFP) is compared to the SSE of a more complete model (i.e., ... UFP + UFP²), the significance of the F test is the significance of the additional variable in the model (i.e., ... UFP²). The logarithmic transformation [$\ln(e^2 - \text{UFP})$] may not be compared to the other models by this F test. The prediction error sum of squares (Press) is used to compare all models for the same parameter and is a measure of the variation between the observed experimental values and those values predicted by the model (Gill, 1978). A lower Press statistic is indicative of less variation and generally represents a better fit of the model to the experimental data. Coefficients of determination (R^2) and the significance level of the F tests for each model are also included in table 11. Both dry matter intake and average daily gain were significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .004$ and $P < .003$, respectively). This is indicative that optimal daily dry matter intake and optimal average daily gain occurred between the diets with -1.4 and -3.9 UFP values. Feed efficiency (dry matter/gain) decreased logarithmically with decreasing UFP values ($P < .02$). The logarithmic model is chosen to represent the relationship between feed efficiency and UFP, because the linear relationship only tended to be significant ($P < .06$), the sequential addition of the quadratic and cubic variables only tended to be significant ($P < .10$) and the

TABLE 11. STATISTICAL INTERPRETATION OF FEEDLOT PERFORMANCE DATA FOR DIETS VARYING IN UFPe

Regression model ^f	SSE ^g	Pr>F ^h	R ²	Press ⁱ
Daily dry matter intake				
UFP	1.51 ^a	.004	.44	2.62
UFP + UFP ²	.56 ^a	.004	.79	1.44
ln (e ² - UFP)	1.11	.01	.59	1.82
Average daily gain				
UFP	.106 ^b	.03	.46	.170
UFP + UFP ²	.037 ^b	.003	.81	.064
ln (e ² - UFP)	.073	.006	.63	.114
Dry matter/gain				
UFP	4.45 ^{ac}	.06	.37	7.30
UFP + UFP ²	2.54 ^{cd}	.03	.64	5.26
UFP + UFP ² + UFP ³	1.36 ^{ad}	.01	.81	3.78
ln (e ² - UFP)	3.43	.02	.52	5.54

abcd SSE values for the same parameter with the same superscript are significantly different ($P < .10$)^{cd}, ($P < .05$)^a, ($P < .01$)^b; analysis used an F test to compare a reduced model with a complete model (Cornell, 1981).

^e Feedlot performance data given in table 10; urea fermentation potential values calculated from data obtained in present study.

^f Model was not included if additional variable was not significant.

^g Model error sum of squares.

TABLE 11-CONTINUED

- h Level of F test significance for model.
- i Prediction error sum of squares represents a statistical measure of the variation between observed and predicted values (Gill, 1978).

slight reduction in Press statistic value does not justify the use of the more complex models. There was a significant logarithmic relationship ($P < .02$) for feed efficiency to improve with decreasing UFP values. However, there is still considerable variation ($R^2 = .52$) unaccounted for by this logarithmic relation. The combined observations of dry matter intake, average daily gain and feed efficiency indicate that optimal feedlot performance occurred at a slightly negative UFP (-1.4 to -3.9), when determined from TDN, bypass protein and rumen degraded protein as described by Burroughs et al. (1975b). This slightly negative UFP range corresponds to the point of maximal metabolizable protein synthesis.

Using the metabolizable energy values determined in the metabolism trial and the energy gained in the comparative slaughter feedlot trial, the partitioning of dietary energy intake by feedlot steers consuming diets varying in UFP is summarized in table 12. ME intake, energy balance and energy gain are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .004$, $P < .0001$ and $P < .0004$, respectively, table 13). Because the diets are isocaloric ME intake follows the same parabolic pattern observed for DM intake (table 10). Both energy balance and energy gain indicate that increased energy deposition occurs with increased energy intake. The energy balance data was derived by comparing the empty body energy content after the feedlot trial with the estimated content before the feeding period using the initial slaughter group data. The energy content of the empty body was calculated from the equations of Garrett and Hinman (1969). The energy gain data was calculated from the

TABLE 12. ENERGY PARTITIONING DATA OF DIETS VARYING IN UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
ME intake, Mcal/day**	18.42	20.00	21.13	21.33	20.79
Energy balance, ^b Mcal/day***	4.78	6.19	6.66	6.76	6.50
Heat production, Mcal/day	13.64	13.81	14.47	14.57	14.29
NE _m heat, ^c Mcal/day	5.96	6.20	6.10	6.18	6.19
Heat increment, Mcal/day	7.68	7.61	8.37	8.39	8.10
NE _m , Mcal/kg diet DM	1.46	1.45	1.44	1.46	1.46
Energy gain, ^d kcal/W _{kg} ^{.75} ***	41.26	60.11	65.26	65.82	64.24
NE _g , Mcal/kg diet DM*	.84	1.11	1.05	1.07	1.11

* Means are significantly related to a logarithmic transformation of UFP by linear regression analysis ($P < .05$); the logarithmic transformation used is $\ln(e^2 - \text{UFP})$.

** Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .005$).

*** Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .001$).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b Energy balance from equations of Garrett and Hinman (1969).

^c NE_m heat equals 0.077 Mcal per W_{kg}^{.75}.

^d Energy gain from equations of Lofgreen and Garrett (1968).

TABLE 13. STATISTICAL INTERPRETATION OF ENERGY PARTITIONING DATA FOR DIETS VARYING IN UFP^c

Regression Model ^d	SSE ^e	Pr>F ^f	R ²	Press ^g
Metabolizable energy intake				
UFP	7.05 ^a	.02	.50	12.334
UFP + UFP ²	3.00 ^a	.004	.79	7.761
ln (e ² - UFP)	5.13	.006	.64	8.420
Energy balance ^h				
UFP	106 ^b	.0001	.33	122
UFP + UFP ²	89 ^b	.0001	.44	105
ln (e ² - UFP)	97	.0001	.39	112
Energy gain				
UFP	400 ^b	.01	.56	675
UFP + UFP ²	95 ^b	.0004	.90	183
ln (e ² - UFP)	243	.002	.74	400
Net energy for gain				
UFP	.083	.06	.38	.137
ln (e ² - UFP)	.068	.02	.49	.110

^{ab} SSE values for the same parameter with the same superscript are significantly different ($P < .05$)^a, ($P < .001$)^b; analysis used an F test to compare a reduced model with a complete model (Cornell, 1981).

^c Energy partitioning data given in table 12; urea fermentation potential values calculated from data obtained in present study.

^d Model was not included if additional variable was not significant.

TABLE 13-CONTINUED

- e Model error sum of squares.
- f Level of F test significance for model.
- g Prediction error sum of squares represents a statistical measure of the variation between observed and predicted values (Gill, 1978).
- h Energy balance models also contained initial age and initial metabolic body weight as covariates.

empty body weight gain using the regression equation of Lofgreen and Garrett (1968). Optimal energy intake and energy deposition occurred between -1.4 and -3.9 UFP values. This follows the same parabolic pattern observed in feedlot performance data (table 10), with the optimal response occurring near the point of maximal metabolizable protein synthesis. While the NE_m did not change with variation in UFP, NE_g increased in a logarithmic manner with decreasing UFP values ($P < .02$). This indicates that for isocaloric rations, there is a minimal protein requirement for optimal energy utilization. The energy deposition data further indicates that for isocaloric diets, there is an optimal dietary nitrogen level at which maximal tissue energy deposition occurs. Dietary nitrogen in excess of this level decreased energy deposition. This decreased energy gain is due more to a decreased energy intake (MEI) than to an effect on the efficiency of energy utilization (NE_g).

Empty Body and Carcass

Empty body and carcass data were analyzed following the format outlined for feedlot performance data. Empty body composition and tissue gains in steers fed diets varying in UFP are summarized in table 14. From the equations of Garrett and Hinman (1969), the daily empty body gains in weight, fat, total energy and energy from protein and fat are significantly ($P < .0001$) related by simple regression analysis with linear and quadratic UFP variables (tables 13 and 15). The low coefficients of determination (R^2) for the

TABLE 14. EMPTY BODY COMPOSITION AND TISSUE GAINS IN STEERS FED DIETS VARYING IN UFP^a

Empty body item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Average initial weight, kg	281.3	281.2	273.3	276.8	275.3
Average final weight, kg	373.9	409.4	407.0	413.5	412.3
Daily weight gain, kg**	.76	1.05	1.09	1.12	1.12
Final percent fat	26.19	27.69	28.88	28.94	28.11
Daily fat gain, kg**	.463	.591	.641	.650	.618
Final percent protein	16.26	15.96	15.73	15.72	15.88
Daily protein gain, kg*	.062	.099	.099	.102	.109
Final energy, Mcal/kg	3.36	3.49	3.59	3.59	3.52
Daily energy gain, ^b Mcal**	4.78	6.19	6.66	6.76	6.50
Daily fat-protein energy gain, Mcal**	4.69	6.10	6.57	6.66	6.41

* Means are significantly related to a logarithmic transformation of UFP by linear regression analysis ($P < .05$); the logarithmic transformation used is $\ln(e^2 - \text{UFP})$.

** Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .001$).

^a Empty body composition calculated using specific gravity from equa-

TABLE 14-CONTINUED

tions of Garrett and Hinman (1969); urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b Equivalent to energy balance in tables 12 and 13.

TABLE 15. STATISTICAL INTERPRETATION OF EMPTY BODY DATA FOR DIETS VARYING IN UFP⁹

Regression model ^h	SSE ⁱ	Pr>F ^j	R ²	Press ^k
Daily weight gain				
UFP	1.79 ^{ab}	.0001	.38	2.05
UFP + UFP ²	1.37 ^{ac}	.0001	.53	1.60
UFP + UFP ² + UFP ³	1.30 ^{bc}	.0001	.55	1.58
ln (e ² - UFP)	1.54	.0001	.47	1.76
Daily fat gain				
UFP	1.18 ^d	.0001	.32	1.37
UFP + UFP ²	1.02 ^d	.0001	.41	1.22
ln (e ² - UFP)	1.10	.0001	.36	1.27
Daily protein gain				
UFP	.0422 ^{ef}	.0001	.33	.049
UFP + UFP ²	.0386 ^{ce}	.0001	.39	.046
UFP + UFP ² + UFP ³	.0365 ^{cf}	.0001	.42	.045
ln (e ² - UFP)	.0394	.0001	.38	.045
Daily fat-protein energy gain				
UFP	104 ^a	.0001	.33	120
UFP + UFP ²	87 ^a	.0001	.44	103
ln (e ² - UFP)	95	.0001	.38	110

abcdef

SSE values for the same parameter with the same superscript are significantly different ($P < .10$)^c, ($P < .025$)^{ef}, ($P < .005$)^d, ($P < .001$)^{ab} analysis used an F test to compare a reduced model with a complete model (Cornell, 1981).

TABLE 15-CONTINUED

- ^g Empty body data given in table 14; urea fermentation potential values calculated from data obtained in present study.
- ^h Model was not included if additional variable was not significant; all models also contained initial age and initial metabolic body weight as covariates.
- ⁱ Model error sum of squares.
- ^j Level of F test significance for model.
- ^k Prediction error sum of squares represents a statistical measure of the variation between observed and predicted values (Gill, 1978).

empty body data indicate that although empty body data are very significantly related to variation in UFP, a large portion of the total variation remains unaccounted for. The regression models contained initial age and initial metabolic body weight as covariates to minimize the large amount of animal variation within the groups. At the initiation of the feedlot trial, steer weights ranged from 240 to 350 kg. Steers of similar breed and frame score would be at different points on the growth curve with this variation in initial weight (Berg and Butterfield, 1976). Initial animal variation was expected to be a major factor affecting ultimate empty body and carcass composition. Subsequent research should consider slaughtering animals at the same point on the growth curve or at the same final composition rather than at the same point in time. In agreement with the feedlot performance data (table 10) and the energy partitioning data (table 12), the empty body composition and tissue gain data indicate that optimal weight, fat and energy gains occurred with a slightly negative UFP value (between -1.4 and -3.9). Daily protein gain is logarithmically related to decreasing UFP values ($P < .0001$). This suggests that there are different protein and fat tissue deposition responses with respect to optimal nitrogen to energy balance. For isocaloric diets there is a minimal nitrogen content necessary for optimal tissue deposition of protein and fat. However, when nitrogen is in excess, there is a decreased energy (fat) deposition, while protein tissue deposition remains unchanged or increases slightly. This decreased adipose tissue deposition is probably due to a decreased energy intake (table 12).

The carcass characteristics and their statistical interpretation are summarized in tables 16 and 17, respectively. The regression models contained initial age and initial metabolic body weight as covariates to minimize initial animal variation. Even with the analysis of covariance, the coefficients of determination (R^2) for the carcass characteristics are extremely low. These low R^2 values suggest that while specific gravity, yield grade, texture of lean, fat over the ribeye, ribeye area and dressing percentages are significantly related to UFP variation, a substantial portion of the overall data variation still remains unaccounted for. This unaccounted portion may be in part due to the large initial animal variation within each group, to slaughtering animals at different points in the growth curve and to the overall difficulty of changing carcass characteristics by manipulating dietary composition. Berg and Butterfield (1976) postulated that level of nutrition only affects carcass composition indirectly by affecting the rate of growth or the rate of progression along the growth curve. At the same point on the growth curve, cattle have comparable carcass characteristics. The effect of nitrogen to energy balance on carcass characteristics could be better evaluated by slaughtering steers at comparable carcass compositions. The evaluation is then in terms of the rate of reaching a specific carcass composition rather than comparing carcass compositions after a specific length of feeding. In these terms, optimal nitrogen to energy balance is reflected in terms of a greater degree of finish (fattening) at the end of the feedlot trial. Consistent with the feedlot performance data (table 10), the energy partitioning

TABLE 16. CARCASS CHARACTERISTICS OF STEERS FED DIETS VARYING IN UFP^a

Carcass, item	UFP ^a			
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)
Specific gravity ^a	1.0535	1.0505	1.0482	1.0480
Marbling ^b	4.64	5.18	5.00	4.77
Quality grade ^c	3.07	3.25	3.26	3.16
Yield grade, % ^{***}	50.58	49.94	49.36	49.64
Maturity of lean ^d	1.71	1.65	1.63	1.72
Maturity of bone ^d	1.68	1.76	1.74	1.70
Color of lean ^e	4.71	4.50	4.50	4.78
Texture of lean ^{f*}	3.78	3.50	3.00	3.36
Firmness of lean ^g	1.86	1.71	1.86	1.93
Color of fat ^h	2.07	2.21	2.07	2.14
Hot carcass weight, kg ^{***}	245.8	270.4	269.6	273.8
Fat over ribeye, cm ^{***}	.89	1.14	1.32	1.12
Ribeye area, cm ² ^{***}	64.30	68.59	66.10	65.20
Kidney-pelvic-heart fat, %	2.32	2.43	2.25	2.21

Dressing percent*	59.08	59.86	60.22	60.96	59.90
Warner-Bratzler shear, kg	4.89	4.13	4.05	5.28	4.39

* Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .05$).

** Means are significantly related to UFP by linear regression analysis ($P < .005$).

*** Means are significantly related by simple regression analysis with linear and quadratic UFP variables ($P < .001$).

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b Small = 4.0; modest = 5.0; moderate = 6.0.

^c Choice = 3.0; prime = 4.0.

^d A maturity = 1.0; B maturity = 2.0.

^e Cherry red = 4.0; moderately dark red = 5.0.

^f Moderately fine = 3.0; slightly coarse = 4.0.

^g Very firm = 1.0; firm = 2.0.

^h Cream = 2.0; slightly yellow = 3.0.

TABLE 17. STATISTICAL INTERPRETATION OF CARCASS DATA FOR DIETS VARYING IN UFP^d

Regression model ^e	SSE ^f	Pr>F ^g	R ²	Press ^h
Specific gravity				
UFP	.00254 ^a	.047	.14	.00296
UFP + UFP ²	.00239 ^a	.019	.19	.00287
ln (e ² - UFP)	.00248	.025	.16	.00287
Yield grade				
UFP + UFP ²	54.2	.0001	.33	64.9
ln (e ² - UFP)	63.8	.004	.21	74.1
Texture of lean				
UFP	24.1 ^b	.14	.10	28.0
UFP + UFP ²	21.9 ^b	.02	.18	26.4
ln (e ² - UFP)	23.4	.06	.13	27.3
Hot carcass weight				
UFP	13977 ^c	.0001	.76	16166
UFP + UFP ²	9929 ^c	.0001	.83	11646
ln (e ² - UFP)	11972	.0001	.80	13756
Fat over ribeye				
UFP + UFP ²	3.53	.0001	.32	4.23
ln (e ² - UFP)	4.36	.02	.16	5.10
Ribeye area				
UFP	1749	.002	.22	2042
ln (e ² - UFP)	1742	.002	.23	2030

TABLE 17-CONTINUED

Dressing percent

UFP	199 ^a	.06	.13	234
UFP + UFP ²	187 ^a	.02	.18	226
ln (e ² - UFP)	195	.03	.14	228

-
- ^{abc} SSE values for the same parameter with the same superscript are significantly different ($P < .05$)^a, ($P < .025$)^b, ($P < .001$)^c; analysis used an F test to compare a reduced model with a complete model (Cornell, 1981).
- ^d Carcass data given in table 16; urea fermentation potential values calculated from data obtained in present study.
- ^e Model was not included if additional variable was not significant; all models also contained initial age and initial metabolic body weight as covariates.
- ^f Model error sum of squares.
- ^g Level of F test significance for model.
- ^h Prediction error sum of squares represents a statistical measure of the variation between observed and predicted values (Gill, 1978).

data (table 12), and the empty body composition data (table 14), the carcass characteristics (table 16) show the greatest degree of finish (fattening) between the -1.4 and -3.9 UFP diets. Specific gravity, yield grade, texture of lean, hot carcass weight, fat over the ribeye and dressing percentages are significantly related by simple regression analysis to linear and quadratic UFP variables. These carcass characteristics generally have maximum or minimum values between the -1.4 and -3.9 UFP diets. Lower specific gravity, lower yield grade percentages, finer textured lean, heavier carcass weight, more fat over the ribeye and higher dressing percentages are consistent with a higher energy intake occurring between the -1.4 and -3.9 UFP diets. This corresponds to the maximum metabolizable protein content of the diets. Ribeye area increased ($P < .002$) with decreasing UFP values. Since the linear and logarithmic models both fit the data equally (table 17), the simpler linear model was chosen to represent the increasing ribeye area with increasing dietary nitrogen content. The increased ribeye area is consistent with the logarithmic increase observed in empty body protein gain (table 14). While the low R^2 for most carcass characteristics indicates a substantial amount of variation remains unaccounted for by the models. The observed changes in various carcass characteristics is consistent with feedlot performance and energy partitioning results, suggesting that optimal carcass finish (fattening) was obtained between -1.4 and -3.9 UFP values.

Nitrogen to Energy Balance

Using the multiple regression equation of Satter and Roffler (1977), ruminal ammonia concentration was predicted from the dietary TDN and CP (not including CP from urea). These predicted ruminal ammonia concentrations and the upper limit of utilizable crude protein are presented for the diets in table 18. If natural crude protein is lower than those calculated from the upper limit values, then urea may be added as crude protein to make up the difference. Before addition of urea, the rumen $\text{NH}_3\text{-N}$ levels need to be below 5 mg per 100 ml rumen fluid, which was demonstrated to be the point of ammonia accumulation by Satter and Slyter (1974). The upper limit of utilizable crude protein is the maximal crude protein obtainable by the addition of urea to the diets and is calculated from the dietary TDN concentration. The dietary crude protein is N multiplied by 6.25. The upper limit of utilizable crude protein is the maximum obtainable from the addition of urea. The actual predicted crude protein is determined by the total dietary crude protein or the upper limit of utilizable crude protein whichever value is lower. The predicted dietary crude protein has an optimal value of about -3.9 UFP. The predicted CP values follow a similar parabolic pattern observed with the data of feedlot performance, energy partitioning, empty body energy, fat gain and carcass characteristics indicative of fattening. This suggests that the optimal nitrogen to energy balance as predicted by Satter and Roffler (1977) may serve as an indicator of increased animal performance and body fat gains due to increased energy intake.

TABLE 18. PREDICTED RUMINAL AMMONIA CONCENTRATION AND UPPER LIMIT FOR UREA UTILIZATION FOR DIETS VARYING IN UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Total digestible nutrients, %	69.6	69.3	69.0	71.0	71.2
Total crude protein, %	9.71	10.62	11.42	12.21	13.00
Urea, %	-	-	.10	.56	1.01
NH ₃ -N, ^b mg/100 ml rumen fluid	2.85	3.30	3.70	3.06	2.77
Upper limit of crude protein, ^b %	11.35	11.69	11.87	11.82	11.65
Predicted crude protein, ^c %	9.71	10.62	11.42	11.82	11.65

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b NH₃-N and upper limit of utilizable crude protein calculated by equations of Satter and Roffler (1977); NH₃-N levels do not include dietary urea NH₃.

^c Limited to the lower value of either total dietary crude protein or the upper limit of utilizable crude protein.

Metabolizable protein (MP) was calculated using the equations of Burroughs et al. (1975b). The percentages of corn grain, corn silage and soybean meal degraded in the rumen, and utilized in the calculations, were 62, 68 and 75%, respectively, as reported by Burroughs et al. (1975b). A comparison of MP values calculated using the TDN and CP values determined in the present study and those values given for feedstuffs by Burroughs et al. (1975b) is presented in table 19. Total MP, calculated from TDN and CP values determined in the present study follow the same parabolic pattern observed in feedlot performance and energy retention data. This indicates that the MP system of Burroughs et al. (1975b) has merit with respect to predicting animal performance. With isocaloric diets, increasing MP density resulted in increased dietary dry matter intake. Increased dietary energy intake resulted in increased animal performance and increased empty body fat and energy gains. While dietary MP concentrations determined in the present study are correlated with increased dietary energy intake, MP concentrations predicted for feedstuffs by Burroughs et al. (1975b) continues to increase with decreasing dietary UFP values and is not correlated with increasing dietary energy intake. The primary difference between the feedstuffs of Burroughs et al. (1975b) and those used in the present study is the TDN content. The TDN content of feedstuffs of Burroughs et al. (1975b) are similar to the values used by the NRC (1976), and both sources tend to overestimate TDN values for comparable Northwest Florida feedstuffs. Several other digestibility studies, conducted at the Agricultural Research Center near Jay, Florida (Maxson et al., 1973; Maxson, 1973; Brommelsiek, 1974, 1977; Brommelsiek et

TABLE 19. METABOLIZABLE PROTEIN (MP) AND UREA FERMENTATION POTENTIALS FOR DIETS VARYING IN UFP^a

Item, per kg feed DM	UFP ^a				
	+3.8	+1.2	-1.4	-3.9	-6.9
Undegraded abomasal protein (UAP), g	35.1	37.1	38.2	37.2	36.2
Rumen degraded protein (RDP), g	62.1	69.1	73.2	69.3	65.4
TDN times .1044, ^b g	72.7	72.4	72.0	74.1	74.3
Maximum MP from urea, g	-	-	2.2	12.5	22.5
Total MP, g	69.2	76.6	80.1	80.8	80.0
Predicted UFP, ^c g	+9.8	+6.9	+4.3	+1.2	-1.8
Predicted UAP, g	33.4	35.7	37.1	35.9	34.8
Predicted RDP, g	58.9	66.8	71.5	67.2	62.9
Predicted TDN times .1044, g	86.3	86.3	86.3	86.2	86.2
Maximum MP from urea, g	-	-	2.2	12.5	22.5
Predicted MP, g	65.1	73.6	80.8	86.5	88.2

^a Urea fermentation potential values calculated from data obtained in present study.

^b Total digestible nutrients.

^c Predicted UFP values given for feedstuffs by Burroughs et al., (1975b).

al., 1979), also indicate that energy values from the NRC (1976) and Burroughs et al. (1975b) are higher than energy values found for similar feedstuffs grown in Northwestern Florida. This was especially true for sorghum grain and silage diets.

Protein utilization, in accordance with the MP system (Burroughs et al., 1975a, b), was compared with observed protein deposition in tissues (table 20). MP intake was calculated from the feedlot DM intake (table 10) and the MP content of the diets (table 19). Net protein (NP) was calculated at 47% of MP according to Burroughs et al. (1975a). The NP for maintenance was estimated from the equation of Smuts (1935), and the remaining NP was available for gain. The observed empty body protein gain represents approximately one third of the expected NP_g derived from the MP system. While the MP system has a correlation with feedlot performance and energy retention, it overestimates the NP_g available for tissue deposition. This overestimation could occur in metabolic fecal values and in the efficiency of conversion of MP to NP. Chalupa (1980) and Bull et al. (1979) reviewed various methods for calculating NP requirements and found considerable variation in estimates for both these areas.

The NP system presented by Fox et al. (1977) predicts lower NP_g requirements, using the equation of Reid (1974). These NP_g requirements (table 21) exceed the observed tissue protein gain by substantial percentages. In general, the systems, which estimate NP_g requirements (Chalupa, 1980; Hogan, 1975; Roy et al., 1977; Fox et al., 1977; Burroughs et al., 1975 a, b), overestimate NP_g

TABLE 20. COMPARISON OF PROTEIN INTAKE AND PROTEIN TISSUE DEPOSITION IN STEERS FED DIETS VARYING IN UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Protein intake, g/day					
Crude	769	920	1047	1119	1158
Digestible, true ^b	700	837	953	1018	1054
Digestible, apparent	392	489	565	676	723
Metabolizable	548	664	734	740	713
Net ^c	258	312	345	348	335
Net protein utilization, g/day					
Maintenance ^d	62	64	64	64	64
Gain (NP _g)	196	247	282	283	271
Protein tissue gain, g/day	62	99	99	102	109
Protein gain/NP _g , %	32	40	35	36	40

^a Urea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b Estimated at 91% of CP.

^c 47% of MP (Burroughs et al., 1975a).

^d From the equation of Smuts (1935).

TABLE 21. COMPARISON OF NET PROTEIN (NP) REQUIREMENTS FOR PROTEIN TISSUE DEPOSITION IN STEERS FED DIETS VARYING IN UFP^a

Item	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
NP _m requirement, g/day ^b	62	64	64	64	64
NP _g requirement, g/day ^c	119	158	170	164	162
NP, % diet DM ^d	2.94	3.27	3.56	3.86	4.15
NP, % diet CP	30.3	30.8	31.2	31.6	31.9
Daily protein gain, g	62	99	99	102	109
Tissue gain/NP _g , %	53	63	58	62	67

^a Urea fermentation potential values calculated from data obtained in the present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^b From the equation of Smuts (1935).

^c From the equation of Reid (1974).

^d Not considering ammonia utilization potential.

compared to observed protein tissue deposition in the present feedlot trial. The percentages of daily protein gain with respect to average daily gain in feedlot steers for a number of literature references is given in table 22. When DES was utilized as an implant the percent protein deposition was greater than when Ralgro or no implant was used. The NP_g estimates using the MP system of Burroughs et al. (1975b) predicts more NP_g available for tissue deposition than was found in the studies cited in table 22. Estimates of NP_g are generally determined using short term nitrogen retention and metabolism studies (Burroughs et al., 1973b; Fox et al., 1977; Chalupa, 1980). The use of short term trials to estimate NP_g , compared to extended feedlot trials, appears to overestimate NP_g availability.

TABLE 22. DAILY PROTEIN TISSUE GAIN AS A PERCENT OF AVERAGE DAILY GAIN IN FEEDLOT STEERS

Breed of steers	Implant	Initial wt, kg	Days on feed	Protein gain, %		Reference
				avg.	daily gain ^a	
Angus-Hereford	DES	359	121,168,170	11.7,11.5,10.2		Fowler et al., 1970
Angus-Hereford	none	366	121,168,170	10.0,8.0,8.0		Fowler et al., 1970
Angus-Hereford	DES	326	128	14.6,15.3,15.9		Maxson, 1973
Angus-Hereford	Ralgro	307	127	9.0,9.7,10.6		Brommelsiek, 1977
Charolais-Brahman	DES	254	124	13.3,13.4,13.9,14.2		Richter, 1977
Charolais-Brahman	Ralgro	178	113	11.4,11.7,12.0		Harris, 1981
Angus-Hereford	Ralgro	313	119,126	7.8,8.5,9.0,9.2,9.7		Present study

^a Listed individually by treatment group.

CHAPTER FIVE

SUMMARY

A 5 x 5 Latin square metabolism trial and a comparative slaughter feedlot trial were conducted with British type steers to evaluate diets with various urea fermentation potentials (UFP) for feed efficiency, feed intake, total digestible nutrients (TDN), digestible energy (DE), metabolizable energy (ME), nitrogen utilization, deposition of protein and fat in tissues, net energy for maintenance (NE_m), net energy for gain (NE_g) and carcass characteristics. Corn grain and silage diets were fed. With increasing dietary nitrogen, UFP values were calculated to be +3.8, +1.2, -1.4, -3.9 and -6.9 g urea per kg diet dry matter, corresponding to a crude protein range of 9.7 to 13.0%. The dietary metabolizable protein (MP) levels were determined to be 69.2, 76.6, 80.1, 80.8 and 80.0 g per kg diet dry matter, respectively. Crude protein digestibility increased with decreasing UFP values ($P < .005$), but TDN showed no significant relationship to variation in UFP. Dry matter intake increased ($P < .005$) with decreasing dietary UFP, and thereby increased dietary energy and nitrogen intakes ($P < .005$). There were corresponding increases ($P < .001$) in urinary energy and nitrogen excretions. DE and ME showed no significant relationship with dietary UFP.

Eighty steers were randomly assigned to ten groups of eight in a comparative slaughter feedlot trial. The five diets with decreasing UFP were each fed to two groups of steers. One steer from each group was slaughtered at the beginning of the trial to determine initial body composition. While NE_m was not significantly related to UFP, feed efficiency improved and NE_g increased logarithmically ($P < .05$) with decreasing dietary UFP levels.

Average daily gain, DM intake, ME intake and energy balance were parabolically related ($P < .005$) to dietary UFP levels. Optimal feedlot performance and energy utilization were observed at -1.4 to -3.9 UFP levels, which corresponds to maximum dietary MP concentration.

Carcass specific gravity was utilized to determine empty body fat and protein. Daily gains in empty body weight, fat and energy were parabolically related ($P < .001$) to dietary UFP levels. Optimal empty body gains were also observed to occur between -1.4 and -3.9 UFP levels, which corresponds to maximum dietary MP concentration. Empty body protein gain per day increased logarithmically ($P < .05$) with decreasing dietary UFP levels. Carcass specific gravity, yield grade, texture of lean, hot carcass weight, fat over the ribeye and dressing percentage followed similar parabolic patterns with changes in dietary UFP. Their respective maxima and minima suggested that an increased degree of carcass finish (fattening) occurred with increased dietary MP concentration. Ribeye area increased with decreasing dietary UFP levels.

While the MP system (Burroughs et al., 1975b) has merit with respect to predicting animal performance, it overestimated NP_g availability for protein gained in the tissues over the 119 to 126 day feedlot trial. The use of short term nitrogen retention studies to establish NP_g requirements may lead to overestimation of NP_g availability. Further studies should be undertaken to determine the optimal MP concentration for other dietary energy levels, to determine NP_g available for tissue deposition and to establish specific NP_g requirements.

APPENDIX

TABLE 23. BODY COMPOSITION DATA OF STEERS IN INITIAL COMPARATIVE
SLAUGHTER GROUP

Item	Data
No. of steers	10
Shrunk weight, kg	311.3
Empty body weight, kg	280.1
Carcass specific gravity	1.0766
Empty body ether extract, %	14.68
Empty body protein, %	18.88
Empty body energy, Mcal/kg	2.39

TABLE 24. COMPARISON OF OBSERVED AND EXPECTED AVERAGE DAILY GAINS OF STEERS

Item, kg per day	UFP ^a				
	+3.8 (+9.8)	+1.2 (+6.9)	-1.4 (+4.3)	-3.9 (+1.2)	-6.9 (-1.8)
Observed average gain	.80	1.09	1.16	1.13	1.12
Expected average gain ^b	.86	.94	1.05	1.09	1.03

^aUrea fermentation potential values calculated from data obtained in present study; values in parenthesis given for feedstuffs by Burroughs et al. (1975b).

^bDetermined from TDN (Church, 1980): $TDN = 0.0553 (1b \text{ body wt})^{.67} [1 + 0.805(1b \text{ gain})]$.

TABLE 25. CORRELATION COEFFICIENTS BETWEEN VARIABLES OF FEEDLOT PERFORMANCE, ENERGY PARTITIONING AND DIETARY METABOLIZABLE PROTEIN

Variable	ADG	Feed/gain	MEI	EG ^a	NE _g	UFP ^b	MP ^c	NH ₃ -AP ^d
DMI	.84	-.63	1.00	.89	.49	-.66	.88	.85
ADG		-.95	.83	.97	.84	-.68	.91	.84
Feed/gain			-.62	-.90	-.95	.61	-.83	-.74
MEI				.88	.48	-.71	.88	.86
EG					.82	-.75	.96	.90
NE _g						-.62	.77	.86
UFP							-.83	-.91
MP								.97

^a Energy gain from empty body weight gain by the equation of Lofgreen and Garrett (1968).

^b Urea fermentation potential values calculated from data obtained in present study.

^c Dietary metabolizable protein content calculated from equations of Burroughs et al. (1975b).

^d Maximal dietary crude protein predicted by point of ruminal ammonia accumulation (Satter and Roffler, 1977).

TABLE 26. CORRELATION COEFFICIENTS BETWEEN VARIABLES OF DAILY EMPTY BODY COMPOSITION, CARCASS CHARACTERISTICS AND DIETARY METABOLIZABLE PROTEIN

Variable	Protein gain	Specific gravity	YG ^a	REA ^b	FOE ^c	HCW ^d	UFP ^e	MP ^f	NH ₃ -AP ^g
Fat gain	.02	-.92	-.50	.27	.46	.70	-.32	.43	.41
Protein gain		.25	-.02	.24	.05	.27	-.46	.52	.49
Specific gravity			.45	-.07	-.42	-.42	.22	-.30	-.29
YG				.27	-.82	-.49	.13	-.30	-.27
REA					.06	.55	-.15	.14	.11
FOE						.43	-.14	.37	.30
HCW							-.25	.33	.31
UFP								-.83	-.91
MP									.97

^a Yield grade percent.

^b Ribeye area.

^c Fat over the ribeye.

^d Hot carcass weight.

^e Urea fermentation potential values calculated from data obtained in present study.

^f Dietary metabolizable protein content calculated from equations of Burroughs et al. (1975b).

^g Maximal dietary crude protein predicted by point of ruminal ammonia accumulation (Satter and Roffler, 1977).

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Animal Science

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