Growth production and meat

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ABSTRACT

The growth of an animal from birth to slaughter includes aspects of development of cells, tissues and organs, and the endocrine and metabolic factors that regulate them. These factors in turn are subject to genetic and environmental control. At the opposite end of the production system, the conversion of living muscles to meat involves a series of metabolic, chemical and physical transformations that continue the sequence begun during growth. Metabolic manipulation of growth generally promotes anabolic or inhibits catabolic processes, and may be accomplished by genetic, nutritional or pharmacological means. These modifications often continue to exert their effects during the *post-mortem* period. For example, β-adrenergic agonists stimulate protein deposition by reducing protein degradation, but the reduced proteolysis continues *post-mortem*, resulting in tough meat. In contrast, stimulation of the somatotropic axis increases the rate of protein synthesis, and proteolysis (and meat quality) are unaffected. New techniques to improve growth patterns and product quality will arise from molecular biotechnology. Moreover, for extensive production systems the objectives of enhanced productivity and product quality must be balanced against the ability of the animal to withstand the rigors of its environment. Development of such techniques that improve production without impairing product quality or adaptability will require deeper understanding of the mechanisms involved in survival, growth and meat quality.

INTRODUCTION

The typical growth curve for a given animal is sigmoid, that is growth is initially slow, then accelerates, and finally declines so that weight reaches its asymptotic maximum (Fig. 1). The allometric growth curves for the main components of the carcass (bone, muscle and fat) show that the amounts of bone and muscle increase at a slower rate than total carcass weight, whereas the reverse is true for fat (Fig. 2). These allometric growth patterns determine the development of economically important traits in meat animals. As an animal matures, the proportion of fat in its body (and carcass) increases even more rapidly (Berg & Butterfield, 1976). Clearly, these patterns vary among animals, with important consequences for efficiency and quality of meat production. For example, a large-frame animal usually matures later than a small one, so that the rapid accretion of fat takes place at heavier weights. Therefore, the large-frame animal will be leaner than its smaller counterpart at any given weight. Because it is more efficient to deposit lean tissue than fat, the leaner animal converts feed more efficiently. In markets that penalize over-production of fat, the late-maturing animal thus has a double advantage: more efficient growth, and a more valuable product. There are, however disadvantages: increased mature size (and maintenance requirement) of females, and a greater likelihood of inferior meat quality. This paper will examine some interactions among growth patterns, productive efficiency, and carcass and meat quality, from the perspective of production systems that must fit their particular environments.

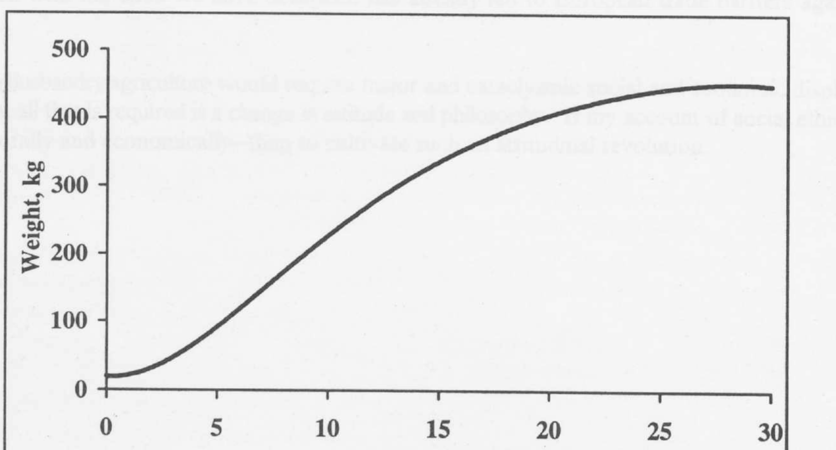

Fig. 1. Typical cattle growth curve

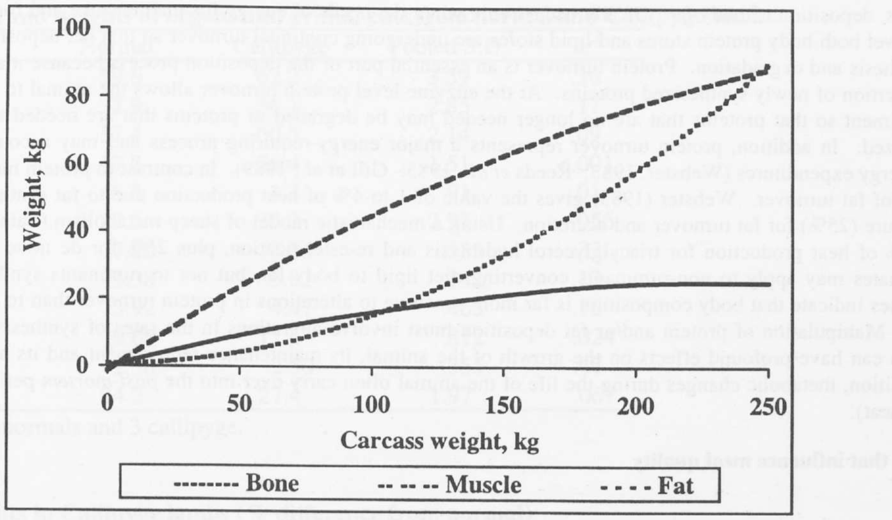

Fig. 2. Allometric growth curves for bone, muscle and fat

Current concepts of growth

Since the major tissues of the carcass are bone, muscle and fat, the development of these tissues is of both scientific and economic interest. Development and growth of bones can occur through endochrondal ossification or intra-membranous ossification. In long bones, a cartilage model is laid down by chondrocytes which develop into osteocytes, which in turn secrete the osteoid matrix which is them mineralized (Burwell, 1986). After long bone formation, further longitudinal growth takes place through the proliferation and maturation of chondrocytes at the epiphyseal (growth) plates. In terms of determining the mature size or frame of an animal the critical event is the closure of the growth plates, which occurs at different but specific points during the animal's development. The earlier this closure and ossification occurs, the smaller the frame or eventual size of the animal. The proliferation and maturation of chondrocytes at the growth plates is stimulated by growth hormone, IGF-1 and other growth factors, as well as by low levels of sex steroids (Burwell, 1986). This latter effect accounts for the growth spurt often seen during early puberty. On the other hand, high concentrations of sex steroids cause closure of the plate and results in the animal reaching its ultimate size, as occurs during late puberty. Mature size is a highly heritable trait and so the genetic control of skeletal growth is very finally tuned, probably operating at many levels. These probably include the expression of specific genes within chondrocytes as well as their endocrine, autocrine and paracrine regulation. To date, the specific genes responsible for chondrocyte differentiation, proliferation and maturation have not been identified.

Skeletal muscle arises from mesoderm cells which migrate to various parts of the body from somites arranged along the neural tube. These cells become myoblasts and begin expressing genes specific to muscle cells. Over time these myoblasts fuse forming multi-nucleated myotubes that eventually give rise to muscle fibers (Dayton & Hathaway, 1991). It is generally recognized that the number of muscle fibers in an animal is fixed around the time the animal is born. Subsequent growth of muscle then occurs through elongation of muscle fibers by addition of sarcomeres and increases in the cross-sectional area through the addition of nuclei from satellite cells and myofibrillar proteins. Proliferation of myoblasts and fusion and formation of myotubes are stimulated by IGF-I and other growth factors. The terminal differentiation step, that is fusion of myoblasts into myotubes is inhibited by transforming growth factor-β (TGF-β; Massague *et al.*, 1986). This inhibitory effect may allow for an increase in the number of myoblasts available for fusion and possibly in the number of muscle fibers. The number of muscle fibers is positively correlated with ultimate muscularity, as seen in runt pigs (Handel & Stickland, 1987) and double-muscled cattle (Rollins *et al.*, 1980). A family of myogenic regulatory factors (MRFs) that determine the differentiation of myoblasts has been identified. These genes include myogenic, MyoD, MRF-4, myf-5 and others (Rudnicki & Jaenisch, 1995). There is a specific sequence of expression that leads to myogenesis, but it is recognized that either MyoD or myf-5 expression is necessary and sufficient to initiate the sequence.

As in all tissues, growth of adipose tissue comprises both hyperplastic (i.e., increase in cell number) and hypertrophic (i.e., increase in cell size) growth. Hyperplasia includes the processes of proliferation and differentiation of fibroblast-like mesenchymal cells into adipocytes (Vernon, 1986). The process of differentiation is regulated or influenced by a number of external hormones, such as insulin, growth hormone, insulin-like growth factor-I, glucocorticoids, and triiodothyronine (Kovacs & Graves, 1996). In addition, a number of genes have been identified, whose expression is linked to the terminal differentiation of adipocytes. Among these, c/EBPα and PPARγ appear most important, with the latter gene being the most likely candidate for the role of deciding factor.

Postnatal fat accretion occurs primarily though hypertrophy of existing adipocytes (through accumulation of intracellular lipid) with a smaller contribution of hyperplasia (Allen, 1976; Hood, 1982; Robelin, 1981). For example, in Friesian bulls the amount of total body fat increases 197-fold between birth and maturity, whereas the number of adipocytes only increases 6.7-fold and the mean adipocyte volume increases 29-fold during the same period (Robelin, 1986). This general observation, however, may obscure the fact that individual fat depots vary in their rates and timing of hyperplastic and hypertrophic growth. Cianzio *et al.* (1985) found that from 11 to 19 months, subcutaneous, intermuscular, kidney and mesenteric fat depots in steers grew by hypertrophy, with little or no change in cell numbers. Intramuscular fat accretion, on the other hand, was due to the appearance of new adipocytes as well as increases in their lipid content. Therefore, we may conclude that during the finishing phase the earlier developing depots (i.e., subcutaneous, intermuscular, kidney and mesenteric fat) have completed their hyperplastic development and deposit fat by filling existing adipocytes, whereas the intramuscular depot continues to recruit new adipocytes as well as filling existing cells with lipid.

All aspects of animal growth including development of tissues mentioned above are under fine genetic control, so that animal size, muscularity, and fat content and distribution are all heritable traits. They are therefore susceptible to genetic selection or manipulation. Moreover, there is considerable scope for manipulation of the animal's environment, nutrition and physiological state to alter those variables. Manipulation of growth patterns will have a wide range of consequences, possibly including altered nutritional requirements, meat quality, and environmental adaptability. The nature of these consequences will depend upon the mechanisms involved in the growth alteration. Growth involves the deposition of dietary energy into body protein and fat, and can only occur when energy intake exceeds the energy expended for maintenance. Therefore, increases or decreases in maintenance energy expenditures will produce inverse changes in the energy available for growth. Since metabolic processes in different tissues vary in their priorities, deposition of body fat typically occurs only when the needs of energy for maintenance and for protein accretion have been met. A the metabolic level both body protein stores and lipid stores are undergoing continual turnover so that net deposition represents the difference betwe the rates of synthesis and degradation. Protein turnover is an essential part of the deposition process because it allows re-modeling of the myofibril structure for insertion of newly synthesized proteins. At the enzyme level protein turnover allows the animal to adapt to changes in its nutritional an climatic environment so that proteins that are no longer needed may be degraded or proteins that are needed to cope with a new challenge may b rapidly synthesized. In addition, protein turnover represents a major energy-requiring process and may account for between 25 and 40 percent maintenance energy expenditures (Webster, 1983; Reeds *et al.*, 1985; Gill *et al.*, 1989). In contrast to protein metabolism, there is disagreement abo the energy cost of fat turnover. Webster (1983) gives the value of 1 to 4% of heat production due to fat synthesis, whereas Gill *et al.* (1989) cite much higher figure (25%) for fat turnover and accretion. Using a mechanistic model of sheep metabolism (Sainz & Wolff, 1990a), these costs can b estimated as 1% of heat production for triacylglycerol hydrolysis and re-esterification, plus 25% for de novo lipogenesis from acetate. Therefor Webster's estimates may apply to non-ruminants converting diet lipid to body fat, but not to ruminants synthesizing fat from acetate. Moreover modeling analyses indicate that body composition is far more sensitive to alterations in protein turnover than to changes in lipid metabolism (Sainz & Wolff, 1990b). Manipulation of protein and/or fat deposition must involve alterations in the rates of synthesis and breakdown of protein and lipi Such alterations can have profound effects on the growth of the animal, its maintenance requirement and its adaptability to different environment stresses. In addition, metabolic changes during the life of the animal often carry over into the *post-mortem* period, thus influencing the quality of th final product (meat).

Factors that influence meat quality

Genotype:

Large differences exist among breeds with large- and small-frames, or with high or low degrees of muscling. The large-frame animal grows mo rapidly, and deposits less fat than the small-frame animal. For example, Charolais steers had faster weight gains (+11%), higher meat yields (+9%) and le intramuscular fat (-30%) as compared to Angus steers (Shackelford *et al.*, 1994). If these animals were slaughtered at the same age, the Charolais wou produce a much leaner carcass than the Angus. This result may be generalized to compare Continental beef cattle breeds (i.e., Charolais, Limousi Gelbvieh) against British breeds (i.e., Angus, Hereford, Shorthorn; Koch *et al.*, 1982). When cattle are finished on high-concentrate diets, early-maturin breeds (especially females) reach the fattening phase sooner, and should therefore be slaughtered at younger ages and lighter weights. On the other han males of those breeds may be slaughtered at heavier weights without production of excess fat.

There is some controversy about genetic differences in the proportions of muscle in different cuts, and their relationship to animal conformatio Zebu cattle tend to have higher dressing percentages (+ 2 to 4%) than non-humped cattle (Johnson *et al.*, 1990a; Koch *et al.*, 1982; McIntyre, 1994). Th is due to the smaller size and capacity of their digestive tracts (McIntyre, 1994). The work of Berg & Butterfield (1976) and Thonney (1990), based carcass dissections, showed that muscle weight distribution did nor vary among beef and dairy cattle breeds. On the other hand, selection of animals w superior conformation implies that it should be possible to select an animal with a greater yield of high-value cuts of meat. There is some evidence that th is indeed the case: Norman & Felicio (1980-81) showed that at similar body and carcass weights, Nellore and Guzerat cattle had higher meat:bone rati than Charolais cattle, whereas Canchim (3/8 Nelore, 5/8 Charolais) cattle were intermediate. Another more extreme example is the Callipyge lamb, which there is marked hypertrophy of the muscles of the loin and hindquarters (Tables 1 and 2). Given that the legs are more valuable than the shoulde this conformation is highly desirable. Of course, this improvement in conformation will only confer an advantage to these animals if meat quality is n adversely affected. Unfortunately, this is not the case; due to high levels of calpastatin, *post-mortem* myofibrillar fragmentation is impaired and the meat very tough (Table 3).

Table 1. Carcass characteristics and weights of organs and primal cuts from normal and Callipyge lambs

	Normal	Callipyge	Pooled S.D.[1]	P[2]
Body wt, kg	59.6	62.2	3.59	.36
Hot carcass wt, kg	32.9	36.1	2.85	.17
Dressing %	57.4	60.5	2.14	.09
Loin eye area, cm^2	17.8	26.4	1.51	<.001
Back fat, mm	6.8	4.3	.91	.01
Carcass fat, %	28.5	23.3	2.97	.056
Shoulder, kg	7.20	7.65	.585	.33
Rack, kg	3.38	3.82	.342	.13
Loin, kg	3.92	4.47	.465	.16
Oven-ready legs, kg	9.65	11.4	.812	.024
Breast, kg	2.30	2.50	.355	.47
Shoulder + rack + loin + legs, kg	24.2	27.4	1.97	.067

[1] Pooled standard deviation, n = 5 normals and 3 callipyge.
[2] Probability of a Type I error.

Table 2. Increased muscle weights in Callipyge lambs (% difference from normal)

Trait	Koohmaraie *et al.*, 1995	Jackson *et al.*, 1997b	Sainz et al 1997	Jackson *et al.*, 1997a
Infraspinatus	+6.9[a]	+6.1[a]		
Supraspinatus	+2.9[a]	+6.4[a]		
Longissimus	+32.1	+51.0		
Psoas group	+20.4	+45.1		
Adductor	+30.0	+47.5		
Semimembranosus	+38.3	+63.0		
Semitendinosus	+26.4	+27.0		
Leg + Loin + Rack + Shoulder			+13	+10.4

[a] P>0.10.

Table 3. Carcass and meat traits in Callipyge lambs (% difference from normal)

Trait	Koohmaraie *et al.*, 1995	Field *et al.*, 1996	Sainz *et al.*, 1997	Jackson *et al.*, 1997a
Dressing %	+4.5	+7	+5	+6.3
Loin eye area	+33.8	+72.6	+48	+70.9
Back fat	-29.4	-36.5	-37	-13.6
Calpastatin activity in LD	+82.8		+113	
Myofibrillar fragmentation	-33.6 (21 d)		-41.8 (14 d)	
Shear force	+144.7 (21d)	+53.4 (14d)		

In relation to meat quality, *Bos indicus* breeds and their crosses are known for their inferior (tougher) meat relative to *Bos taurus* breeds (Crouse *et al.*, 1989; Johnson *et al.*, 1990a; Koch *et al.*, 1982; Norman, 1982; Shackleford *et al.*, 1991, 1995; Wheeler *et al.*, 1990; Whipple *et al.*, 1990). There may be breed differences in collagen content and cross-linking (Norman, 1982), although others have not confirmed this result (Johnson *et al.*, 1990a; Whipple *et al.*, 1990). Several reports have demonstrated high levels of calpastatin in meat from Zebu cattle, relative to levels found in meat from non-humped animals (Johnson *et al.*, 1990b; Shackelford *et al.*, 1991; Wheeler *et al.*, 1990; Whipple *et al.*, 1990). The resulting inhibition of calpain activity results in reduced myofibrillar fragmentation during the *post-mortem* period (Fig. 3), and this in turn results in tougher meat (Fig. 4). From another point of view, this meat does not undergo the normal aging process. As recently shown by Koohmaraie et. al. (1996), muscles are tender at slaughter but become tough during development of rigor and contraction of the sarcomere. This toughness is alleviated through the fragmentation of myofibrils. When muscles are restrained so they cannot contract and shorten, the toughness does not develop and the meat remains tender. Under normal processing conditions however, myofibrillar fragmentation is an essential process to ensure tenderness of the meat. On the other hand, Zebu meat is tougher even one day *post-mortem*, so that it is likely that other mechanisms also contribute to the increased toughness. It is worth pointing out although that most studies focus on the longissimus muscle (LD), Shackelford *et al.* (1995) found that 1) the tenderness of the LD has a low relationship to that of other muscles, and 2) five of the ten muscles used in that study were not different between Zebu and European cattle.

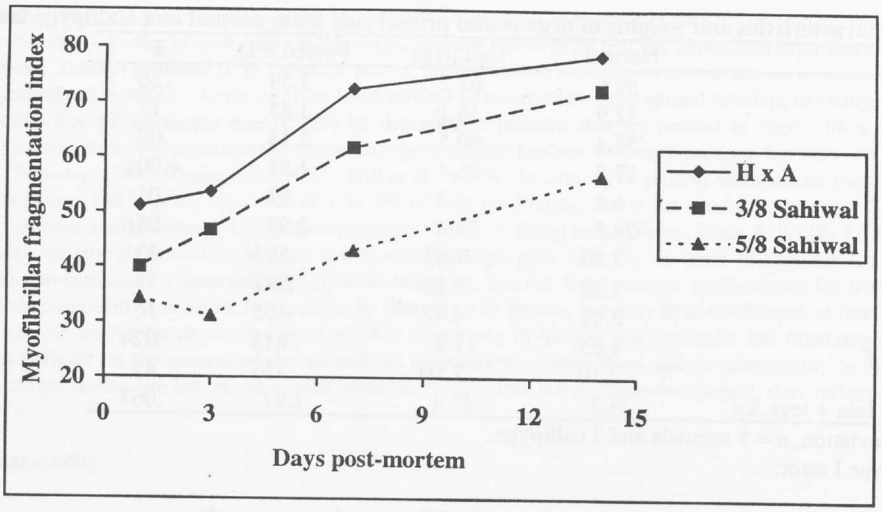

Fig. 3. Effects of Zebu breeding on myofibrillar fragmentation
From: Whipple *et al.*, 1990

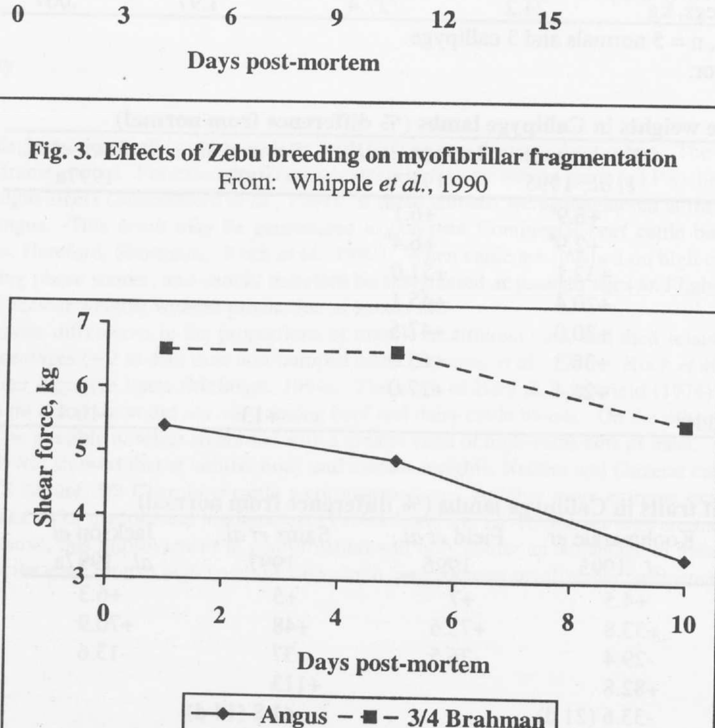

Fig. 4. *Post-mortem* aging of meat from purebred Angus or Angus-Brahman crossbreds
From: Johnson *et al.*, 1990a

Gender:

Sexual differences in carcass composition resemble breed effects, inasmuch as the greatest effects are those related to mature size and muscularity. Except in pigs, males grow more rapidly and deposit less fat than females, with castrated males being intermediate (Burrow *et al.*, 1991; Shahin *et al.*, 1993). The pig departs from this general pattern in that the barrow grows most rapidly and deposits most fat; this is likely due to their greater appetite, but the mechanisms responsible for these differences are not fully understood. For ruminants, however, intact males produce heavier, leaner carcasses than females, with castrates being intermediate. Unfortunately, meat from bulls may be inferior (tougher and darker) to that from castrates, although this may depend upon age, pre- and post-slaughter management, and consumer preferences. Intact males produce tougher meat than castrates, due to differences in collagen structure (Maiorano *et al.*, 1993) and reduced myofibrillar fragmentation caused by elevated calpastatin (Table 4; Morgan *et al.*, 1993). Other problems occur due to the propensity of bulls to fight during transport and lairage, especially when mixed with strange animals. Under those conditions, stressed bulls arrive at slaughter with low muscle glycogen reserves, which results in dark-cutting meat (Hood & Tarrant, 1981).

Age:

The relationship between chronological and physiological age varies among breeds and individuals within a breed. Early-maturing animals are normally smaller than later-maturing animals at the same age, but may be more physiologically mature. Maturity should therefore be discussed in reference to the growth and composition curves for that specific type of animal. The main effect of age on meat quality refers to the accumulation and maturation (i.e., increased cross-linking) of collagen fibers, which leads to toughening of meat.

Table 4. Differences between bulls and steers in carcass and meat quality

	Steers	Bulls	Significance
Carcass weight, kg	242	273	*
Dressing %	60.0	60.0	ns
Back fat, mm	7.1	2.1	*
Kidney, pelvic and heart fat, %	3.0	1.0	*
Rib eye area, cm^2	67.7	76.7	*
Marbling score	4.34	3.60	*
Meat color[b]	2.0	2.5	*
Shear force, kg	4.2	5.0	*
Myofibrillar fragmentation index[c]	62.0	53.5	*
Calpastatin (U/g, 24 h)	1.33	2.41	*

[a] Marbling: 3 to 4, Slight; 4 to 5, Small.
[b] Color: larger numbers represent darker meat.
[c] MFI measured 7 d *post-mortem*.
From: Morgan *et al.*, 1993.

Nutrition:

The effects of nutrition on carcass conformation and composition are controversial. Carcass yield (dressing percentage) is greater in concentrate-fed than in forage-fed animals, due to reduced gastrointestinal tract contents (Sainz *et al.*, 1995). The relationship between body weight and fatness is stronger in ruminants than in non-ruminants (Greenhalgh, 1986). For example, backfat is easily manipulated in swine by altering feeding level, but this is more difficult in cattle and sheep. It seems reasonable that animals on a higher plane of nutrition are more likely to deposit fat, since there is more energy available after meeting the needs for maintenance and lean growth. Feeding level is positively related to carcass fatness, but results are often confounded by the increased body weight at the same age of concentrate-fed animals (Byers, 1982). In order to make valid comparisons among dietary treatments, animals should be compared at the same weight or composition. When this is done, nutrition has smaller effects on body composition at the same weight (Greenhalgh, 1986). Nevertheless, nutrition can have substantial effects on the patterns of bone, muscle and fat development. For example, steers that underwent compensatory growth produced carcasses that had less subcutaneous fat than full-fed controls, even though there was no change in marbling scores (Carstens *et al.*, 1991; Sainz *et al.*, 1995). Differences in tenderness due to nutrition are also confounded with the effects of age, since slow-growing animals on a low plane of nutrition reach slaughter finish at a later age than those that grew more rapidly (Loxton *et al.*, 1990). Finally, there are important effects of vitamin supplements, such as vitamin E. Steers fed vitamin E for 120 days pre-slaughter produce meat with improved color and prolonged shelf-life relative to non-supplemented controls (Liu *et al.*, 1995; Sherbeck *et al.*, 1995). This result is consistent with a reduction in myoglobin oxidation, in view of vitamin E's activity as a biological anti-oxidant.

Manipulation of growth

A great deal of research effort has been expended over the years in various efforts to manipulate animal growth. These have typically had two primary objectives; firstly to increase production or productive efficiency, and secondly to increase product quality. In the latter case this has typically been viewed as a reduction in carcass fat. A number of approaches have been used both experimentally and commercially to accomplish these objectives. Traditional systems of livestock production have evolved using both intact and castrated males, with a smaller contribution by females. The superior performance of intact males relative to castrates provided early impetus for the use of exogenous anabolic (sex) steroids, which continue to find useful application in the United States and elsewhere (but not legally in the European Community). Other classes of exogenous agents which have been investigated include the direct or indirect manipulation of the growth hormone axis, β-adrenergic agonists, and feed additives (including ionophores such as monensin). These classes of compounds have quite different effects in ruminants and non-ruminants; this discussion will draw mainly from studies using cattle and sheep. In addition, novel techniques arising from immunological and direct genetic manipulation hold promise for the future. In devising new methods for growth manipulation, the objectives given by Buttery & Dawson (1988) are relevant: to "(i) produce meat which is safe for the consumer as judged by the regulating authorities; (ii) produce meat which has as good, if not better, eating quality than meat from untreated animals; (iii) do not unduly alarm the general public; and (iv) are financially sound".

Genetic selection:

The fundamental tool at the producers disposal is genetic selection because it is not only highly cost effective, it is permanent and without so impediments to its use. Traditional methods of selection have relied a great deal upon visual confirmation and there are numerous examples in w various fads in conformation have led the livestock industries to produce animals that were (are) inappropriate for the production environment an their eventual market. More recently quantitative techniques for estimating transmitting ability for economic traits have gained wide spread popula within the livestock industries and this has meant that selection decisions have been placed on a far more objective footing. Genetic selection pe does not require a very profound understand of the animals physiology or basic function, but does require caution to ensure that the animals are be selected in an environment similar to that in which they will be expected to produce.

Nutrition:

Buttery & Dawson (1988) suggest closer examination of current feeding to achieve the wanted improvements to growth. Techniques achieving this include stimulating food intake and improving nutrient availability, bioactive peptides, and enhancements of hormone release. Since deposition of fat only occurs after the energy needs for maintenance and lean growth have been met, restriction of energy intake can result in dram reductions in the accretion of fat and the overall fat content of the carcass (Sainz *et al.*, 1995). In fact moderate restriction of intake can actually re in an increase in feed conversion efficiency, although the mechanisms for this are poorly understood as yet (Sainz, 1995).

Anabolic Steroids

The superior growth performance of intact males has been alluded to above. However, most anabolic implants used in cattle contain some fo of estrogen. Estrogens (e..g., estradiol 17-β, E2) are generally preferred over androgens due to the reduced amount required for estrogen ver androgen response. However, trenbolone acetate (TBA) has recently gained popularity. TBA seems to decrease protein breakdown and basal metabo rate, though the mechanisms for each are disputed (Hunter & Vercoe, 1987; Hunter & Magner, 1990; Hayden *et al.*, 1992; Buttery & Dawson, 198 Some studies have failed to show any growth improvement with TBA alone, but have seen synergistic effects with combined E_2+TBA treatm (Hayden *et al.*, 1992, Schanbacher, 1984). TBA may also affect feed intake, so dietary protein content may need to be increased with its use (Hunte Vercoe, 1987). In addition to increased rate of gain (+15 to 20%; Roche & Quirke, 1986), carcass (including marbling or intramuscular) fat conten decreased by anabolic implants. The net effect is equivalent to an increase in mature size (Owens *et al.*, 1995).

These improvements in protein gain can be brought about by increases in the rate of protein synthesis or decreases in the rate of prot degradation, or some combination of the two. Lobley *et al.* (1987) concluded that testosterone decreased rates of synthesis and degradation of bo protein in wethers but the rate of degradation was reduced more than the rate of synthesis. Most studies reporting actual rates of protein metaboli show reductions of 10 to 35% in the rate of protein synthesis. Since protein deposition is increased, one must conclude that the rate of prot degradation decreases to an even greater extent. In fact, those studies reporting rates of protein degradation generally do show decreases ranging from to 49%. Actual rates of lipogenesis and lipolysis are quite difficult to measure in vivo and few data are available, but circulating concentrations of no esterified fatty acids (NEFA) reflect NEFA entry rates, and indirectly, lipolytic rates. Thus, in a study by Coelho *et al.* (1981), circulating NEF concentrations were reduced by only 2%, a difference which was not significant. Similarly, a study by Galbraith & Geraghty (1982) also showed difference in circulating NEFA concentrations. It therefore appears that lipolytic rates are unaltered in ruminants receiving anabolic steroids. The sa cannot be said for amino acid catabolism, as reflected in plasma urea nitrogen (PUN). PUN and amino acid catabolism are consistently reduced anabolic steroids (-13 to -49%), reflecting the redirection of amino acids towards protein accretion.

In the future, use of exogenous anabolic steroids in meat production will probably depend upon societal acceptance of such techniques. Pub concern over hormone residues in meat seems to be unfounded, considering that typical levels of hormones in meat from treated animals are mu lower than in intact animals (0.0006 μg vs. 0.13 μg testosterone in 250 g of meat from a treated steer and an untreated bull, respectively; Buttery Dawson, 1988). One novel approach that could be more acceptable is prenatal androgen treatment, either chronic (Jenkins *et al.*, 1987) or acute (Gill Hosking, 1995). A time critical, brief exposure to testosterone yielded increased birth weights and ADG, as well as altering wool growth, plasm insulin levels and ano-genital distance in lambs. This effect was seen in both males and females, though females increased more relative to contro Final testosterone levels were not altered; therefore, this technique should be safe for production use. Further study is needed to confirm the results a investigate possible side effects.

Growth Hormone:

In whole animal experiments, growth hormone or somatotropin (GH) increases growth rates and protein accretion, and lowers fat percent, fe intake, and feed to gain ratios (Schanbacher, 1984; Beermann *et al.*, 1990). Similar effects are seen using GH releasing factor (GRF; Sainz *et al* 1994a,b). Superficially, the growth-enhancing effects of GH and GRF are quite similar to those seen with anabolic steroids. For example, GH a GRF increase rates of gain on average by 23%, ranging from 16 to 42%. However, and unlike the effects of anabolic steroids, this is genera accompanied by a decrease of feed intake (-7%). Improved rates of gain, in spite of decreased feed intake, means that feed efficiency is dramatica improved by GH (+30%). These effects are accompanied by consistent reductions (-15 to -30%) in body fat content. Therefore, with the exception the effects on feed intake, the overall effects of GH and GRF are quite similar to those of the anabolic steroids. Since plasma GH concentrations often increased in animals treated with anabolic steroids, some have hypothesized that the effects of anabolic steroids are mediated, at least in pa through GH. This issue was discussed in detail by Hancock *et al.* (1991), who concluded that major differences in their metabolic effects arg against mediation of steroid effects through GH.

The reductions in fat content produced by GH and GRF are a result of both increased protein gain and decreased fat deposition. Increases protein gain average 51%, ranging from 31 to 138%. GH seems to increase protein synthesis (+20%), with a smaller increase in degradation (+15 Buttery & Dawson, 1988; Eisemann *et al.*, 1986; MacRae & Lobley, 1991; Schanbacher, 1984;). The effect on protein synthesis is system including skeletal as well as kidney and liver protein accretion. This yields a decrease in dressing percentage, but this is deceiving as the increase variety meats (e. g., liver and kidney) can be profitable (Beermann *et al.*, 1990). In addition to increased protein gain, GH-treated animals consiste deposit less fat (-20 to -35%). This comes about as the result of lower rates of lipogenesis (-50%), as well as increased rates of lipolysis (+50% probably due to the insulin-antagonistic effects of GH (Etherton *et al.*, 1987; Vernon, 1982). Additional actions of GH includes lengthening of lo bones, directly or through stimulation IGF-I. These effects are quite different from the effects of anabolic steroids, which tend to depress rates protein turnover with little or no effect on lipolysis. As seen with the anabolic steroids, however, GH decreases rates of amino acid catabolism (-24 both measured through radioisotope dilution or estimated from PUN. Therefore, this summary supports the conclusions of Hancock *et al.* (1991), that the growth-promoting effects of anabolic steroids are unlikely to be mediated by GH.

Nutrition is an important factor in the efficacy of GH. The increase in protein synthesis and accretion can only be expressed to its full potential with an increase in amino acid intake (MacRae & Lobley, 1991). Because feed intake is often reduced in GH-treated animals, the amino acid content and balance and density in diet must be increased to supply the increased demand. Failure to do so limited the responses seen in early experiments with this hormone. This factor will restrict the use of GH and GRF to situations in which protein status is adequate. Moreover, it has been difficult to design an administration method compatible with modern production systems. One novel technique that holds promise is the use of monoclonal antibodies to GH. These seem to increase or extend GH binding to receptors, thus potentiating its effects (Holder *et al.*, 1985; MacRae & Lobley, 1991). This approach would offer a relatively easy treatment not requiring frequent re-applications, and could prove commercially viable.

β-Adrenergic agonists:

β-adrenergic agonists are catecholamine-like compounds that bind to and activate β-adrenergic receptors on cell membranes. Compounds specific for β1- (e. g., ractopamine) and β2-adrenoceptors (e. g., clenbuterol, cimaterol, salbutamol) possess powerful repartitioning activity, so named because of the redirection of nutrients away from fat and towards muscle growth. These agents increase weight gain and reduce body and carcass fat content in a variety of species (Hanrahan, 1987; Kim *et al.*, 1987; Ricks *et al.*, 1984).

The effects of β-adrenergic agonists on weight gain in domestic and laboratory species are both smaller and more variable than those seen with anabolic steroids and GH. As several reviews have pointed out, this may result from failure to meet the increased nutrient requirements of β-agonist treated animals (Boyd *et al.*, 1991; NRC, 1994; Reeds & Mersmann, 1991). Improvements in rates of gain average 15 to 20%; changes in feed intake have been inconclusive; on average, feed intake increases by only 3% (probably non-significant), but this varies from -12% to +23% (Bohorov *et al.*, 1987; Emery *et al.*, 1984; Kim *et al.*, 1987; Reeds *et al.*, 1986). Likewise, feed efficiency improves on average (+17%), but changes in feed efficiency vary from -10% to +69% (Claeys *et al.*, 1989; Kim *et al.*, 1987; Moloney *et al.*, 1990). In contrast, changes in body composition with β-agonist treatment have been much more consistent: body (and/or carcass) fat content is reduced (mean, -22%), with changes varying from -14% to -34% (Baker *et al.*, 1984; Ricks *et al.*, 1984; Sainz *et al.*, 1990; Williams *et al.*, 1987). Although their effects are seen in all animals, ruminants and swine are more responsive than poultry.

As seen for GH, the improvements in carcass and body leanness in β-agonist treated animals come about as a result of increased (+25%) rates of protein gain and decreased (-37%) rates of fat gain (Kim *et al.*, 1989; MacRae *et al.*, 1988; Reeds *et al.*, 1986; Sainz & Wolff, 1988; Sainz *et al.*, 1990). However, the mechanisms responsible for these changes are unclear at present. In the case of protein metabolism, rates of protein synthesis, as reported in the literature, tend to show an increase in the rate of protein synthesis in muscles of β-agonist treated animals (+16%), but ranging from -5% to +75%. Likewise, rates of protein degradation are reduced (-14%), but the changes range from -55% to +50% of controls (Claeys *et al.*, 1989; Reeds *et al.*, 1986). Few data are available on lipid turnover rates in β-agonist animals, particularly for rates of lipogenesis. Thornton *et al.* (1985) showed that clenbuterol reduced acetate incorporation into lipid (-81%) and increased lipolysis (+100%) in isolated ovine adipocytes. This compares well with in vivo rates of lipolysis (estimated from NEFA concentrations; Eisemann *et al.*, 1988; O'Connor *et al.*, 1991), which increase similarly (+99%). Similar to anabolic steroids and GH, β-agonists depress PUN (-34%) and presumably amino acid catabolism. Differences in species, β-agonist dosage, and timing of measurements are known to be important (Kim & Sainz, 1992; Sainz *et al.*, 1993a,b); therefore, the above observations must be viewed with extreme caution.

The β-agonists have very specific actions on certain muscle groups. β-agonist response is seen primarily in the muscles of the hindquarters and the loin, with minimal changes in the forequarters. The hypertropic response is limited to white muscle fibers, and is accompanied by consistently elevated activities of calpastatin and in some cases reduced levels if μ-calpain (Kretchmar et al., 1990; Sainz et al., 1993b). The result is a decrease in myofibrillar fragmentation *post-mortem*, and very tough meat. This can be overcome by infusion of calcium chloride (Koohmaraie & Shackelford, 1991), providing further support for the importance of the calpain system in meat tenderness.

The substantial repartitioning effects of β-agonists offer very promising opportunities improving carcass leanness, as well as a valuable tool for studying the mechanisms of muscle growth and meat quality. Commercial application, however, has not received legal approval, due to possible residue problems. Moreover, the problem of tough meat would negate any benefit of increased lean content. The first issue might be resolved by treating animals pre-natally (Kim et al., 1994), or through immunological stimulation of β-adrenoceptors using anti-idiotypic antibodies (Y.S. Kim, pers. comm.). The toughness issue could be overcome with improved *post-mortem* processing techniques. These techniques could include calcium chloride infusion, freezing-thawing regimes (Sainz *et al.*, 1997), or the use of high-pressure shock waves (M.B. Solomon, pers. comm.).

Feed additives

In addition to hormones and hormone-like compounds, a variety of feed additives are in use that are effective, in varying degrees, to improve growth rate and/or efficiency in beef cattle. Among these, ionophore antibiotics are probably most widespread, with monensin being the foremost example of the class. The effects of ionophores such as monensin on rumen function are relatively well-known, but hard information about their metabolic effects is scarce (Bergen & Bates, 1984). Certainly, monensin is known to reduce feed intake (-6%) without altering rates of gain, therefore feed efficiency is improved (+6 to +8%) as well (Byers, 1980; Goodrich *et al.*, 1984; Buttery & Dawson, 1988). Carcass fatness is reduced (-10%), due to improved protein gain (0 to +6%) and decreased fat deposition (-5 to -6%; Byers, 1980). The mechanisms responsible for observed changes in protein and fat gain have not been studied, but acute effects of large i.v. doses of monensin include stimulation of lipolysis (Armstrong & Spears, 1988). Fasting heat production is unchanged (Johnson *et al.*, 1985) or reduced (-5%; Garrett, 1982). Maintenance energy requirements are consistently lower (-4 to -8%, mean -6%), and efficiency of gain is unchanged (Byers, 1980) or reduced (-9 to -16%; Johnson *et al.*, 1985). In non-ruminants at least, ionophores reduce the thickness of the intestinal epithelium, aiding nutrient uptake and probably reducing energy expenditures (Buttery & Dawson, 1988).

Immunological Manipulation

The consuming public has legitimate concerns regarding the use of chemicals in animal production, and the possibility of residues in meat. Therefore, strategies that could achieve the same goals without the use of exogenous agents would be expected to allay consumers' fears. Manipulation of the animal's own immune processes to produce the appropriate metabolic modifications has therefore received a great deal of attention. Because GH secretion is inhibited by somatostatin, administration of anti-somatostatin is expected to raise endogenous GH levels and thereby stimulate growth. Spencer (1986) reported on several studies that found increases in ADG and feed efficiency in anti-somatostatin treated lambs, but other studies have been less encouraging. According to Buttery & Dawson (1988), it is difficult to get high titers for both anti-somatostatin and glucocorticoids, and as a result findings have been mixed. Antibodies to specific regions of GH also enhance growth when complexed with GH and injected into animals (Holder *et al.*, 1985). The potentiation of GH seems to occur via increased affinity for receptors and/or reduced clearance rate. To date, only complexes formed before injection have been used, so the problem of acceptance still remains. With further research, this may provide a reasonable alternative. Studies with rodents passively immunized against IGF-I have failed to demonstrate the essentiality of circulating IGF-I for normal or accelerated growth (Spencer et al, 1991; McGarry *et al.*, 1994). Rather than alter protein metabolism to partition nutrients, some researchers have reduced b fat by immunizing animals against fat cell membranes (Nassar & Hu, 1991). Lastly, active immunization of bulls against gonadotrophin-releas hormone reduced testes size and testosterone production (Adams *et al.*, 1996). Immunocastration allows sufficient testosterone production to stimu growth and reduce carcass fat (relative to steers), without the aggressive behavior and meat quality problems of bulls. Problems with all of the abo mentioned immunological techniques are related to the variability in the immune response. Further work will be required to develop succes immunological strategies to enhance growth.

Transgenics

One major advantage of using genetically manipulated animals is that the modifications are heritable, eliminating the need for administratio exogenous compounds, even between generations (MacRae & Lobley, 1991). Additionally, using the right promoter can selectively turn on transgene(s). To date, production of transgenic rodents has been successful, but transgenic livestock have been problematic. Apart from the gre difficulty in producing large transgenic animals, problems have occurred with incorporation and controlled expression of the transgenes. In addit developmental abnormalities (e. g., skeletal deformities, infertility) have hindered progress. The major drawback to application of gene tran technologies in meat production, however, is vehement public distrust of genetically manipulated products. As genetically engineered foods (e tomatoes and other plant products) become more common, public perceptions may change.

The growth of animals is not controlled by one simple growth factor that can merely be increased. Rather, a complex interaction between m factors is closer to reality. Many methods currently exist to modify growth of farm animals. Many are prohibitive due to either public concerns (implants) or adverse side effects (toughness of β-agonist treated animals). To counter this, novel methods of growth modification need to investigated to ascertain their feasibility, acceptance, and potential impacts on the final product.

Meat production

Meat production systems may be classified as intensive or extensive. Intensive systems involve management of animals in artificial environme i.e., climatic, dietary, and disease factors are closely controlled by the producer (Hahn, 1981). In temperate zones, these are exemplified by the swine poultry industries, although some ruminant feedlots could also be considered in this category. In tropical and less-developed areas, pigs and poultry often raised under extensive conditions, and ruminants are rarely fed cereal diets for prolonged periods. Extensive production systems require little hu manipulation of the environment, so that livestock must survive, reproduce and grow under the prevailing conditions. Due to variations in latitude, alti and other meteorological factors, livestock are thus exposed to temperatures ranging from below 0°C to over 40°C, and relative humidities from 0 to 10 Depending upon location, there are a variety of ecto- and endo-parasites that can impair performance directly or indirectly, by transmitting disease. F availability and quality also varies tremendously among locations and throughout the years. In temperate zones, livestock must cope with cold stress low feed availability, depending on the season (Young, 1981). In comparison, animals raised extensively in the tropics often have abundant feed of v low quality, and must deal with heat stress and more intense parasitism (Payne, 1966). Clearly, desirable animal characteristics will vary depending on type of production system and environmental constraints, so that no one type of animal could fit all locations and markets. Because the most extre ranges in production systems and environments are found in the beef industries, beef cattle will be used for most of the following examples.

Bos taurus cattle tend to perform well in temperate environments and produce meat that is of high quality. There is significant variation amo breeds as well as within breeds in growth potential and fattening characteristics, as exemplified by the difference among the medium- framed Brit breeds such as Angus, Hereford or Shorthorn as compared to the larger-framed continental breeds such as Charolais, Limousin and Gelbvieh. Gene differences become much more pronounced when we compare these European types of cattle, *Bos taurus* with the humped (Zebu) cattle or *Bos indic* Zebu cattle tend to have significant advantages in hot environments, whether they are dry or wet, as compared to *Bos taurus*. These advantages related to their ability to dissipate heat, to withstand the higher temperatures without suffering a loss of intake and to their resistance to ecto- and end parasites (Payne, 1966; Turner, 1980). These advantages allow the Zebu to survive and produce in tropical environments which can be detrimental fatal to their European cousins. The NRC (1996) guidelines include a 10 percent adjustment in maintenance requirement recognizing that Zebu ca have a lower fasting heat production than *Bos taurus*. Since *Bos indicus* cattle tend to have higher activities of calpastatin and lower rates of prot turnover, this is likely one of the mechanisms for the reduced maintenance requirement. It should therefore not be surprising that these animals a produce meat that is significantly tougher than that from *Bos taurus* cattle. Zebu cattle also tend to marble less than *Bos taurus* (Wheeler *et al.*, 199 which probably accounts for the persistence of the marbling score as the primary quality grading variable in the U.S. market, in spite of the lack significant relationship between marbling and tenderness (Fig. 5). It should be noted that the advantage of the Zebu under tropical conditions becom a disadvantage under extreme cold, where it's ability to dissipate heat rapidly and its lack of insulating sub-cutaneous fat then becomes a liabil North American producers understand that Brahman cattle in cold environments will actually require more feed. Nevertheless in the hot environme of the south and southwest of the U.S. a certain proportion of Zebu (usually between 1/4 and 3/8) is essential for survival and productivity of cattle those environments.

As seen previously, manipulation of animal growth to enhance growth or carcass leanness is possible through a variety of means. In examining Fi 1, it becomes clear that shifting the curve to the left (so that the animal is heavier at any given age) will usually entail increasing mature size. Similar decreasing carcass fat content at a given weight implies slaughtering animals that are less mature, which also entails higher mature weights. Large-fram animals grow more efficiently and produce leaner carcasses, so that these changes would appear to be totally positive, with no negative implications. Up closer examination, we see that higher mature weights mean higher maintenance requirements for the reproductive herd, so that the improvements in to efficiency are much smaller than expected or zero (Table 5). It is true that at the same slaughter weight the offspring of 700 kg cows will be much lea than those of 500 kg cows, but it is equally true that the smaller cows are better able to cope with the inevitable fluctuations in feed supply, etc..

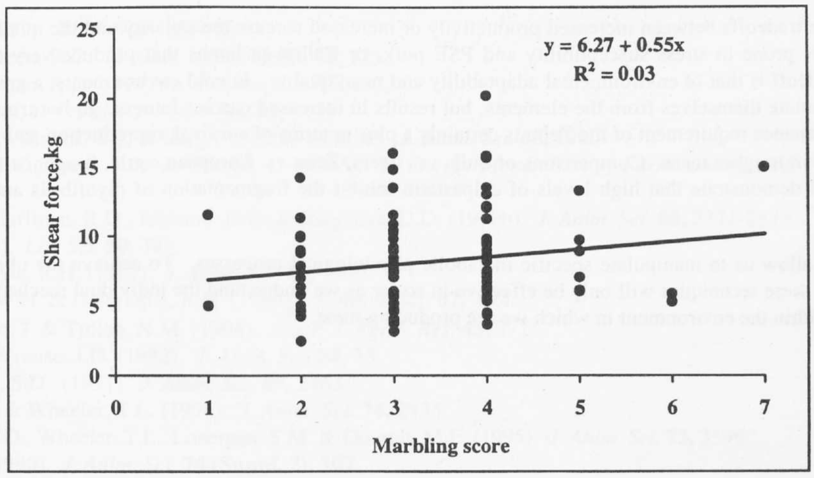

Fig. 5. Relationship between marbling score and beef tenderness

Table 5. Effects of mature size on efficiency of beef production

Cow mature weight, kg	Total ME intake, MJ Cow	Calf	MEI:slaughter wt (calf)	MEI:slaughter wt (total)
500	22,000	35,000	70	113
600	26,000	29,000	57	109
700	31,000	21,000	44	107

Assumptions: 1) Daily feed intake is 2% of body wt. for cows and calves on range, 3% for steers in the feedlot; 2) Metabolizable energy (ME) contents are 8 and 11.5 MJ/kg feed for range and feedlot diets, respectively; 3) Cows wean 50% of their body wt. at 8 months; 4) Calves reach slaughter finish (~30% fat) at cows' mature weight at 15 months of age under intensive feeding; 5) All calves slaughtered at 500 kg for consistency.

Conclusions

Biotechnology is rapidly giving us more and more powerful tools to manipulate animal function. This manipulation can occur at the level of the genome, at the level of expression of different genes, or through specific and effective chemical agents and immunological techniques. In short, we are developing a formidable array of technological tools which we can bring to bear upon the problem of how to improve animal production and product quality. We have also gained a great deal of insight about the mechanisms involved in controlling these factors, although there is still much to be learned about the interactions among growth, survival and product quality. The foregoing discussion should serve to illustrate the fact that regardless of our technologies and our knowledge of underlying mechanisms, one basic fact remains: livestock raised under extensive conditions must first of all survive in their environment. On a global basis this introduces an enormous variation in the survival requirements for livestock and these must be met first. After survival, the next requirement is reproduction. Again, unless we are willing or able to completely control the environment we have to consider the carrying capacity of a particular environment or production system. For example, cattle growers in very arid regions in western Queensland and the Northwest Territory of Australia are content with cows that are able to produce one calf every two years, because that is what the environment will support (Frisch & Vercoe, 1982). Likewise, swine producers in the tropics that raise pigs in sheds that are not totally climate controlled understand that farrowing percentages will decline in the hottest parts of the year (Dan & Summers, 1996). These expectations can become derailed when we blindly introduce "improved genotypes", because often these genotypes have been improved in temperate regions and are totally unsuitable for hotter climates. Once a production system has been devised that fits its environment, and the appropriate type of animal placed within it that is able to survive and reproduce within that environment, then and only then can we look to the growth of the offspring in terms of their meat production. There may also be tradeoffs between increased productivity or increased carcass muscularity and the quality of the product. For examp the highly muscular pig that is prone to stress susceptibility and PSE pork, or Callipyge lambs that produce very tough meat both represent s tradeoffs. Another kind of tradeoff is that of environmental adaptability and meat quality. In cold environments, a greater propensity to fatten enab cows to store nutrients and insulate themselves from the elements, but results in increased carcass fatness. In hot tropical environments with varia feed supply, the reduced maintenance requirement of the Zebu is certainly a plus in terms of survival, reproduction and growth, but the associated low rates of protein turnover result in tougher meat. Comparisons of bulls vs. steers, Zebu vs. European cattle, β-agonist treated animals vs. controls, a Callipyge vs. normal sheep all demonstrate that high levels of calpastatin inhibit the fragmentation of myofibrils and result in significantly tough meat.

New technologies will allow us to manipulate specific metabolic physiological processes. To achieve the objectives of improved producti efficiency and product quality, these techniques will only be effective in so far as we understand the individual mechanisms and how they interact a whole within the animal and within the environment in which we are producing meat.

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