Studies on Compensatory Growth in Dairy Steers in Relation to Changes in Plane of Nutrition

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Introduction

Higher animals show retarded growth associated with nutritional stress. When adequate levels of nutrition are available, after the period of undernutrition, growth rates are accelerated in comparison with those of continuously growing animals of the same chronological age. In addition to demonstrating the ability to recover from depressed growing conditions, such animals reach their mature size very rapidly.

Animals have long been subjected to natural changes in seasonal nutritional environments as for example, the dry and wet periods in certain torrid zones, and the summer and winter seasons in temperate and sub-frigid climates. The nutritional conditions of herbivora are especially closely related to seasonal environment. Cattle, which have a relatively long growing period, will accelerate their depressed growth rate in summer or a wet period following poor nutritional conditions in winter and drought periods, and recover rapidly to their natural mature size. This accelerated rapid growth has been termed compensatory growth.[1] The compensatory growth after a period of undernutrition has been expressed as the restoration of disturbed normal relationship between chronological and physiological ages.[9] Furthermore, it is thought that compensatory growth phenomena are exhibited not only in rapid increment of body weight, but also in rapid growth of body dimensions and organs, as well as changes in body composition arising from the physiological changes associated with the rapid advance of growth.[5]

Compensatory growth studies in beef cattle in most pasture regions in Europe and the United States are commonly concerned with the animal's ability to exhibit compensatory growth under favorable summer grazing conditions following a period of undernutrition in winter as a result of both qualitative and quantitative deficiencies of diet. Compensatory growth studies conducted in Hokkaido[4,5] were also based on the same conception as those in Europe and the United States, but studies conducted in southern Japan[8] tried to regain body weight by fattening in winter following a decreased gain rate on summer pasture. In northern Australia[11], southern[6] and eastern[3] Africa, the body weights of cattle vary greatly as a result of the extreme changes in nutritional conditions from dry to wet periods.

The main purpose of this experiment was to investigate the influence of growth stage at the commencement of undernutrition, duration of the period of undernutrition and severity of undernutrition in relation to growth rate, feed utilization and changes in conformation and composition during both undernutrition and re-alimentation periods.

Experimental design

Four trials(Trial I, II, III and IV) were made from February 3, 1970 to March 4, 1977 using a total of 65 Holstein steers.[5] Each experimental plan is summarized in Table 1. Animals

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Table 1. Nutritional treatments

(Trial I)

Group	No. of animals	Planned TDN intake (%)*	
		Period I (211–360 days of age)	Period II (361–510 days of age)
A	3	100	100
B	3	60	60
C	3	60	140
D	3	80	80
E	3	80	120
F	3	hay ad lib	hay ad lib

Note: All group members were slaughtered at 511 days of age.

(Trial II)

Group	No. of animals	Planned TDN intake (%)*	
		Period I	Period II
A	3	100 (121–210 days of age)	100 (211–330 days of age)
B	3	60 (121–210 days of age)	140 (211–330 days of age)
C	3	100 (61–150 days of age)	100 (151–270 days of age)
D	3	60 (61–150 days of age)	140 (151–270 days of age)

Note: Animals for Groups A and B, and animals for Groups C and D were slaughtered at 331 and 271 days of age, respectively.

(Trial III)

Group		No. of animals	Planned TDN intake (%)*	
			Period I (211–360 days of age)	Period II (361–510 days of age)
A	a	3	100 (slaughtered at 361 days of age)	
	a′	4	100	100 (slaughtered at 511 days of age)
B	b	4	40 (sluaghtered at 361 days of age)	
	b′	4	40	140 (slaughtered at 511 days of age)

(Trial IV)

Group		No. of animals	Planned TDN intake (%)*	
			Period I (91–240 days of age)	Period II (241–420 days of age)
A	a	4	100 (slaughtered at 241 days of age)	
	a′	4	100	100 (slaughtered at 421 days of age)
B	b	4	60 (slaughtered at 241 days of age)	
	b′	4	60	140 (slaughtered at 421 days of age)

Note: * Planned TDN intake is expressed by percentage of TDN requirement of the NRC feeding standard (1966) for dairy heifers.

Concentrate mixture: Hay=1: 4 on air dry weight base in Trial I, and 1: 4 on TDN base in Trial III, 1: 2 in Trial II, and 1: 2 for first 30 days, 1: 3 for second 30 days and 1: 4 for remaining experimental period in Trial IV, respectively.

Table 2. TDN and DCP contents of feed used in the four trials

Trial / Items	I		II		III		IV	
	TDN	DCP	TDN	DCP	TDN	DCP	TDN	DCP
	%	%	%	%	%	%	%	%
Calf starter			81.0	17.0				
Conc. mixture	74.0	11.0	74.0	11.0	74.0	11.0	74.0	11.0
2nd cut hay	59.9	7.7	55.0	8.5	55.0	6.0	55.0	6.0

Table 3. Mean body weight, mean gain and daily gain

Trial	Group	Period I						Period II				Whole period	
		Days of age at beginning	Period	First weight	Final weight	Gain	Daily gain	Period	Final weight	Gain	Daily gain	Gain	Daily gain
		days	days	kg	kg	kg	kg	days	kg	kg	kg	kg	kg
I	A	211	150	182.4	251.5	69.1	0.46	150	317.0	65.5	0.44	134.6	0.45
	B	211	150	181.7	179.3	−2.4		150	198.5	19.2	0.13	16.8	0.06
	C	211	150	181.8	189.0	7.2	0.05	150	318.0	129.0	0.86	136.2	0.45
	D	211	150	181.3	214.5	33.2	0.22	150	268.8	54.3	0.36	87.5	0.29
	E	211	150	181.4	218.0	36.6	0.24	150	330.7	112.7	0.75	149.3	0.50
	F	211	150	181.7	259.3	77.6	0.52	150	335.8	76.5	0.51	154.1	0.52
II	A	121	90	131.5	210.7	79.2	0.88	120	305.0	94.3	0.79	173.5	0.83
	B	121	90	134.3	137.7	3.4	0.04	120	281.5	143.8	1.20	147.2	0.70
	C	61	90	83.7	155.2	71.5	0.79	120	258.5	103.3	0.86	174.8	0.83
	D	61	90	89.2	105.7	16.5	0.18	120	238.3	132.6	1.11	149.1	0.71
III	A	211	150	193.1	288.1	95.0	0.63	150	389.0	111.0	0.74	204.9	0.68
	B	211	150	193.2	156.1	−37.0		150	355.4	203.4	1.36	162.2	0.54
IV	A	91	150	104.5	212.4	107.9	0.72	180	310.1	97.6	0.54	205.6	0.62
	B	91	150	104.3	110.9	6.6	0.04	180	294.3	180.9	1.01	190.0	0.58

were fed a concentrate mixture and second cut hay according to planned Total Digestible Nutrient (TDN) intake of the U.S. National Research Council (NRC) feeding standard (1966).

Trial I was designed to determine the effect of changes in the levels of nutrition on the demonstration of compensatory growth in steers which were re-alimented at different planes of nutrition following a low TDN intake period. Trial II was designed to investigate the effects of starting age (61 vs. 121 days) in steers subjected to undernutrition and re-alimentation following deprivation. Trial III was designed to investigate any increased compensatory growth following re-alimentation after severe undernutrition. Trial IV was planned to investigate the relationship between the mechanism of compensatory growth phenomena and certain aspects of water metabolism.

Results and discussion

Digestible Crude Protein (DCP) and TDN contents of feed used in the four trials are shown in Table 2.

1) *Recovery of weight from the effect of undernutrition*

Results of the long term effects of undernutrition and re-alimentation imposed at different stage of growth, duration of the period and severity of undernutrition on body weight gain and daily weight gain are summarized in Table 3. It has been reported that calves over 3 months of age can show compensatory growth.[10] There were no significant differences in the recovery of growth due to different early starting age, at least at 61, 91 and 121 days of age (Trial II and IV). Growth retardation periods of animals were set at 90 days and 150 days in all four trials. All underfed steers exhibited compensatory growth during re-alimentation irrespective of duration of undernutrition period (Trial I, II, III and IV), although it has been reported that the prolonged undernutrition in the first 8–12 months of post-natal life causes permanent stunting in cattle.[2] Growing steers which were forced to decrease to 80% of initial body weight by severe undernutrition had an ability to continue growing extensively and demonstrate compensatory growth by re-alimentation (Trial III). It was concluded that the more severe the degree of undernutrition, the greater the gain in body weight and daily weight during re-alimentation (Trial I and III). But the body weight gain of underfed animals during whole experimental periods totaled approximately the same (Trial I) or less than those of controls (Trial II, III and IV).

2) Recovery of conformation from the effect of undernutrition

Body growth measurements for the experimental periods in Trial III are given in Table 4. Body measurements indicated that body length, chest width, hip width, thirl width, rump length, shin circum and face width were retarded in their growth, while withers height, hip height, chest depth and face length were relatively able to tolerate and continue to grow during undernutrition. Relative growth rates during re-alimentation were higher for the parts which were rather severely retarded, and lower for the parts which were rather mildly retarded during undernutrition. Differences in the extent of growth during undernutrition and re-alimentation were observed between the body parts which grew horizontally, such as width and length, and those growing vertically, such as height and depth. Skeletal parts which were most severely retarded by undernutrition were the pelvis and metacarpal bones. The growth of withers height during re-alimentation remained relatively low in comparison with that of other parts.

3) Effect of plane of nutrition on the efficiency of food utilization

TDN and DCP intake of each group, expressed as TDN and DCP percentages of the feed requirement of the NRC feeding standard, at the periods of digestion trials are summarized in Table 5. TDN intake for the high plane of nutrition ranged from 119 to 130%. It was impossible to feed 140% of TDN throughout the experimental period as planned. TDN, DCP and Digestible Energy (DE) required per kg of body weight gain during the experimental period in each trial are given in Table 6. TDN, DCP and DE required per kg of gain in compensatory animals were improved significantly during re-alimentation. But the total amounts of nutrient required per kg of gain for compensatory animals were approximately the same (Trial I and II) or less than those for controls over the whole period. Compensatory animals can take and utilize large amounts of feed during the recovery period and thus those steers show higher efficiency for weight gain. This improved efficiency is due to an ability of steers to use more of energy ingested for growth than for maintenance. Compensatory animals slowly raise their basal metabolic rate to the normal for the period of re-alimentation.[9] To estimate the basal metabolism of steers, Thyroxine Secretion Rates (TSR)[7] were examined as shown in Table 7. TSR of steers (Trial III) at the end of undernutrition and at the beginning of re-alimentation were compared to those for controls. Low TSR values observed 2 weeks before the end of undernutrition were recovered after 3 weeks of re-alimentation. It was suggested that the low basal metabolic rate induced by undernutrition could recover to normal rate relative to metabolic body size ($W^{0.75}$) within a very short term of re-alimentation. Improved feed efficiency would be temporary, and gradually reduce and not continue

Table 4. Results of body measurements

(Trial III)

Body measurement parts	Group	Period I Gain	Period I Underfed/Control	Period II Gain	Period II Fullfed/Control	Whole period Gain	Whole period Testing/Control
		cm	%	cm	%	cm	%
Withers height	A	14.39		7.98		22.37	
	B	4.16	28.91	11.22	140.60	15.38	68.75
Hip height	A	12.41		7.94		20.35	
	B	3.06	24.66	11.87	149.50	14.93	73.37
Body length	A	17.69		12.90		30.59	
	B	1.11	6.27	21.96	170.23	23.07	75.42
Chest depth	A	8.57		5.34		13.91	
	B	2.13	24.85	9.17	171.72	11.30	81.24
Chest width	A	8.75		4.88		13.63	
	B	0.30	3.43	9.69	198.57	9.99	73.29
Hip width	A	6.11		5.39		11.50	
	B	0.11	1.80	9.33	173.10	9.44	82.09
Thirl width	A	5.63		4.52		10.15	
	B	0.36	6.36	7.04	155.75	7.40	72.91
Rump length	A	5.58		4.53		10.11	
	B	0.32	5.74	7.71	170.20	8.03	79.43
Chest girth	A	19.55		15.11		34.66	
	B	1.01	5.22	28.41	188.02	29.43	84.91
Belly girth	A	20.87		18.72		39.59	
	B	−10.53		54.26	289.85	43.74	110.46
Shin circum	A	1.47		1.20		2.67	
	B	−0.15		2.28	190.20	2.13	79.78
Face length	A	5.36		4.52		9.88	
	B	1.62	30.22	5.84	129.20	7.46	75.51
Face width	A	2.46		1.53		3.99	
	B	0.27	10.98	2.70	176.47	2.93	74.44

Note: Face length and face width are the length between the tip of os occipital and the edge of os incisivum, and between the both edges of os zygomaticum, respectively.

thoroughout the recovery period.[9] It is difficult to explain the cause of improved feed efficiency in steers observed at early stage of re-alimentation only by the low metabolic rate of compensatory animals, because the basal metabolism as expressed by TSR data (Table 7) showed a rapid recovery at the beginning of re-alimentation. Compensatory steers were more efficient than the controls in protein utilization as well as in feed utilization during the recovery period (Table 8), they showed improved nitrogen balance and accumulated higher rates of nitrogen during re-alimentation following undernutrition.

4) *Effect of plane of nutrition on the composition of muscle*

The chemical compositions and calorific values of M. longissimus thorasis in 9–11 rib cut (Trial IV) are shown in Table 9. Higher amounts of moisture and lower amounts of protein and fat were contained in muscles from underfed steers than those from controls which had heavier body weights but identical ages at the end of both underfed and fullfed periods. When the plane of nutrition on which they feed are not extremely low, steers may have the definite percentages of chemical compositions

Table 5. TDN and DCP intake expressed as percentage of the feed requirement of the NRC feeding standard

(Trial I)

Group	Period I		Period II	
	TDN	DCP	TDN	DCP
	%	%	%	%
A	85.6	93.1	95.5	136.6
B	54.3	57.1	46.9	59.3
C	53.6	56.5	130.1	172.5
D	68.4	72.2	75.1	97.2
E	69.1	72.5	110.1	150.5
F	99.2	104.2	123.7	179.9

(Trial II)

Group	Period I		Period II	
	TDN	DCP	TDN	DCP
A	98.0	132.5	97.1	114.8
B	46.7	63.0	120.5	127.4
C	96.6	127.0	97.9	105.5
D	61.0	79.7	118.9	120.0

(Trial III)

Group	Period I		Period II	
	TDN	DCP	TDN	DCP
	%	%	%	%
A	102.9	102.2	99.7	125.6
B	49.3	43.5	125.6	125.8

(Trial IV)

Group	Period I		Period II	
	TDN	DCP	TDN	DCP
A	90.2	97.7	99.4	134.4
B	50.8	49.2	118.9	146.9

Note: TDN and DCP intake were estimated by two digestion trials in each period conducted during Periods I and II. The values of TDN and DCP used for Period I and II in Trial I are average values of the first and second digestion trials and the third and fourth digestion trials.

Table 6. TDN, DCP and DE each required per kg of body weight gain

(Trial I)

Group	Period I			Period II			Whole period		
	TDN	DCP	DE	TDN	DCP	DE	TDN	DCP	DE
	kg	kg	Mcal	kg	kg	Mcal	kg	kg	Mcal
A	6.04		29.55	8.41		35.17	7.19		32.29
B				11.36		50.85	26.86		124.19
C	32.29		157.44	5.46		25.20	6.88		32.19
D	9.64		48.70	7.22		32.82	8.14		38.85
E	8.70		41.50	5.49		25.13	6.28		29.14
F	6.30		31.88	9.67		45.30	7.96		38.54

(Trial II)

Group	Period I			Period II			Whole period		
	TDN	DCP	DE	TDN	DCP	DE	TDN	DCP	DE
A	3.53			5.35			4.52		
B	37.58			3.82			4.60		
C	3.07			4.18			3.71		
D	6.50			3.48			3.81		

(Trial III)

Group	Period I			Period II			Whole period		
	TDN	DCP	DE	TDN	DCP	DE	TDN	DCP	DE
A	5.99	0.63	26.41	5.88	0.64	27.44	5.96	0.66	27.11
B				3.88	0.37	15.79	5.43	0.60	24.92

(Trial IV)

Group	Period I			Period II			Whole period		
	TDN	DCP	DE	TDN	DCP	DE	TDN	DCP	DE
A	3.38	0.45	16.83	6.60	0.96	34.08	4.91	0.69	25.02
B	22.00	17.46	113.11	3.84	0.56	19.84	4.51	0.65	23.27

Table 7. Thyroxine secretion rate of steers estimated 2 weeks before the end of Period I and 3 weeks after the beginning of Period II

(Trial III)

Group	No. of animals	Normal plasma thyroxine (μg/100 ml)	TSR (mg T_4/day)	$W^{0.75}$ ($kg^{0.75}$)	$TSR/W^{0.75}$ (μg T_4/day)
	(2 weeks before the end of Period I)				
A	4	9.10	1.24	71.26	17.40
B	4	6.26	0.15**	44.71**	3.35**
A/B (%)		68.79	12.10	62.74	19.25
	(3 weeks after the beginning of Period II)				
A	4	7.87	1.25	73.04	17.11
B	4	7.00	0.86*	51.46**	16.71
A/B (%)		88.95	68.80	70.45	97.66

Note: **,*: significant at 1% and 5% levels between Groups A and B.

Table 8. Nitrogen balance

(Trial II)

Group	Period I				Period II			
	Income	Out go		Balance	Income	Out go		Balance
		in urine	in feces			in urine	in feces	
	g/day	g/day	g/day	g/day	g/day	g/day	g/day	g/day
A	108.7 (100.0)	37.3 (34.3)	38.3 (35.2)	33.1 (30.5)	120.4 (100.0)	44.7 (37.1)	54.5 (45.3)	21.2 (17.6)
B	48.3 (100.0)	26.2 (54.2)	19.5 (40.4)	2.6 (5.4)	127.0 (100.0)	30.2 (23.8)	60.0 (47.2)	36.8 (29.0)
C	87.1 (100.0)	32.9 (37.8)	32.5 (37.3)	21.7 (24.9)	103.0 (100.0)	27.8 (27.0)	47.3 (45.9)	27.9 (27.1)
D	50.1 (100.0)	23.3 (40.5)	16.7 (33.3)	10.1 (20.2)	106.6 (100.0)	27.7 (26.0)	49.1 (46.1)	29.8 (27.9)
(Trial III)								
A	105.8 (100.0)	40.6 (38.4)	41.1 (38.8)	24.1 (22.8)	132.0 (100.0)	49.5 (37.5)	54.4 (41.2)	28.1 (21.3)
B	37.5 (100.0)	23.4 (62.4)	14.3 (38.1)	−0.2	142.1 (100.0)	43.3 (30.5)	61.2 (43.0)	37.6 (26.5)

relative to individual body weight.

Conclusion

Under the conditions used for this experiment, steers can continue to grow intensively for a certain period of re-alimentation following decreased growth resulting from undernutrition, irrespective of the degree, duration and severity of undernutrition, and the stage of growth at the beginning of undernutrition.[5] This compensatory growth is supported by an excellent appetite which underfed animals usually demonstrate whenever they are released to full feeding. This ability to make good recovery of growth after undernutrition has improtant implications for cattle production where seasonal food shortages exist.

Table 9. Chemical composition and calorific values of M. longissimus thoracis in 9–11 rib cut

(Trial IV)

Group	Moisture	Protein	Fat	Ash	Calorie (wet)
	(241 days of age)				
	%	%	%	%	cal/g
A	76.7	20.0	0.6	1.2	1270
B	78.5**	19.1*	0.3**	1.0*	1157**
	(391 days of age)				
A	74.6	21.8	0.9	1.1	1390
B	76.2*	20.3*	0.8	1.0	1300*

Note: **,*: significant at 1% and 5% levels between groups A and B.

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