

Compensatory Growth in Ruminants

(Pertumbuhan Kompensatori pada Ternak Ruminansia)

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Abstrak

Faktor biologis yang menyebabkan terjadinya pertumbuhan compensatory adalah, naiknya konsumsi pakan per unit bobot badan, naiknya efisiensi penggunaan pakan dan kecendrungan menggunakan nutrien untuk sintesa protein. Respons ternak setelah diberi pakan kembali, tergantung pada umur dan tingkat berat dan lamanya pembatasan pakan. Keberlanjutan suasana hormonal atau turunnya kebutuhan pokok atau keduanya akan menentukan berlanjutnya pertumbuhan kompensatori.

Kata Kunci: Pertumbuhan Kompensatori, Feed Intake, Ruminansia

Introduction

In many part of the tropics, animals often suffer extended periods of poor nutrition during the dry season. Green pastures are rare at the time and, even if available are usually mature and consequently of low nutritive value. This often results in poor growth in young animals, severe liveweight loss, delays in onset of puberty or prolonged postpartum anoestrus. However, soon after the wet season, when the quantity and quality of the grasses are improved, animals increase their live weight markedly. During this time animals are compensating for their weight loss during the dry season and often superior liveweight gain compared to animals which had not undergone poor nutrition. Thus compensatory or "catch up" growth is a phenomenon which is fairly common in areas where marked fluctuations in forage supply occur.

The physiological events associated with compensatory growth are increase in

feed intake per unit liveweight, increase in efficiency of nutrient utilization and preferential partitioning of nutrients to protein synthesis. However, response of animals may be variable depending on factors such as, age of the animal at which the feed restriction is imposed and the degree and duration of feed restriction.

Although feed supplement may enhance the growth of an animal on poor quality feed, it may not necessary be economical. However, certain conditions it has been considered practical to give the animal an appropriate feed supplement which allow it to subsist at maintenance level during the dry season. The producer has a need for information to use in his decision making process, on whether to feed a supplement or to allow his animals to suffer a period of static even negative growth, followed by compensatory growth. In relation to that, this paper could provide some understanding of feed utilization by growing ruminant animals during period of undernutrition and compensatory growth.

Age of the Animal

Evidence showed that restricting feed intake of animals for a period soon after birth did not stimulate compensatory growth when animals resume ad libitum feeding compared to those subjected to the same treatment when they were older (Everitt and Jury 1977; Tudor and O'rouke 1980).

Sheep restrictively fed for the first 6 months after birth required more time (56 months) when ad libitum fed to catch up in live weight of those ad libitum fed from birth (Allden, 1968). On the other hand those restrictively fed during the second 6 months require less time (11 months) on resumption of ad libitum feeding, to catch up in live weight with their ad libitum fed counterparts. This results, however, were confounded by the degree of feed restriction.

Compensatory growth of animals, restrictively fed in early life, may persist for different periods when ad libitum feeding is resumed. For example, Everitt and Jury (1977) who raised twin calves on either high or low plane of nutrition for 16 weeks found that the difference in live weight between the two groups was 41.2 kg at the beginning of resumption of feeding. This weight differences was further reduced to 29.2 kg by 20 months and to 25.6 kg by 35 months, illustrating a persistent compensatory growth phase.

In studies with sheep (Hopkins and Tulloh, 1985) where the animals were restrictively fed immediately after birth, compensatory growth was observed to persist for only 35 days after resumption of feeding.

Animals close to maturity may not exhibit compensatory growth. Hight and Barton (1965) restricted feed intakes of Ramney ewes (mean live weight 73 kg; 4–5 years old) for 21 and 42 days to lose 10 and 19 % of their live weight respectively. During 40 days of resumption of feeding the ewes did not exhibit compensatory growth

nor had they regained the weight they had lost.

Degree and Duration of Feed Restriction

The degree of feed restriction imposed can be above, below or maintenance energy requirement. Therefore, depending on the degree of restriction, the animals may be maintaining, losing or gaining a small weight during feed restriction.

Evidence suggests that increasing the degree of feed restriction prior to resumption of feeding is likely to result in compensatory growth, which will persist for a longer period. Saubidet and Verde (1976) restrictively fed steers, 8 months old, to different degrees ranging from 6.06 MJ to 11.95 MJ metabolisable energy (ME)/kg dry matter (DM). They found that animals subjected to the greatest degree of feed restriction were those that showed a higher feed intake per unit of live weight and a greatest weight gain during resumption of feeding. Scales and Lewis (1971) fed steers at three levels; ad libitum, maintenance and submaintenance during the three months winter period. On resumption of ad libitum feeding, the maintenance and sub-maintenance groups exhibit compensatory growth, which persisted for 82 days and 180 days respectively, after which their growth rates were similar to those for the ad libitum group.

Ryan *et al.* (1993) restricted steers of 9–10 months old for a period of 89 days. During this period, the steers lost on average 16.4 % or 41 kg of their initial body weight. Upon feed resumption, using high quality diet, the restricted steers were found to compensate completely within 11 months.

In sheep, restricted feeding resulting in live weight loss (Aldren, 1968) or maintenance (Graham and Searle, 1979) resulted in compensatory growth, which persisted for 10 and 12 months respectively. However, Ryan *et al.* (1993) found that his restricted sheep did not compensate completely in 11 months after feed resumption, and remained lighter than the controls. The difference in response of the animals may be due to the severity of the restriction and or the quality of diet used during feed resumption. Severe restriction in growth rate during feed restriction however, will result in compensatory growth later on but may jeopardize attainment of market specification for heavy carcasses at a young age (Warren *et al.*, 1998).

In cattle, Robinson *et al.* (2001) found that when the difference in live weight at the end of grow-out (about 230 kg) was greater than 15 kg, increased growth rate during finishing was insufficient to permit catch up of live weight by the end of finishing (about 400 kg).

The duration of feed restriction also affects the growth response to resumption of ad feeding. Sheep that were maintained at the same live weight for 6 months grew faster during resumption of feeding than those maintained at the same weight for 4 months (Graham and Searle, 1979). In cattle, those subjected to restricted feeding for 24 weeks showed greater growth rate (140%) during resumption of feeding than those that were restrictively fed for 12 weeks and then ad libitum fed (Ledger, 1973).

The variation in compensatory growth which have been recorded are likely to be due to variations in digestive function or utilization of absorbed nutrient or both.

Feed Intake

When animals are on resumption of feeding after a period of feed restriction, feed intake is usually increased (Table 1). It is advisable to measure feed intake per unit live weight since during feed resumption there would be a dramatic live weight change.

The increased feed intake is caused by the increase in the nutrient requirement, particularly protein for the recovery of digestive tract and liver. The size of digestive tract and metabolic capacity of digestive tract and the liver are reduced during feed restriction (Stangassinger and Gieske, 1986; Burrin *et al.*, 1990; Ryan *et al.*, 1993; Aziz *et al.*, 1993; Yambayamba *et al.*, 1996b) and increase during feed resumption (Stangassinger and Gieske, 1986; Yambayamba *et al.*, 1996 b). This adaptation period usually take 3 to 4 weeks (Searle and Graham, 1975), therefore feed consumption measured at different time would be different.

Increased feed intake usually is accompanied by increase digesta load. If increased feed intake is higher than the increase in digesta load, the residence time of feed particle in the rumen will be shorter or in other word rate of passage is increased. This results in reduced digestibility as found by Drew and Reid (1975); Graham and Searle (1979) and Mahyuddin and Teleni (1995). However, the reduced residence time of feed particle in the rumen would only reduced feed digestibility if the feed is fibrous. It is unlikely that digestibility of feed will be reduced if feed is highly degradable in the rumen (Thomson *et al.*, 1982). If the increased feed intake is proportional to increased digesta load, the retention time for feed in the rumen may not influence digestibility (Asplund *et al.*, 1975).

Table 1. Feed intake (g per kg live weight) and feed efficiency (kg feed per kg live weight gain) of animals in normal growth (NG) and compensatory growth (CG)

Animal	Feed Intake		Feed Efficiency		Reference
	NG	CG	NG	CG	
Calf					
male	22.0	24.5	7.1	6.3	Tudor and O'Rourke (1980)
female	22.3	23.0	8.3	6.3	Tudor and O'Rourke (1980)
Lambs	29.0	30.7	8.9	7.0	Turgeon <i>et al</i> (1986)
Steers	26.5	25.0	6.9	3.5	Ellenberger <i>et al</i> (1989)
Steers	30.0	28.8	8.4	5.9	Cartens <i>et al</i> (1991)
Steers	27.0	25.9	7.3	6.5	Hayden <i>et al</i> (1993)
Heifers	20.8	22.7	7.7	5.9	Yambayamba <i>et al</i> (1996)
Lambs	34.5	41.7	12.9	7.3	Mahyuddin and Teleni (1996)
Calf	22.6	24.6	12.1	10.0	Santra and Pathak (1999)

Table 2. Maintenance requirements (KJ/Kg LW ^{0.75}) of animals during feed restriction and ad libitum feeding.

Animals	Feed Restriction	Ad Libitum Feeding	Reference
Sheep			
Weight stasis	300	450	Graham and Searle (1975)
Weight loss	340	470	Graham and Searle (1979)
Weight stasis	250	375	Gingins <i>et al</i> (1980)
Steers			
185 kg, weight stasis	350	720	Ledger and Sayer (1977)
275 kg, weight stasis	350	720	Ledger and Sayer (1977)
450 kg, weight stasis	320	480	Ledger and Sayer (1977)

Efficiency of Feed Utilization

In most cases animals undergoing compensatory growth have a higher feed efficiency than those growing normally (see

Table 1). The variability of feed efficiency shown in Table 1 may be due to variability of degree and duration of feed restriction and the period at which measurement was taken during

feed resumption. Increased efficiency of feed utilization of animals during feed resumption may be explained by a number of studies, that animals tended to lower their maintenance energy requirements when they have been either loosing or maintaining live weight for a period of time. If this reduced maintenance energy requirements is extended well into the period of feed resumption, it could explain the observed increased efficiency of feed.

The reduction in maintenance requirements has been shown to be higher for animals maintaining lower liveweights rather than higher liveweights (see Table 2). Generally, when animals are loosing or maintaining live weight over period of time, their basal metabolic rate (BMR) might be reduced (Cartens *et al*, 1989; Lapicere *et al*, 1992 ; Yambayamba *et al*, 1996) resulting in lower maintenance requirements.

While the amount of energy required to meet maintenance requirement in ruminant is usually taken as 420 – 450 kJ/kg LW^{0.75} (ARC, 1980) it is clear that animals are capable of reducing their maintenance requirement when their feed intake is reduced. It was found that the tissue losses of digestive tract and the liver during feed restriction are responsible for the reduced maintenance requirement, and that the lowered maintenance requirement persisted during re-alimentation until these tissues had been fully repleted (Ryan *et al* 1993).

This is suggested to be a mechanism of survival during poor nutrition. Depending on the time taken by the animal to adapt to the increased intake during resumption of feeding, the extra amount of energy resulting from a reduction in maintenance energy required would be available for compensatory growth. Thus the longer the reduced maintenance requirement persists the longer the compensatory growth response would be anticipated to last.

Another possible reason which might explain the increase in efficiency of nutrient utilization by animals undergoing compen-

satory growth is the hormonal/enzyme milieu which is stimulated by feed resumption after a period of feed restriction (see Table 3). The sudden increased influx of nutrients in the body pools during feed resumption, could have a "rebound" effect on the hormonal milieu. This milieu might be sustained for a period, thus facilitating the phenomenon of compensatory growth. The sustainability of such milieu or decreased maintenance requirement or both would probably determine the persistence of compensatory growth. In relation to animal production, it certainly would be useful if ways can be developed to sustain processes such as these, which facilitate compensatory growth.

Endocrine and Metabolic Changes

The response of hormones and metabolites to feed resumption following a period of feed restriction is presented in Table 3. The levels of hormones and metabolites concentration represent the balance between supply, utilization and excretion.

Feed restriction is associated with higher plasma concentration of GH and lower plasma concentration of insulin, IGF-I, T4 and T3. In contrast, during feed resumption plasma concentration of GH are lower, while insulin, IGF-I, T4 and T3 are higher. During this period, plasma levels of T4, T3, IGF-I and insulin was positively, and GH was negatively correlated with empty body protein and empty body fat (Hayden *et al.*, 1993).

The increased insulin, concentration during feed resumption are probably a result of increased availability of substrates such as glucose, propionic acid and amino acids. The increased concentration of plasma insulin would facilitate uptake of these substrates by muscle tissues for protein synthesis. The observation (e.g. Thomson *et al* 1982; Blum *et al*, 1985; Mahyuddin 1995; Mahyuddin and Teleni 1995; Santra and Pathak, 1999) that protein deposition was significantly increased

Table 3. Plasma concentrations of hormones and metabolites in ruminants subjected to different dietary regimes.

	P1		P2		
	Control	Restricted	Control	Restricted	Reference
Hormones:					
Insulin (ug/l)	0.89	0.65	-	0.76	Henricks <i>at al.</i> , (1993)
	1.30	0.47	1.4	1.79	Hayden <i>at al.</i> , (1993)
	0.75	0.37	0.8	0.90	Yambayamba <i>at al.</i> , (1996a)
IGF-1 (µg/l)	168.4	118.3		151.2	
	270.0	153.0	350	345.0	Henricks <i>at al.</i> , (1993)
	188.8	106.2	210	205.0	Hayden <i>at al.</i> , (1993) Yambayamba <i>at al.</i> (1996a)
Growthhormone (ug/l)	11.5	24.3		16.9	
	11.5	20.0	4.0	5.0	
	8.5	13.8	8.5	8.4	Henricks <i>at al.</i> , (1993) Hayden <i>at al.</i> , (1993)
Thyroxine (ng/ml) (T4)	75	48	76	68	Yambayamba <i>at al.</i> , (1996a)
	65	52.5	67.5	70	
					Hayden <i>at al.</i> , (1993)
Triiodothyronine (ng/ml) (T3)	1.9	1.3	2.4	2.7	Yambayamba <i>at al.</i> , (1996a)
	1.25	0.95	1.3	1.25	
					Hayden <i>at al.</i> , (1993) Yambayamba <i>at al.</i> , (1996a)
Metabolites:					
Glucose (nM)	5.2	4.2	4.3	5.3	
	4.7	3.7	4.6	4.8	
	3.4	3.0	3.4	3.6	Ellenberger <i>at al.</i> , (1989)
	5.8	4.8	5.6	5.4	Hayden <i>at al.</i> , (1993) Mahyuddin & Teleni (1996)
FFA (nM)	0.22	0.22	0.23	0.09	Yambayamba <i>at al.</i> , (1996a)
	0.27	0.35	0.25	0.25	
	0.25	0.53	0.20	0.20	Ellenberger <i>at al.</i> , (1989) Hayden <i>at al.</i> , (1993)
Urea (mg/dl)	8.4	8.3	11.8	12.5	Yambayamba <i>at al.</i> , (1996a)
	11.0	14.5	12.5	10.0	
	60.2	54.6	63.9	59.9	Ellenberger <i>at al.</i> , (1989)
	13.0	9.0	22.0	25.0	Hayden <i>at al.</i> , (1993) Mahyuddin&Teleni (1996) Yambayamba <i>at al.</i> , (1996a)

P1 is period when animals are on a restricted diet

P2 is a period when animals are fed *ad libitum*

on resumption of feeding following a period of restricted feeding is consistent with this. Growth hormone (GH) induces a lipolytic response in adipose tissue (Goodman and Kostyo, 1981). During feed restriction, GH production is enhanced to induce lipolysis, so that FFA is mobilized to bridge energy deficit. However, the degree of lipolysation to increase FFA concentration is dependent on the severity of dietary restriction imposed. Ellenberger *et al* (1989) found no difference in FFA concentration between restricted and ad libitum fed animals. In his study, the restricted animals were allowed to have a small gain of 0.35 kg/d. When animals are on feed resumption, FFA concentration is reduced as a result of reduced GH production.

During normal growth thyroid hormones (T4 and T3) are involved in both synthesis and degradation of protein (Golberg *et al*, 1980), whereas during limited nutrient availability, decreased thyroid function and (or) lowering of circulating levels of thyroid hormones could be metabolically desirable to minimize protein degradation (Ellenberger *et al*, 1989).

Plasma levels of glucose usually varied in direct relation to nutrient supply. However, blood glucose level does not increase as rapidly during feed resumption as does feed intake. Mahyuddin and Teleni (1996) found that during compensatory growth, animals showed an increase in glucose production, glucose taken up and that was oxidized by the hind-limb muscle. There was a dramatic increase in the actual rate of glucose oxidation per unit muscle weight.

The level of plasma urea reflects the degree of protein degradation. Unfortunately, during feed resumption when protein intake is increased the level of urea is also increased. However, animals undergoing compensatory growth were found to be more efficient in utilizing dietary protein for body protein than

animals growing normally as discovered by Mahyuddin and Teleni (1996).

Body Composition

A high proportion of the live weight gained in the initial stages of compensatory growth appears to be water in gut tissue (Drew and Reid, 1975). This is due to the relatively greater amount of protein deposited to replace protein depleted from tissues such as digestive tract and liver (Stangassinger and Giesecke, 1986; Ryan *et al*, 1993; Yambayamba *et al*, 1996 b).

The restoration of the digestive tract and the liver tissue, after a period of restricted feeding, is probably an adaptation mechanism which allows the animal to process the increased influx nutrients caused by resumption of feeding. For every 1 g protein deposited, 3 – 4 g of water retained (Searle, 1970).

In gut and liver tissues

These two tissues are the most metabolically active tissues in the body (Stangassinger and Giesecke, 1986). It is possible that a large proportion of energy expenditure during compensatory growth would be accounted for by the increased size of digestive tract and the liver. This could delay net fat accretion.

Mahyuddin and Teleni (1995) found that during the first 3 to 4 weeks of resumption of feeding following a period of feed restriction at half maintenance energy level, animals were depositing nearly 5 times as much protein as the control animals. However, this was followed by a marked increase in fat deposition, approximately 3 times the rate in control animals. The rates of both protein and fat deposition in interrupted growth animals

Table 4. The ratios of protein : fat content in cattle and sheep loosing/gaining live weight (LW) at different rates in compensatory growth (CG).

Animal	Feed Restriction		LW Change (g/d)	Protein: Fat Ratio		References
	Degree (Intake)	Length (d)		Control	CG	
Calf	14.2 g/kg	200	-60	0.51	0.41	Tudor and O'Rourke (1980)
Sheep	LW	140	-159	0.40	0.39	
Lamb	15 g/kg LW	144		0.33	0.42	Burton <i>et al.</i> , (1974)
Lamb	Maintenance	58	-100	0.63	0.95	Thomson <i>et al.</i> , (1982)
Lamb	20%	70	-140	0.56	0.55	
Lamb	<i>ad libitum</i>	140		0.46	0.47	
Lamb	70%	147	-47	0.66	0.74	
Lamb	<i>ad libitum</i>	56	-155	0.40	0.87	Drew and Reid (1975)
Steers	Maintenance	92	+250	0.65	0.72	Searle and Graham
Lambs	half	207	+42	0.66	0.72	(1975)
Steers	maintenance	189	+400	0.46	0.68	Searle <i>et al.</i> , (1979)
	half					Mahyuddin and Teleni (1995)
	maintenance					Hayden <i>et al.</i> , (1993)
	2 % LW					Turgeon <i>et al.</i> , (1986)
	23 g/kg LW					Cartens <i>et al.</i> , (1991)
	14 g/kg LW					

continued to be higher to the end of experiment (15 weeks after resumption of feeding, and protein: fat ratio was also higher than the control (see Table 4). Reports on body composition of animals undergoing compensatory growth have been variable. Compensatory growth may result in a higher rate of fat than protein deposition (Searle and Graham, 1975; Tudor and O'Rourke, 1980), a higher rate of protein than fat deposition (Burton *et al.*, 1974; Little and Sandland, 1975; Mahyuddin, 1995), or no changes in body

composition (Thornton *et al.*, 1975; Graham and Searle, 1979) relative to control.

Buttler-Hogg (1984) and Yambayamba *et al.* (1996 b) observed that at the same live weight, animals did not differ in body composition irrespective whether they were on normal or compensatory growth curve. From the discussion above, it can be concluded that animals undergoing compensatory growth are leaner than those growing normally; however, at the same live weight both groups would have similar body composition.

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