COMPENSATORY GROWTH IN BEEF CATTLE
Gordon E. Carstens
Department of Animal Science
Texas A&M University

ABSTRACT

A number of mechanisms are involved that enable cattle to adapt metabolically to periods of nutritional restriction, and to subsequently exhibit compensatory growth once ad libitum access to high-energy diets are provided. Reductions in energy density of growth and energy requirements for maintenance, and increases in net efficiency of growth, feed intake and gut fill all have been shown to contribute toward compensatory growth in cattle. The interdependency of these mechanisms, and the fact that few studies have been conducted to examine these mechanisms concurrently make it difficult to predict their relative contributions to compensatory growth. Furthermore, differences in stage of maturity, severity and duration of the growth restriction period and type of diet fed during realimentation all may influence the magnitude of the compensatory growth response that is observed, and likely will alter the degree to which each mechanism contributes to compensatory growth.

INTRODUCTION

Beyond marketing, profitability in the cattle feeding business is dependent upon optimizing the utilization of available feed and cattle resources. In producing slaughter beef, a diverse array of feeding systems are used ranging from direct placement of calves into feedlots on high-grain diets, to use of extensive backgrounding programs. These backgrounding programs vary widely in their duration, as well as in the number and types of diets used. Typical backgrounding programs utilize harvested forages in feedlots or stocker grazing systems, although in recent years programmed feeding of high-grain diets also has been used. An inherent aspect of backgrounding programs that restrict growth by limiting feed quantity or quality is a period of accelerated growth once cattle are realimented on a high-grain diet; this commonly is called compensatory growth.

Backgrounding programs by design restrict growth rates during the growing phase, thereby extending the time to reach final slaughter weights and increasing the cost of animal maintenance. Therefore, the extent to which backgrounding programs are used economically in feeding systems depends upon relative costs of backgrounding vs feedlot diets, as well as the degree to which growth during the compensation period is faster or more efficient than growth during continuous ad libitum feeding of high-grain diets. Furthermore, the degree to which carcass composition or weight (i.e., carcass value) is modified during the growth restriction and compensation periods also will influence the economics of feeding systems that use backgrounding programs. Therefore, in deciding which feeding system to use for a given set of calves, it is critical to predict as accurately as possible the performance and carcass compositional changes during the compensation periods.

The current feeding standard (NRC, 1984), however, is less accurate in predicting performance responses of cattle during compensatory than continuous growth periods, especially when considering short-term feeding intervals (Oltjen and Carret, 1988). This is because the degree of compensation following periods of growth restriction is highly variable, and it is affected by a number of factors including: (i) stage of maturity at the start of growth restriction, (ii) severity of growth restriction, (iii) duration of growth restriction, and (iv) pattern of growth during realimentation.

Adding to the complexity of predicting the performance of cattle exhibiting compensatory growth is the fact that numerous mechanisms interact to produce more rapid, efficient growth following periods of growth restriction. These mechanisms include a(n): (i) reduction in energy density of tissue growth, (ii) reduction in maintenance energy requirements, (iii) increase in the net efficiency of tissue growth, (iv) increase in feed intake, and (v) increase in gut fill. An improved understanding of the degree to which each of these mechanisms contribute to compensatory growth will further improve the development of feeding standards/growth models (NRC, 1984; Oltjen...
et al., 1986; Fox et al., 1988) to predict cattle performance more accurately.

**MECHANISMS CONTRIBUTING TO COMPENSATORY GROWTH**

**Energy Density of Tissue Growth**

Lean tissue requires less energy per unit of liveweight gain than fat, due to a lower energy density of protein plus water and mineral than of fat (1.24 vs 9.39 kcal/g). Therefore, to the degree that growth patterns can be modified during growth restriction and realimentation to increase the proportion of lean gain, NEg requirements will be reduced and growth rates accelerated during the compensation period. Accordingly, NRC (1984) recommended that NEg requirements be reduced by 11.5% for compensating yearling steers relative to steer calves (Table 1).

In agreement with NRC’s recommendation, Carstens et al. (1991) found that compensatory growth steers, previously restricted to 0.4 kg/d for 6 mo, contained 12% more empty-body protein and 25% less empty-body fat than continuous growth steers at 450 kg empty-body weight (EBW). This change in empty-body composition resulted in an 18% reduction in NEg requirements (5.72 vs 4.69 Mcal/kg EBW at 400 kg EBW) for compensatory growth steers. In comparing carcass composition at equal carcass weights, Smith et al. (1977) and Harris (1994) found that compensatory growth steers deposited less carcass fat than continuous growth steers. Likewise, Rompala et al. (1984), Mader et al. (1989), Dolezel et al. (1993) and Gill et al. (1993a) found that carcass weights adjusted to a similar degree of carcass fatness were heavier in cattle that were previously backgrounded than in cattle fed high-grain diets continuously.

**Stage of Maturity Effects.** As shown in Table 2, not all experiments have found compensatory growth to be leaner. The inconsistencies in these results imply that degree of maturity at the time growth is restricted is an important factor that directs the compositional change that occurs during subsequent compensatory growth. In experiments that have reported reduced fat deposition during compensatory growth (Butterfield, 1966; Smith et al., 1977; Sully and Morgan, 1982; Mader et al., 1989; Carstens et al., 1991; Harris, 1994), initial ages of the cattle were 8 mo or older, whereas in the experiments that found increased fat deposition during compensatory growth (Stuedemann et al., 1968; Tudor et al., 1980, Aballa et al., 1988), cattle were less than 2 mo of age at the point of growth restriction. For the experiments in which composition was not affected by growth pattern, ages at the point of growth restriction tended to be intermediate (Table 2). Exceptions to this trend include the experiments of Henricks et al. (1994) and Ryan et al. (1993b). Nine-mo old Angus bulls were used in the study of Henricks et al. (1994). Bulls are known to be later maturing than steers, and thus would be expected to be younger physiologically than steers at the same age. In the experiment of Ryan et al. (1993b), 9 to 10 mo old Hereford steers were restricted in growth for only 90 d prior to realimentation. The relatively short duration of this growth restriction period likely contributed to the lack of an effect on body composition at final slaughter (see discussion latter in this section).

The effects of stage of maturity at the point of growth restriction on alterations in composition are shown more clearly in Table 3. Restricting growth for 200 d in young (4 d of age) Hereford calves prior to realimentation increased empty-body fat by 14% in contrast, restricting growth for 189 d in older (10

<table>
<thead>
<tr>
<th>Steer type</th>
<th>NEg, Mcal/kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medium-frame calves</td>
<td>.0635 EBW.75 EBG1.097</td>
</tr>
<tr>
<td>Medium-frame compensating yearlings</td>
<td>.0562 EBW.75 EBG1.097</td>
</tr>
<tr>
<td>Large-frame calves</td>
<td>.0562 EBW.75 EBG1.097</td>
</tr>
<tr>
<td>Large-frame compensating yearlings</td>
<td>.0498 EBW.75 EBG1.097</td>
</tr>
</tbody>
</table>

†EBW = empty body weight; EBG = empty body gain.

71
Table 2. Comparison of empty-body or carcass composition at constant weight endpoints for continuous and compensatory growth cattle†.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Initial age or wt, kg</th>
<th>Final wt, kg</th>
<th>Continuous growth</th>
<th>Compensatory growth</th>
<th>Change in composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tudor et al., 1980</td>
<td>4 days 330</td>
<td>29.2</td>
<td>33.3</td>
<td>fatter</td>
<td></td>
</tr>
<tr>
<td>Abdalla et al., 1988‡</td>
<td>2 mo ~475</td>
<td>25.2</td>
<td>27.2</td>
<td>fatter</td>
<td></td>
</tr>
<tr>
<td>Yambayamba &amp; Price, 1991§</td>
<td>6 mo 410</td>
<td>34.2</td>
<td>37.3</td>
<td>similar</td>
<td></td>
</tr>
<tr>
<td>Fox et al., 1972</td>
<td>238 kg 341</td>
<td>23.0</td>
<td>17.0</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td>Rompala et al., 1985</td>
<td>7 mo 400</td>
<td>15.2</td>
<td>12.2</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td>Wright &amp; Russel, 1991</td>
<td>8 mo 322</td>
<td>16.9</td>
<td>11.7</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td>Henricks et al., 1994†</td>
<td>9 mo 400</td>
<td>21.7</td>
<td>19.1</td>
<td>similar</td>
<td></td>
</tr>
<tr>
<td>Ryan et al., 1993</td>
<td>9-10 mo 590</td>
<td>35.0</td>
<td>34.2</td>
<td>similar</td>
<td></td>
</tr>
<tr>
<td>Smith et al., 1977‡‡</td>
<td>small-frame 8-9 mo NA</td>
<td>43.2</td>
<td>33.0</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td></td>
<td>large-frame 8-9 mo NA</td>
<td>31.1</td>
<td>20.7</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td>Carstens et al., 1991</td>
<td>10 mo 450</td>
<td>32.4</td>
<td>24.2</td>
<td>leaner</td>
<td></td>
</tr>
<tr>
<td>Harris, 1994§</td>
<td>8 mo 510</td>
<td>33.6</td>
<td>29.8</td>
<td>leaner</td>
<td></td>
</tr>
</tbody>
</table>

†Experiments presented were limited to those which reported composition at weight constant endpoints. Values listed are empty-body fat unless otherwise specified.
‡Trial 2 results reported from compensatory growth treatment which followed 210 days of growth restriction on low-protein diet.
§Dissected carcass fat composition was measured.
††9-10-11 rib chemical fat composition was measured.
‡‡9-10-11 rib chemical fat composition, adjusted to a constant carcass weight of 300 kg, was measured. Results from continuous steers fed a 2.84 Mcal ME/kg diet and compensatory steers fed the same diet following 267 d of growth restriction are presented.

(8 mo of age) Angus/Hereford steers reduced empty-body fat by 25%. Empty-body fat was not altered significantly during compensatory growth in steers that were intermediate in physiological age (8 mo old, later-maturing Charolais steers). It is interesting to note that the relative growth advantage of compensatory vs continuous growth steers in these studies was closely related to the magnitude of change that occurred in tissue composition during the compensation period. Compensatory growth was not exhibited in the Hereford calves restricted at an early stage of maturity (Tudor et al., 1980). However, over equal weight intervals, ADG were 24 and 37% greater in compensatory than continuous growth steers in the experiments of Wright and Russel (1991) and Carstens et al. (1991).

Thornton et al. (1979) conducted one of the few studies to compare directly the effects of stage of maturity at the point of growth restriction on composition of growth upon realimentation. They examined compensatory growth patterns following a 25% weight-loss period in both immature (23 kg) and mature (43 kg) lambs. Although not different statistically, the authors noted that empty-body composition of compensatory growth lambs tended to be fatter (45% empty-body fat) than of continuous growth control lambs (42% empty-body fat) when weight loss was imposed on immature lambs, but leaner (39% empty-body fat) than of controls when weight loss was imposed on mature lambs.
Table 3. Effects of stage of maturity at time of growth restriction on noncarcass, carcass and empty-body composition in continuous and compensatory growth cattle.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Noncarcass Protein</th>
<th>Noncarcass Fat</th>
<th>Carcass Protein</th>
<th>Carcass Fat</th>
<th>Empty-body Protein</th>
<th>Empty-body Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tudor et al., 1980 [Composition at 330 kg EBW]:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>continuous growth</td>
<td>16.3</td>
<td>27.8</td>
<td>15.3</td>
<td>29.9</td>
<td>15.7</td>
<td>29.2</td>
</tr>
<tr>
<td>compensatory growth</td>
<td>15.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>31.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>34.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>33.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>difference, %</td>
<td>-6.7</td>
<td>14.7</td>
<td>-8.5</td>
<td>14.0</td>
<td>-7.6</td>
<td>14.0</td>
</tr>
<tr>
<td>Wright and Russel, 1991 [Composition at 365 kg EBW]:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>continuous growth</td>
<td>19.5</td>
<td>15.9</td>
<td>18.7</td>
<td>15.7</td>
<td>19.0</td>
<td>15.8</td>
</tr>
<tr>
<td>compensatory growth</td>
<td>21.0</td>
<td>11.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>18.8</td>
<td>15.0</td>
<td>19.6</td>
<td>13.8</td>
</tr>
<tr>
<td>difference, %</td>
<td>7.7</td>
<td>-26.4</td>
<td>0.5</td>
<td>-4.5</td>
<td>3.2</td>
<td>-12.7</td>
</tr>
<tr>
<td>Carstens et al., 1991 [Composition at 450 kg EBW]:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>continuous growth</td>
<td>15.5</td>
<td>28.6</td>
<td>14.7</td>
<td>34.1</td>
<td>14.8</td>
<td>32.4</td>
</tr>
<tr>
<td>compensatory growth</td>
<td>17.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>18.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>27.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>16.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>24.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>difference, %</td>
<td>9.7</td>
<td>-37.0</td>
<td>10.2</td>
<td>-20.2</td>
<td>12.2</td>
<td>-25.3</td>
</tr>
</tbody>
</table>

<sup>a</sup>Growth rates were restricted to: 0.05 kg/d in Hereford calves for 200 d beginning at four d of age (Tudor et al., 1980); 0.45 kg/d in Charolais crossbred steers for 216 d beginning at 8 mo of age (Wright & Russel, 1991); and 0.40 kg/d in Angus/Hereford crossbred steers for 189 d beginning at 10 mo of age (Carstens et al., 1991).

A computer model (Keele et al., 1992) was used to assess the effects of stage of maturity on compositional changes during continuous and compensatory growth, independent of the effects of duration or severity of growth restriction. The computer model, developed specifically to predict the effects of plane of nutrition on empty-body composition in cattle, was used to simulate empty-body fat of steers following a 6-mo period of growth restriction (0.45 kg/d) imposed at 3, 6, 9 or 12 mo of age (Figure 1; top panel). The model predicted little change in empty-body fat when growth restriction was imposed at 3 mo of age, but differences in empty-body fat between continuous and compensatory growth steers increased as age at the point of growth restriction was increased.

Collectively, the aforementioned studies imply that at earlier stages of maturity, when the impetus for fat deposition is low, the ability to manipulate the composition of growth during restriction and compensation periods is limited. At later stages of maturity, when the potential for fat deposition is greater, composition of growth is more likely to be leaner during the compensation period.

**Effects of Severity of Growth Restriction Period.** The different responses to growth restriction in the three experiments described in Table 3 cannot be attributed due solely to differences in stage of maturity, as the severity of growth restriction obviously was greater in the experiment of Tudor et al. (1980). However, based on limited studies, it appears that the level of nutritional restriction, independent of stage of growth, also affects composition of growth during the compensation period. Smith et al. (1977) found that as the degree of growth restriction was increased, the proportion of carcass fat (9-10-11 rib fat adjusted to 300 kg carcass weight) deposited during compensatory growth was reduced further. Small-frame steers backgrounded previously on a low-energy diet (2.18 Mcal ME/kg) were leaner than steers backgrounded previously on a moderate-energy (2.40 Mcal ME/kg) diet (33.3 vs 38.1% rib fat), and substantially leaner than steers fed the high-energy diet continuously (43.1% rib fat). The proportion of rib fat for large-
frame steers in the same experiment was 20.7, 25.9 and 31.1%, respectively. Likewise, Meyer et al. (1965) found that steers backgrounded previously on a moderate-energy diet to gain .30 kg/d were leaner than steers fed the high-energy diet continuously. However, when steers were restricted more severely on a low-energy diet to gain .35 kg/d, carcass composition tended to be similar to that of continuous growth steers. Although not specified by Meyer et al. (1965), their steers likely were younger (initial BW of 180 kg) than the 8- to 9-mo old steers used in the experiment of Smith et al. (1977). The implication is that at earlier stages of maturity, more severe rates of growth restriction (less than ~.3 kg/d) are less likely to change carcass composition (Meyer et al., 1965) or to increase carcass fat (Tudor et al., 1980; Abdalla et al., 1988) during the compensatory period.

Effects of Duration of Growth Restriction Period. The magnitude of the compensatory growth response appears to increase as the duration of the growth restriction period is extended. Ledger (1973) found that ADG during realimentation were .81 and 1.16 kg/d for steers previously restricted to maintain BW for 12 and 24 wk, respectively. Differences in the length of the growth restriction period may have contributed to the differences in carcass composition noted in the experiment of Smith et al. (1977) discussed above. Steers were restricted on the low-energy diet for ~80 d longer than steers restricted on the moderate-energy diet. Dolezal et al. (1993) finished steers on a high-grain diet as calves (initial age ~8 mo), and following 112- (yearlings) or 280-d (long yearlings) backgrounding periods on a corn silage-based diet. Carcass weights adjusted to a constant sc. fat thickness endpoint of 13.5 mm were similar for calves and yearlings (323 and 334 kg), but were heavier for the long yearlings (370 kg). These results suggest that carcass composition, adjusted to a common carcass weight endpoint, would have been leaner for the 280-d backgrounded steers than for steers backgrounded for only 112 d, or steers fed high-grain diets as calves. This observation concurs with simulation results (Figure 1; lower panel) that compared empty-body composition of steers fed high-grain diets continuously to steers restricted to .45 kg/d for 3, 6, 9 or 12 mo prior to realimentation. Increasing the duration of the growth restriction period further reduced the proportion of fat deposited during the compensatory period.

Differential Effects on Carcass and Noncarcass Tissues. Composition appears to be altered to a greater extent by plane of nutrition for noncarcass than carcass tissues (Murray et al., 1975; 1977). Moreover, Wright & Russel (1991) and Carsiens et al. (1991) found that the proportion of fat in noncarcass tissues was reduced by 26 and 37% in compensatory growth steers, whereas the reduction in carcass fat in compensatory growth steers was only 4 and 20%, respectively (see Table 3). This phenomenon also was demonstrated using lambs (Kabbali et al., 1992). Compensatory growth lambs deposited 24% less fat in noncarcass tissues than continuous growth lambs even though carcass composition was not affected. Therefore, experiments that rely on carcass measurements alone (i.e., indicator cut, specific gravity) to determine empty-body composition will tend to underestimate the impact of growth restriction on subsequent changes in empty-body composition (and thus NE requirements for growth) during the compensatory period.

Maintenance Energy Requirements

Cattle placed on a low plane of nutrition to maintain BW require progressively less feed per day as the length of the growth restriction period is extended (Leder and Sayers, 1977; Foot and Tullloch, 1977). These experiments demonstrated that cattle adapt metabolically to restrictions in dietary energy by lowering their metabolizable energy requirements for maintenance (ME\textsubscript{m}). Current estimates for cattle (Corbett et al., 1987; Birko et al., 1991) suggest that ME\textsubscript{m} is increased ~10% per multiple of increase in maintenance energy feeding. Deviations in ME\textsubscript{m} imposed by nutritional organ manipulation are related to changes in visceral mass, especially the liver and the gastrointestinal tract (GIT) tissues (Ferrell et al., 1986; Table 4). These visceral organs, although weighing less than 10% of total body mass, expend 40 to 50% of the total energy expended by the whole animal (Ferrell, 1988; Johnson et al., 1990). Because the weight of these visceral organs proportionally increases in response to dietary energy restriction, energy requirements for maintenance are reduced.

Upon realimentation, visceral organ mass increases rapidly and ME\textsubscript{m} is elevated. There exist, however, a metabolic lag phase during which ME\textsubscript{m} remains lower and(or) efficiency of energy utilization remains elevated until animals adapt fully to the higher plane of nutrition. A reduction in ME\textsubscript{m} during realimentation would contribute to compensatory growth by increasing the availability of energy for growth, although the extent and duration of this metabolic lag phase is open to question. Ledger and
Sayers (1977), noting that daily feed required to maintain BW continued to decline past 12 wk and did not plateau until 15 wk, postulated that an equal period of time may be required for metabolism to stabilize during realimentation. Turner and Taylor (1983) proposed that the duration of the metabolic lag phase ($t_q$) be expressed as a function incorporating a first order lag constant ($t$):  

$$t_q = \frac{-\ln \left(1 - q\right)}{t}$$

where $q$ is the proportion of maximal heat production response to a change in level of nutrition. The lag constant was estimated to be $28 \text{ d}$, based on results from feeding experiments including Ledger and Sayers (1977). Thus $64 \text{ d}$ would be required to achieve $90\%$ of maximal heat production response upon realimentation. Adaptation periods of this length have not, however, been demonstrated in calorimetry experiments. Graham (1982) suggested that a 3- to 4-wk adaptation period was required to stabilize metabolism in sheep following a change in level of nutrition, which is comparable to the 3-wk lag in the maximal heat production response found in steers (see Figure 2; top panel). A metabolic lag period of this duration appears to parallel the time required to achieve maximal visceral organ mass following realimentation. Johnson (1985) measured proportional weights (g/kg EBW) of liver and fat-free GIT tissues in steers following a 45-d feed restriction period to maintain BW (day 0), and on days 15, 30 and 45 of realimentation. Proportional liver weights were 30, 35 and 39% larger, and GIT tissue weights were 16, 20 and 22% larger on days 15, 30, 45 of realimentation, respectively, than on day 0. Burkin et al. (1990) measured visceral organ weights and their metabolic activities (O$_2$ consumed/g of tissue) in realimented sheep following a 14-d feed restriction period. Relative to day 0 of realimentation, the proportional metabolic activity of whole liver (total liver O$_2$ consumed/kg EBW) was 50, 66 and 75% higher on days 7, 14 and 21 of realimentation, respectively. The large increase in whole-liver oxygen consumption was attributed to an increase in liver mass; oxygen consumption per unit of liver weight was not changed by realimentation. Therefore, the lag in heat production that occurs as animals are switched from a low to a high plane of nutrition closely mimics the proportional change in their visceral organ mass.

Not all experiments, however, have demonstrated an appreciable lag phase in heat production during realimentation. Armstrong and Blaxter (1984), based on the results of Wainman et al. (1972) in sheep and Schytler et al. (1982) in cattle, concluded that maximal heat production was achieved within 5 to 9 d of realimentation. Likewise, Ortizues et al. (1993) found that most of the heat production response to a change in level of nutrition occurred within 10 d. The apparent discrepancies between experiments in the time required for animals to adapt metabolically to an increase in level of nutrition likely is related to differences in severity and/or duration of the previous growth restriction period.

The degree to which a decrease in ME$_m$ imposed by previous growth restriction contributes to faster, more efficient growth during the subsequent compensation period is largely unknown. In sheep subjected to weight loss followed by realimentation, Hogg and Tullch (1982) concluded that compensatory gains were due to a reduction in ME$_m$, whereas Drew and Reid (1975) and Graham and Searie (1979) found that compensatory gains were due to increased feed intakes rather than to reduced ME$_m$. Recent results presented by Sainz (1995) suggest that the type of diet fed during the growth restriction period also may affect ME$_m$ during the subsequent realimentation period. In this experiment, steers were full-fed a high-concentrate diet continuously (controls), or following a backgrounding period during which steers were limited-fed a high-concentrate diet (CL) or full-fed a forage diet (FA) to gain .75 kg/d. Relative to control steers, ME$_m$ during the finishing period (all steers fed the same diet ad libitum) were 7% lower in CL steers, but 28% higher in FA steers. The reduction in ME$_m$ of CL steers occurred even though feed intakes were 21% greater than controls. Sainz suggested that differences in ME$_m$ during the finishing period may have been related to differences in visceral organ mass at the start of realimentation. At the end of the backgrounding period, reticularumen weights of CL steers were 4% lighter than controls, whereas the reticularumen weights of FA steers were 28% heavier than controls, suggesting that a forage-diet effect on visceral organ mass may have prompted higher ME$_m$ in FA steers during the compensation period.
Table 4. Effects of previous growth rates on selected visceral organ weights and fasting heat production in growing lambs.†

<table>
<thead>
<tr>
<th>Previous ADG, g/d</th>
<th>Liver, g</th>
<th>Stomach, g</th>
<th>Small intestine, g</th>
<th>Heat production, kcal/day</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>469 (100)</td>
<td>744 (100)</td>
<td>354 (100)</td>
<td>928 (100)</td>
</tr>
<tr>
<td>100</td>
<td>501 (107)</td>
<td>781 (105)</td>
<td>381 (108)</td>
<td>1010 (109)</td>
</tr>
<tr>
<td>200</td>
<td>536 (114)</td>
<td>819 (110)</td>
<td>411 (116)</td>
<td>1099 (118)</td>
</tr>
<tr>
<td>300</td>
<td>574 (122)</td>
<td>860 (116)</td>
<td>443 (125)</td>
<td>1196 (129)</td>
</tr>
</tbody>
</table>

†Visceral organ weights and fasting heat production were calculated for a 35 kg EBW lamb based on regression equations presented by Ferrell et al. (1986). Numbers in parentheses represent percentage differences relative to lambs gaining 0.0 g/d.

Net Efficiency of Tissue Growth

Fox et al. (1988) concluded that compensatory growth in cattle was due primarily to a reduction in ME_M and an increase in efficiency of ME utilization for growth (k_F); subsequently they developed multiplicative factors to adjust ME_M and k_F according to previous growth rates. They proposed, for example, that a medium-frame steer previously gaining 36 kg/d rather than 68 kg/d must have 4.5% lower ME_M and 10% greater k_F during the realimentation period to account for compensatory growth. Several experiments have demonstrated that k_F is elevated during compensatory growth in sheep and cattle (Table 5). In these experiments, however, estimates of k_F were derived from slaughter balance measurements of retained energy. Estimates of ME available for growth assume equal ME_M. Thus, to the extent that ME_M may have been reduced during the compensation period in these experiments, the estimates of k_F presented in Table 5 for compensatory growth would be overestimated. Few definitive studies have examined ME_M and k_F concurrently during continuous and compensatory growth patterns; therefore, it is difficult to project conclusively to what degree either or both of these factors contribute toward compensatory growth.

Gingins et al. (1980) fed mature sheep (initial BW of 55 kg) after restricting growth to lose 25% of BW and found that k_F was 73% on day 37 of realimentation. This estimate of k_F was substantially higher than 59% predicted by ARC (1983) for continuous fed sheep. Finding no differences in feed intake or ME_M between continuous and compensatory growth sheep (initial BW of 35 kg), Meyer and Clawson (1964) concluded that compensatory gains in their experiment were due primarily to improvements in k_F. Contrary to these studies, when immature lambs (initial BW of 15 to 22 kg) were realimented after weight-loss (Graham and Scarle, 1979) or growth-restriction periods (Thomson et al., 1982), little or no improvement in k_F was observed during compensatory growth. Based on these studies one could surmise that improvements in k_F during compensatory growth are most likely to occur when growth is restricted at later stages of maturity. Results of Orskov et al. (1975) do not support this observation (Table 5), but in this experiment growth was restricted by limiting protein intake.

As with changes in ME_M during realimentation, increases in k_F are most likely to occur during the initial 3 to 4 wk of realimentation (Figures 2, 3). Orskov's estimates of k_F during compensatory growth were 48% higher than controls from 28 to 35 kg BW which lasted 15 d, but only 11% higher from 35 to 45 kg BW which lasted 24 d. Both Turgeon et al. (1986) and Wright and Russel (1991) found that k_F was improved during compensatory growth in sheep and cattle relative to continuous growth controls. In these studies, however, the improvement in k_F was delayed and did not occur until the second half of the compensation period. Furthermore, in these studies compensatory growth animals deposited more protein during the early stages, but more fat during the latter stages of the compensation period, so that empty-body composition was similar to controls at the end of the studies. As stated by Wright and Russel (1991), the apparent increase in k_F during compensatory growth
Table 5. Efficiency of metabolizable energy utilization for growth (\(k_r\)) in sheep and cattle exhibiting continuous and compensatory growth.

<table>
<thead>
<tr>
<th>Experiment†</th>
<th>Species</th>
<th>Continuous growth</th>
<th>Compensatory growth</th>
<th>Difference, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fox et al., 1972</td>
<td>cattle (corn diet)</td>
<td>47</td>
<td>50</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>cattle (soybean diet)</td>
<td>51</td>
<td>58</td>
<td>14</td>
</tr>
<tr>
<td>Thomson et al., 1982</td>
<td>cattle</td>
<td>36</td>
<td>43</td>
<td>19</td>
</tr>
<tr>
<td>Carssen et al., 1989</td>
<td>cattle</td>
<td>35</td>
<td>41</td>
<td>17</td>
</tr>
<tr>
<td>Orskov et al., 1976</td>
<td>sheep</td>
<td>48</td>
<td>57</td>
<td>19</td>
</tr>
<tr>
<td>Reid et al., 1980</td>
<td>sheep</td>
<td>43</td>
<td>57</td>
<td>32</td>
</tr>
</tbody>
</table>

†Estimates of \(k_r\) (retained energy / ME available for growth) were based on slaughter balance measurements of retained energy and estimates of ME available for growth assuming equal maintenance energy requirements. Estimates of \(k_r\) were determined over equal BW intervals for continuous and compensatory growth animals.

coincided with the period of enhanced fat deposition. This would support the current dogma that fat deposition is more efficient energetically than protein deposition (Reid et al., 1980). Turgeon et al. (1986) and Wright and Russel (1991) did not, however, find lower \(k_r\) during the early stage of compensatory growth when protein deposition was higher. Moreover, in the aforementioned studies, protein deposition rates were higher during the early stages of compensatory growth when \(k_r\) were increased. Several studies have suggested that improved \(k_r\) during the early stages of compensatory growth were largely due to an increase in efficiency of protein deposition (Orskov and McDonald, 1976; Gingins et al., 1980; Thomson et al., 1982).

Feed Intake and Gastrointestinal Tract Capacity

An increase in dry matter intake (DMI) per unit of metabolic weight (BW\(^{0.75}\)) is another mechanism that can account for compensatory growth responses in cattle. NRC (1984) concluded that compensating yearling cattle consume 10% more feed than calves of similar weight and frame size. Several studies have demonstrated that DMI/BW\(^{0.75}\) in compensating cattle exceeds that of continuous growth cattle by more than 10% (Mader et al., 1989, Gill et al., 1993b and Sainz, 1995), although Hironaka et al. (1979) and Carstens et al. (1991) found little or no change in DMI in compensatory vs continuous growth cattle over common BW intervals. Hicks et al. (1990) noted that the pattern as well as the level of DMI was different for cattle fed as yearlings and calves. They observed that DMI of calves increased linearly during the initial ~70 d on feed and plateaued thereafter for the remainder of days on feed, whereas DMI of yearlings increased linearly for the first 40 to 50 d, plateaued for ~40 d and declined thereafter for the remainder of days on feed. NRC (1987) also noted that yearling cattle typically reach maximal DMI at 28 to 42 d on feed. Ryan et al. (1993a) reported that DMI were similar during the initial 84 d of reallimentation, and higher thereafter in compensating steers, whereas Carstens et al. (1991) found that DMI/BW\(^{0.75}\) were 10% lower in compensating steers during the initial 44 d of reallimentation and similar thereafter to continuous growth steers for the remainder of the study. Therefore, to the extent that DMI are increased in compensating cattle relative to continuous growth cattle over similar BW intervals, these increases in DMI likely will be delayed until after the initial 30 to 40 d of reallimentation.

A similar delay in maximal DMI occurs in lactating cows, with DMI continuing to increase for several weeks past peak milk yields. Forbes (1985) concluded that the ability of lactating cows to consume increased amounts of feed and to accommodate greater GIT fill relative to nonlactating cows is related to an increased demand for nutrients. Forbes suggested that increased utilization of metabolites induced by lactation will reduce the degree of chemoreceptor stimulation, thereby limiting negative feedback to intake-controlling centers of the brain. A reduction in chemoreceptor feedback in turn would permit
Table 6. Differences in gastrointestinal tract (GIT) fill in sheep and cattle exhibiting continuous and compensatory growth.

<table>
<thead>
<tr>
<th>Experiment†</th>
<th>Species</th>
<th>GIT fill, g/kg EBW</th>
<th>Continuous growth</th>
<th>Compensatory growth</th>
<th>Difference, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tudor et al., 1980</td>
<td>cattle</td>
<td>127</td>
<td>128</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Thomson et al., 1982</td>
<td>cattle</td>
<td>92</td>
<td>99</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Wright and Russel, 1991</td>
<td>cattle</td>
<td>228</td>
<td>245</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Carstens et al., 1991</td>
<td>cattle</td>
<td>109</td>
<td>131</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>McManus et al., 1972</td>
<td>sheep</td>
<td>97</td>
<td>105</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Burton et al., 1974</td>
<td>sheep</td>
<td>70</td>
<td>124</td>
<td>77</td>
<td></td>
</tr>
<tr>
<td>Winter et al., 1976</td>
<td>sheep</td>
<td>95</td>
<td>121</td>
<td>27</td>
<td></td>
</tr>
</tbody>
</table>

†GIT fill weights were determined at equal BW endpoints.

Greater stimulation of abdominal stretch receptors before feed intake limits were reached. As in lactating cows, the impetus to compensate for previous undernutrition will prompt an increase in the demand for nutrients during realimentation, thus inducing enhanced DMI and a greater GIT capacity in compensating cattle. As shown in Table 6, compensating animals typically have increased GIT fill weights. The exception is the study of Tudor et al. (1980) in which compensating calves were previously subjected to severe restriction early in life. Although cattle appear to be able to accommodate greater GIT fill during compensatory growth, DMI still could be limited by physical constraints of the GIT when low-energy diets are fed during realimentation. Fox et al. (1972) found that compensating steers consumed 16% more feed than continuous growth steers when realimented on a corn-based diet (2.60 Mcal ME/kg), but no increase in DMI was observed when steers were realimented on a soybean-based diet (1.50 Mcal ME/kg).

In a series of experiments, Wright et al. (1986; 1987; 1989) demonstrated that organic matter intakes (OMI) of moderately to highly digestible forages were increased in cattle previously subjected to lower planes of nutrition during the winter (Figure 4; right panel). Partial regression coefficients derived from regressing summer ADG on winter ADG were -.50, -.58 and -.61 for the three experiments, respectively (Figure 4; left panel). Increases in forage OMI of compensating cattle were found irrespective of forage availability (Wright et al., 1986), genotype (Wright et al., 1987) or type of summer forage grazed (Wright et al., 1989). In all three experiments, subcutaneous fat (measured ultrasonically) was reduced significantly in cattle fed at lower levels of nutrition during the winter. This led Wright and coworkers to conclude that higher forage OMI/BW during the summer was primarily the result of reductions in body fat. Moreover, Wright et al. (1986) found that low winter-fed singles were similar in BW and subcutaneous fat levels to high winter-fed twins at the end of the winter feeding period, and subsequently consumed similar amounts of forage during the summer (Figure 4). Thus, growth rates immediately preceding the summer grazing period apparently were less important than body fat levels in affecting subsequent intake of forage organic matter.

As reviewed by NRC (1987), Forbes (1986) suggested that physiological control mechanisms associated with lipid metabolism exist to provide negative feedback on DMI as level of fatness in an animal increases. NRC (1987) concluded that DMI/BW 75 begins to decrease as cattle grow beyond 350 kg BW (21.3% empty-body fat; frame-size equivalent basis), and recommended that DMI/BW 75 be adjusted downward 3, 10 and 18% as cattle reached empty-body fat levels of 23.8, 26.5 and 29%, respectively. It is interesting to note that in the experiments of Wright and coworkers, BW of high winter-fed cattle at the beginning of the summer grazing periods ranged from 368 to 406 kg. Meyer et al. (1965), Mader et al. (1989) and Hironaka et al. (1979) all found that increases in DMI by compensating cattle occurred concurrently with reductions in carcass fatness. Carstens et al. (1991), however, found that DMI was not increased in compensatory growth steers even though steers were substantially leaner than continuous growth steers. In the study of Fox et al. (1972), compensating steers were 27% leaner than continuous growth steers at 364
kg BW, but similar in composition at 454 kg BW. Compared to continuous growth steers, DMI of compensating steers was 10% higher at 364 kg BW, and 16% higher at 454 kg BW. This would indicate that compensating steers continued to consume more feed during the latter phase of the experiment even though the composition of growth was fatter. Sainz (1993) likewise reported that DMI were increased 21 to 30% in compensating steers that were similar in composition to continuous growth steers at a common slaughter weight endpoint. Thus increases in DMI during compensatory growth are not always associated with reductions in fat tissue growth.

LITERATURE CITED


Figure 1. Simulation results depicting the effects of stage of maturity at the start of growth restriction (top panel) and length of growth restriction period preceding compensatory growth (lower panel) on changes in empty-body fat relative to continuous growth steers. Simulation conditions: (i) medium-frame Angus steers, (ii) ADG of 75 kg/d from birth to start of continuous or restricted growth periods, (iii) ADG of 45 kg/d during growth restriction periods, (iv) high-energy finishing diet fed during continuous and compensatory growth periods, and (v) empty-body fat assessed at 450 kg EBW. Top panel: continuous and 6-mo growth restriction periods started at 3, 6, 9 and 12 mo of age. Lower panel: continuous growth and growth restriction periods all started at 9 mo of age; length of growth restriction periods varied from 3, 6, 9 to 12 mo. Simulations conducted by C.B. Williams using model as described by Keene et al. (1992).
Figure 2. Changes in energy metabolism and liver mass in steers during realimentation following a 6-mo period of growth restriction. Top panel: changes in daily ME intake, heat production (measured by indirect calorimetry), and retained energy. Lower panel: changes in liver mass and efficiency of ME used for growth ($k_r$: retained energy ÷ ME for growth). Estimates of ME for growth were calculated assuming a 14% increase in ME_{III} from day 0 to 19 of realimentation. Steers were previously limit-fed a 70% concentrate diet to restrict growth to 0.4 kg/d. Adapted from Carsiens et al. (1989; 1991).
Figure 3. Efficiency of metabolizable energy utilization for growth ($k_r$) in lambs fed a high-protein diet continuously, and in compensating lambs previously fed a low-protein diet from 20 to 28 kg BW. Estimates of $k_r$ were determined as described in Table 5. Adapted from Orskov et al. (1976).

Figure 4. Effects of plane of nutrition during the winter period (5 to 6 mo) on ADG and forage organic matter intakes during the subsequent summer grazing period (3 to 4 mo) in cattle. Organic matter intakes were measured on three occasions during the grazing period based on chromic oxide dilution and estimates of in vitro digestibility of esophageal samples. Adapted from Wright et al. (1986, trials I, II; 1987, single- and twin-born calves; and 1989).