

Effects of compensatory growth on protein metabolism and meat tenderness of beef steers

H. L. Bruce¹, R. O. Ball^{1,2,3}, and D. N. Mowat¹

¹Department of Animal and Poultry Science, University of Guelph, Guelph, Ontario, Canada N1G 2W1; ²Department of Nutritional Sciences, University of Toronto, Toronto, Ontario, Canada M5S 1A8. Received 25 Oct. 1990, accepted 23 May 1991.

Bruce, H. L., Ball, R. O. and Mowat, D. N. 1991. **Effects of compensatory growth on protein metabolism and meat tenderness of beef steers.** *Can. J. Anim. Sci.* 71: 659–668. The relationships between meat tenderness and the changes in metabolism and body composition associated with compensatory growth in cattle were examined. Thirty-six steers were randomly allotted to 12 pens of three with three diets assigned randomly to the pens. Diets were alfalfa/grass silage, alfalfa/grass silage supplemented with corn gluten and bloodmeal and corn silage supplemented with soybean meal. Six steers from each treatment were slaughtered on each of days 124 and 175 of the trial to assess carcass characteristics. Following 124 d on trial, the remaining steers received a high-grain finishing diet. Blood and urine samples were collected throughout the trial for analyses of 3-methylhistidine, hydroxyproline and creatinine. At each slaughter, non-carcass components were cleaned and weighed. Lean, fat and bone proportions were estimated with a 9th-10th-11th rib dissection. Following dissection, the longissimus muscles were frozen at -10°C for analysis of shear force, collagen and protein solubility. The steers fed the alfalfa/grass silage experienced compensatory growth within the first 14 d of the finishing phase. Steers fed the alfalfa/grass silage had lower gain throughout the growing phase (0–124 d), and empty body weight was less than that of the steers fed corn silage. Compensatory growth was observed in steers fed corn silage during the first 14 d of the finishing diet, as evidenced by higher gains compared with steers fed the other diets. Differences in body composition among treatments at 124 d and 175 d were related to dietary energy and not compensatory growth. Meat tenderness, measured by shear force, appeared to be affected primarily by dietary energy and intramuscular fat rather than by rate of growth.

Key words: Compensatory growth, steers, meat tenderness, beef

Bruce, H. L., Ball, R. O. et Mowat, D. N. 1991. **Effets de croissance compensatoire sur le métabolisme protéique et sur la tendreté de la viande des bouvillons.** *Can. J. Anim. Sci.* 71: 659–668. On a étudié sur des bouvillons les rapports existant entre la tendreté de la viande et les modifications du métabolisme et de la composition corporelle et également la croissance compensatoire. Trente-six bouvillons ont été répartis au hasard en douze parquets de trois. Trois régimes alimentaires étaient attribués au hasard aux divers parquets. Les régimes étudiés étaient (1) ensilage luzerne-graminée, (2) le même plus un complément de gluten de maïs et de farine de sang, (3) ensilage de maïs complétement par du tourteau de soja. Pour chaque traitement, six bouvillons étaient abattus au 124^e et au 175^e jour de l'essai, pour évaluer les qualités de la carcasse. Après le 124^e jour, les bouvillons restants recevaient un aliment de finition à forte teneur en céréales. Tout au long de l'essai, le sang et l'urine ont été analysés pour leurs concentrations en 3-méthylhistidine, hydroxyproline et créatinine. A chaque abattage, les viscères gastro-intestinaux étaient nettoyés puis pesés. La proportion de maigre, de gras et d'os a été estimée par dissection d'un morceau allant de la 9^e à la 11^e côte. Le muscle longissimus a été congelé à -10°C puis évalué pour la force de cisaillement et pour la solubilité du collagène et des protéines. Les bouvillons au régime ensilage luzerne-graminée avaient un gain de poids moins fort tout au long de la phase de croissance (0 à 124 j) et leur poids à vide était moindre que

³To whom reprint requests should be addressed.

chez les bouvillons à l'ensilage de maïs. Toutefois, une croissance compensatoire a été observée chez ces bouvillons dans les 14 premiers jours de la phase de finition, de sorte que dans cette période leur gain était supérieur à celui des bouvillons exposés aux autres régimes. Les différences de composition corporelle selon les traitements au 124^e et au 175^e jour s'expliquent par le niveau énergétique de l'aliment et non par la croissance compensatoire. La tendreté, mesurée par la force de cisaillement, semble avoir été affectée principalement par le niveau énergétique de l'aliment et par la teneur en graisse intramusculaire, plutôt que par le rythme de croissance.

Mots clés: Croissance compensatoire, bouvillons, tendreté de la viande, boeuf

Compensatory growth in cattle is a well-documented phenomenon (Bohman and Torell 1956; Horton and Holmes 1978) usually accompanied by increased feed intake (Lofgreen and Kiesling 1985) and improved feed efficiency (Bohman and Torell 1956) following a period of underfeeding. Compensatory growth in cattle, particularly market steers, appears to be greatest and most efficient in the period immediately following an inadequate diet (Fox et al. 1972). Despite its renown, the added feed efficiency during compensatory growth is not completely understood. Few studies have documented metabolic changes in cattle throughout restriction and compensation, or the effects of diet on meat quality (Morgan 1972). Consequently, the objectives of this experiment were to examine the effects of compensatory gain following protein and energy restriction during growth on (1) the type and composition of growth, (2) metabolic indicators of protein turnover and (3) meat quality.

MATERIALS AND METHODS

Experimental Design

Thirty-six Charolais-cross steer calves were fed a diet of predominantly alfalfa/grass silage during a 2 mo adjustment period at the Elora Beef Cattle Research Station, University of Guelph. Calves weighing ($x \pm SD$) 262.2 ± 16.3 were randomly allotted to 12 pens of three animals. Three treatments were randomly allotted to the pens: alfalfa/grass silage; alfalfa/grass silage supplemented with corn gluten meal and blood meal (60:40); and corn silage supplemented with soybean meal (Table 1). All calves received injections of vitamins ADE and Ivomec (Merck-Frosst Canada Inc., Kirkland, ON) and were implanted with Synovex-S (Syntex, Mississauga, ON). Cattle

were fed completely mixed diets ad libitum for 124 d. Following 124 d on trial, all animals were fed a high-grain finishing diet (Table 1). Prior to slaughter, feed was withdrawn for 24 h and water for 16 h. Six steers from each treatment were slaughtered at each of 124 d and at 175 d to examine compensatory changes in carcass characteristics.

Metabolic Indicators

Blood and urine were collected from the steers designated for slaughter at 175 d. Samples were collected on day 0 and every 21 d until the diet changed to the finishing ration at 124 d. Samples of blood and urine were collected at 7, 14, 28 and 49 d following the change of diet. Blood was drawn from the jugular vein into heparinized vacutainers that were kept on ice until the plasma was separated and frozen at -20°C . Manual stimulation of the scrotal region was used to encourage urination. Urine was collected and frozen at -20°C .

Blood and urine samples were prepared for HPLC analysis for 3-methyl-histidine (3-MH) and hydroxyproline (Early and Ball 1987). Twenty μL of norleucine was added to 200 μL of blood and the sample was de-proteinized using a 3:1 ratio of acetone to blood. De-proteinized samples were centrifuged at $20\,000 \times g$ for 3 min and freeze-dried overnight. Lyophilized samples received 20 μL of amino acid elution solution (6:2:2 ratio of H_2O :triethylamine:methanol) and were freeze-dried again. Dried samples then received 20 μL of derivatization solution (7:1:1:1 ratio of methanol:triethylamine:phenylisothiocyanate: H_2O) and were incubated for 30 min at room temperature before freeze-drying. Samples were resuspended in a phosphate buffer containing 5% acetonitrile and were filtered through a 0.45- μm nylon filter (Gelman Scientific, Ann Arbor, MI). Samples of urine were prepared similarly, except de-proteinization was not required, and 1 mL of sample was used as the initial volume. Samples of urine and blood were analyzed on a Waters HPLC

Table 1. Composition of diets (percent of dry matter)

Ingredients	Growing phase		Corn silage & soybean meal	Finishing phase
	Alfalfa/grass silage			
	Unsupplemented	Supplemented		
Alfalfa/grass silage	92.20	89.51		28.50
Corn silage			86.65	
Dry corn	4.75			
High moisture corn				68.60
Soybean meal			10.00	
Corn gluten: blood meal		7.50		
Dicalcium phosphate	0.70	0.64	1.00	0.55
TM salt ^z	0.35	0.35	0.35	0.35
Rumensin premix ^y	2.00	2.00	2.00	2.00

^zTrace-mineralized salt. Contained: 96.5% NaCl; 0.4% Zn; 0.16% Fe; 0.12% Mn; 0.03% Cu; 0.007% I; 0.0004% Co.

^yContained: 98.88% corn and 1.12% rumensin providing 29 g monensin sodium per tonne dry matter.

system (Millipore/Waters, Mississauga, ON) consisting of two 6000A pumps, a 440 Fixed-Wavelength Absorbance Detector set at 254 nm, a Temperature control module, a 710B WISPTM Sample Processor and an 840 Data and Chromatographic Control Station. The column used was a Waters Pico-tagTM C₁₈ reverse-phase column maintained at 46°C. Peak identification and quantitation were accomplished by determining retention times and recoveries of 3-MH and 4-trans-hydroxyproline standards (Sigma Chemical Company, St. Louis, MO).

Concentrations of creatinine in blood and urine were analyzed (Sigma Chemical Company, St. Louis, MO) following a tenfold dilution of the samples.

Body Composition

Animals were slaughtered according to conventional abattoir procedure. The head, feet, hide and tail were weighed upon removal, as were the liver, kidneys, heart, lungs, spleen, internal fat and hanging tender. The gastrointestinal tract was removed, cleaned of its contents and weighed to determine gut weight and fill. Carcasses were chilled at 2°C, graded 24 h postmortem and then aged at 2°C for 7 d.

After aging, the 9th, 10th and 11th rib section was removed from the carcass and assessed for rib fat, rib eye area, marbling and color. The lean, fat and bone were separated to discern tissue partitioning, as well as the compartmentalization of body, subcutaneous and intermuscular fat. The loin eyes were vacuum-packaged and frozen at -10°C for subsequent analysis for shear force, collagen and protein solubility.

Meat Quality

Longissimus muscle from the 9th and 10th rib section was used to measure shear force. Longissimus muscles were thawed at 2°C and roasted at 169°C to an internal temperature of 70°C (Salm et al. 1983). Three core samples, 2.2 cm in diameter, were removed parallel to the muscle fibres and the force required to shear each core was measured using an Instron Universal Testing Device (Instron Corp, Caton, MA) equipped with a Warner-Bratzler type shear cell.

A steak for chemical analysis was sliced from the 11th rib section of each frozen longissimus muscle, trimmed of epimysium, cubed and freeze-dried. The dried samples were blended to a powder with dry ice in a blender and stored at -10°C.

Collagen solubility was determined according to the method of Hill (1966) and hydroxyproline concentration was measured using the colorimetric method of Bergman and Loxley (1963), in which 1-mL samples of the resulting supernatants and 0.1 g of each residue were hydrolyzed at 110°C for 6 h in 6 N HCl. The hydrolysis products were evaporated at 50°C and reconstituted with 5 mL of double distilled water. The resulting acidic reconstitute was neutralized with 1.0 M NaOH and 1 mL of this solution was used for analysis. Absorbance was read within 4 h at 558 nm (LKB Ultraspec II, Cambridge, U.K.). Hydroxyproline concentrations were converted to soluble and insoluble collagen concentrations using the factors 7.52 and 7.25 respectively (Cross et al. 1973). A standard curve was constructed using L-4-trans-hydroxyproline (Sigma Chemical Company, St. Louis, MO).

Protein solubilities were determined by the method outlined in Link et al. (1970). Briefly, two 0.5-g samples were extracted for sarcoplasmic and total soluble protein with 15 mL of 0.03 M KH_2PO_4 , pH 7.4, and with 15 mL 1.1 M KI, buffered to pH 7.4 with KH_2PO_4 , respectively. Sarcoplasmic protein was extracted with two 3-h extractions and total soluble protein with two 3-h extractions and one 2-h extraction. All extractions were performed at 2°C. Protein concentrations of the extracts were determined with a BCA reagent kit (Pierce Chem. Co., Rockford, IL). Absorbances were determined spectrophotometrically at 500 nm after a 30-min incubation at 37°C for colour development. Blanks contained each respective extraction buffer and standards were prepared from BSA. Myofibrillar protein content was calculated as the difference between the total soluble and sarcoplasmic protein fractions. Total protein ($N \times 6.25$) in each sample was determined by a micro-Kjeldahl method (Association of Analytical Chemists 1984). Collagen and protein solubilities were expressed as g soluble 100 g^{-1} protein ($N \times 6.25$).

Statistical Analyses

Analysis of variance was used to determine significant differences between the three diets and the two times of slaughter (124 and 175 d) using the General Linear Models procedure of the Statistical Analysis System Institute, Inc. (1985). Pearson correlations were used to determine linear relationships between meat quality, carcass components and metabolic characteristics (SAS Institute, Inc. 1985). Analysis of covariance was used to evaluate

the effect of fat content on shear force. Differences were considered statistically significant at $P < 0.05$.

RESULTS AND DISCUSSION

Growth

Growth during the first 124 d of the feeding trial was less in the steers receiving the unsupplemented alfalfa/grass diet than in steers receiving protein supplementation (Table 2). Overall DM intakes during the growing period with the three diets (Table 1) were 7.35, 7.86 and 7.02 kg d^{-1} , respectively. Intake was significantly higher ($P < 0.05$) for the supplemented alfalfa/grass diet than for the other diets. These data are comparable to those in several earlier studies which suggested that growing steers fed high levels of alfalfa/grass silage were in fact deficient in protein (Viera et al. 1985; Mowat and Buchanan-Smith 1988). However, on the finishing diet, mean average daily gain for these steers was greater than those of steers fed the other diets. This increase in average daily gain was considered indicative of compensatory growth (Bohman and Torell 1956) and is comparable to that reported recently in companion studies with larger numbers of steers (Mowat and Buchanan-Smith 1990).

During the growing phase, the corn silage diet contained 13.6% crude protein on a DM basis (CP), fully adequate by NRC (1984)

Table 2. Effect of growing phase diet on growth rates (kg d^{-1}) of steers during growth (0–124 d) and finishing (124–175 d)

Time period	Growing phase diets			SD
	Alfalfa/grass silage		Corn silage	
	Unsupplemented	Supplemented		
<i>Growth phase</i>				
0 to 25 d	0.56 ^a	1.32 ^b	1.08 ^b	0.22
0 to 53 d	0.76 ^a	1.27 ^b	1.25 ^b	0.20
0 to 91 d	0.89 ^a	1.26 ^b	1.30 ^b	0.15
0 to 124 d	0.93 ^a	1.27 ^b	1.27 ^b	0.12
<i>Finishing phase^z</i>				
124 to 138 d	2.04 ^a	1.21 ^b	1.14 ^b	0.43
124 to 152 d	1.47	1.07	1.09	0.26
124 to 175 d	1.39	1.29	1.20	0.22

^zAll animals received the same finishing diet during the finishing phase.

^{a,b}Means with different letters within a row are different according to Student-Newman-Keuls test ($P < 0.05$).

standards. The alfalfa/grass silage diet supplemented with corn gluten meal and blood meal, two highly rumen undegradable protein sources (NRC 1989), contained 26.7% CP. The unsupplemented alfalfa/grass silage diet contained 21.5% CP. However, 57.2% of the CP in this silage was as non-protein nitrogen, suggesting that extensive proteolysis had taken place during the ensiling process. The finishing diet contained 14.6% CP.

Body Composition

Although protein deprivation did not affect liveweight, it decreased the empty body weight (EBW) of the steers slaughtered at 124 d (Table 3). This difference in EBW appeared to be due to a trend of reduced carcass and non-carcass components ($P < 0.10$). Live weight was not different because steers fed the alfalfa/grass silage diet had slightly more gut-fill than the steers fed

Table 3. Means and standard deviations (SD) of starved liveweight, empty body weight, carcass and noncarcass components, and gut-fill for steers slaughtered at 124 and 175 d

Slaughter day	Diets			SD
	Alfalfa/grass silage		Corn silage	
	Unsupplemented	Supplemented		
124 d				
Liveweight (kg)	377.5	382.1	388.8	20.8
Empty body weight (kg)	309.9 ^a	321.1 ^{ab}	333.9 ^{b(5)} ^z	13.5
Carcass (g kg ⁻¹ EBW)	539.9	552.7	574.6(5)	56.3
Non-carcass (g kg ⁻¹ EBW)	281.4	292.2	286.6	9.8
Gut-fill (g kg ⁻¹ EBW)	298.6	272.3	216.9(5)	80.8
175 d				
Liveweight (kg)	434.3	460.5	449.1	27.4
Empty body weight (kg)	385.4(5)	396.2	383.2	26.5
Carcass (g kg ⁻¹ EBW)	605.8	577.9	570.3	41.2
Non-carcass (g kg ⁻¹ EBW)	284.5(5)	282.1	282.7	13.7
Gut-fill (g kg ⁻¹ EBW)	207.1(5)	219.5	218.9	44.1

^z $N = 6$ except where shown in parentheses ($n = 5$).

^{a, b}Means with different letters within a row are different ($P < 0.05$).

Table 4. Means and standard deviations (SD) of rib weights and fat, lean and bone proportion of 9-10-11th rib section for steers slaughtered at 124 and 175 d

Slaughter day	Diets			SD
	Alfalfa/grass silage		Corn silage	
	Unsupplemented	Supplemented		
124 d				
Rib weight (g kg ⁻¹ EBW)	7.84 ^a	7.72 ^a	9.91 ^b	0.95
Fat (g kg ⁻¹ rib)	176.2	163.7	216.3	45.0
Lean (g kg ⁻¹ rib)	621.0	610.7	588.8	31.1
Bone (g kg ⁻¹ rib)	213.5 ^a	221.0 ^a	186.5 ^b	21.5
175 d				
Rib weight (g kg ⁻¹ EBW)	7.64 ^a	7.82 ^a	9.35 ^b	0.91
Fat (g kg ⁻¹ rib)	231.8	242.7	286.8	42.6
Lean (g kg ⁻¹ rib)	574.5	548.8	535.1	37.9
Bone (g kg ⁻¹ rib)	193.6 ^{ab}	208.3 ^a	177.9 ^b	17.3

^{a, b}Means with different letters within a row are different ($P < 0.05$).

corn silage. Carstens (1988) found that compositional differences in the non-carcass tissues were due to reductions of fat content in the viscera of the underfed steers, and not gut-fill; however, Carstens (1988) fed restricted amounts of the same diet as the control steers to obtain compensatory growth, while in the present experiment dietary inadequacy was achieved through protein deprivation with a forage-based diet. In the present experiment, although there may have been unmeasured changes in visceral fat deposition, there were no differences in dissectible fat in the 9th-10th-11th rib separation for steers at 124 d (Table 4). The confounding effect of food intake versus composition is also shown by the nonsignificant effect of protein supplementation of the alfalfa/grass silage on the EBW of steers (Table 3) probably due to the effect of roughage on gut-fill (Kay et al. 1970) in these cattle.

After receiving the finishing diet for 51 d, EBW of steers fed the unsupplemented alfalfa/grass silage diet equalled the EBW of the steers fed the corn silage diet (Table 3). The compensation was primarily in carcass components since the control diet had the lowest proportion of EBW in carcass components at 124 d but the highest proportion at 175 d. These data agree with studies by Carstens (1988) and Fox et al. (1972) who found no differences in empty body weight, at similar slaughter weights (500 and 454 kg,

respectively), between control and compensatory steers following compensatory growth.

Differences between rib weights and proportion of bone and fat at 124 and 175 d (Table 4) appeared to be related to dietary energy rather than protein deprivation, since these parameters were not different between control and protein supplemented steers at either 124 or 175 d. However, steers fed the alfalfa/grass diets had lighter ribs containing a lower proportion of fat and a higher proportion of bone at both 124 and 175 d compared to steers fed corn silage, probably reflecting the higher dietary energy intake of steers receiving corn silage. Patterson et al. (1985) found that steers on a high-energy diet tended to have less bone in the rib side. Jones (1985) also showed that steers fed forage-based diets had a greater proportion of bone than grain-fed steers. Clearly, dietary energy exerted a greater effect on body composition than protein intake or compensatory growth. Greenhalgh (1986) also found that slow growth followed by fast growth had little effect on lean, fat and bone proportion, while growth stasis produced partitioning differences.

Metabolic Indicators

Hydroxyproline and 3-MH in plasma and urine were both expressed as ratios to creatinine in order to adjust for differences in muscle mass so that changes would reflect muscle metabolism (Gibson 1990). Free

Table 5. Means and standard deviations (SD) of concentrations of hydroxyproline and 3-methylhistidine in urine and plasma for steers slaughtered at 124 and 175 d

Time	Diets			SD
	Alfalfa/grass silage		Corn silage	
	Unsupplemented	Supplemented		
124 d	<i>(mg mg⁻¹ creatinine 100 mL⁻¹)</i>			
Urinary hydroxyproline	0.0080	0.0094	0.0085	0.0320
Plasma hydroxyproline	1.090 ^{ab}	0.6287 ^a	1.6024 ^b	0.0535
Urinary 3-methylhistidine	0.0023	0.0022	0.0029	0.0001
Plasma 3-methylhistidine	0.6228	0.2639	0.6189	0.0649
175 d				
Urinary hydroxyproline	0.0663	0.0433	0.1583	0.0881
Plasma hydroxyproline	0.5190	0.4934	0.5248	0.0677
Urinary 3-methylhistidine	0.0033	0.0034	0.0053	0.0002
Plasma 3-methylhistidine	0.2847	0.2372	0.2290	0.0804

*a,b*Means with different letters within rows are different ($P < 0.05$).

hydroxyproline has been found to be an indicator of collagen turnover (Prockop and Kivirikko 1967), which may influence meat tenderness through changes in intramuscular collagen solubility (Bailey 1985). Concentrations of hydroxyproline and 3-MH in plasma and urine were unaffected by the fluctuations in growth rates produced by dietary manipulation (Table 5).

Significant differences between the diets for plasma hydroxyproline at 124 d appeared to be related to dietary energy and growth rate. Steers fed the protein supplemented alfalfa/grass silage diet had lower concentrations of hydroxyproline in plasma than the steers fed corn silage although growth rates were not different. Although plasma hydroxyproline tends to increase with growth rate because of increased collagen turnover it may also increase as a result

of muscle remodelling or changes in muscle mass even when liveweight gain is not affected (Bailey 1985; Eisemann et al. 1986). No differences were observed by slaughter at 175 d.

Elevation of 3-MH excretion, which reflects protein degradation, appears to require deficiency of dietary protein (Young and Munro 1978). Although a response in concentration of 3-MH to protein deprivation was not shown in plasma and urine samples taken only at 124 d, an indication of a metabolic response occurred when urinary 3-MH was depicted over time (Fig. 1). The steers fed the alfalfa/grass silage diet appeared to excrete more 3-MH than the steers fed the protein supplemented diets within the first 50 d of protein deprivation, but differences were not significant because of large variation among samples.

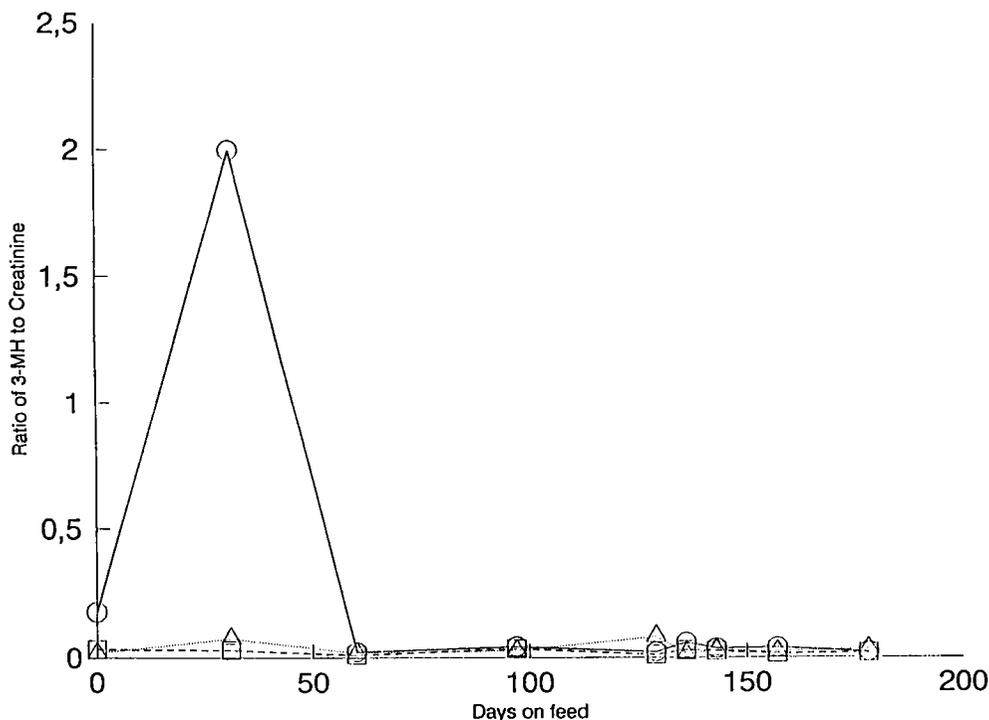


Fig. 1. Effects of diets during growing and finishing phase (175 d total) on urinary 3-methylhistidine (3-MH) concentrations adjusted for muscle mass using creatinine excretion. Diets are: —○—, alfalfa/grass silage; ---□---, alfalfa/grass silage plus protein supplement; ---△---, corn silage plus soybean meal.

Table 6. Effect of diet on collagen and protein solubility^a and shear force

Characteristic	Diets			
	Alfalfa/grass silage		Corn Silage	SD
	Unsupplemented	Supplemented		
Soluble collagen (%) ^z				
124 d	10.69	8.12	9.04	4.89
175 d	9.31	10.59	11.91	3.98
Sarcoplasmic protein (g kg ⁻¹) ^y				
124 d	179.5a	171.0ab	158.1b	11.1
175 d	185.7	179.6	168.6	18.2
Myofibrillar protein (g kg ⁻¹) ^y				
124 d	510.0	437.8	427.8	59.1
175 d	461.1	501.5	486.5	42.5
Shear force (kg)				
124 d	5.19a	5.01a	3.56b	0.82
175 d	4.50ab	5.24a	3.59b	0.84

^zPercent of total collagen.

^yProportion of each total which was soluble.

a,b Means with different letters within rows are different ($P < 0.05$).

Meat Quality Characteristics

No treatment differences were found for soluble collagen expressed as a percent of total collagen (Table 6). Although differences in collagen turnover and crosslinkage formation may have occurred, as suggested by the changes in blood hydroxyproline, the cross-link changes were not sufficient to change the heat lability of the collagen as measured by the method of Hill (1966).

There were also no effects of compensatory growth on total or myofibrillar protein solubility (Table 6). Sarcoplasmic protein solubility was higher in meat from steers of the unsupplemented alfalfa/grass diet than steers fed the corn silage when slaughtered at 124 d.

Shear force was lowest ($P < 0.05$) in meat of steers fed the corn-silage diet (Table 6). The meat of steers fed alfalfa/grass diets were of similar tenderness. These data suggest that shear force was influenced by the dietary energy but was not affected by protein supplementation. These data also suggest that increased sarcoplasmic protein solubility was indicative of decreased tenderness. Indeed, sarcoplasmic protein solubility was significantly correlated to shear force ($P < 0.05$, $r = 0.34$). This association may be indicative of a relationship between protein restructuring

and meat tenderness. Myofibrillar protein solubility has been more frequently reported to be associated with meat tenderness (Herring et al. 1967). Plasma N-3-MH, an indicator of muscle protein turnover, was not related to myofibrillar solubility in our experiment, but was related to sarcoplasmic protein solubility ($r = 0.38$, $P < 0.05$). Rapid muscle protein turnover would increase soluble protein available in the sarcoplasm from muscle accretion and remodelling. Work done in our laboratory (Murch et al. 1991) has shown that the fraction of solubility extractions previously believed to contain primarily sarcoplasmic proteins also contains significant quantities of myosin, actin and myoglobin. Therefore, the proteins soluble in the low ionic extraction solution may be indicative of functions related to meat tenderness.

Time of slaughter and diet affected the fat content of the muscle. Steaks from steers fed for 175 d had more ether extractable lipid (11.1%, SE=0.72) than steaks from steers fed for 124 d (7.2%, SE=0.72). There were no differences between the diets for extractable lipid (corn silage, 11.2%, alfalfa/grass silage supplemented with protein, 8.22%, alfalfa/grass silage 8.15%, SE 0.88). Fat content contributed to differences in shear force

as indicated by a significant correlation to shear force ($r = -0.25$, $P < 0.05$); however, when fat was used as a covariate in an analysis of variance, the effect of diet on shear force remained close to significant ($P = 0.08$).

The compensatory growth exhibited by steers finished on a high energy diet, following growth on diets of reduced protein, did not affect meat tenderness. Differences in body composition appeared to be due to differences in dietary energy rather than compensatory growth. Meat tenderness also appeared to be affected primarily by dietary energy and its relationship to intramuscular fat deposition, rather than the rate of growth.

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