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Nutritional research to meet future challenges

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Abstract. Nutrition is a mature science with well established principles for energy, protein and mineral metabolism based on known metabolic pathways. The quantitative requirements are summarised within various international feeding standards and models. However, when these are applied to specific circumstances, especially in northern Australia, the response of the animal to nutrient supply does not always agree with that predicted from the feeding standards or the error of prediction is not sufficiently accurate for practical use. There is a need for the continual testing of these relationships within production systems. Molecular methods have the potential to discover new metabolic relationships within tissues and characterise the microbial ecology and its relationship to rumen function. Suitable problem models based on growth, meat quality, reproduction, milk and fibre production, and environmental consequences need to be identified. We suggest that production systems designed to meet market weight for age specifications, growth paths and compensatory growth, skeletal growth, parasites, fatty acid isomers, adaptation to low crude protein diets, rumen microbial ecology, epigenetics, remote data acquisition and animal management, greenhouse gas emission, and C balance of various production systems are important problem models, the research of which will benefit the future of the livestock industries in Australia.

Introduction

Nutrition is regarded as a mature science. The first principles of energy metabolism were established by Lavoisier in the 18th century and Ferrell and Oltjen (2008) have outlined the history of, and approaches taken in, the development of various energy feeding standards. The studies they cited epitomised the general approach taken in past nutritional research in that basic physiology and biochemistry underpinned research to answer a quantitative question relating to production. Growth and milk production were the first targets, driven by the need to be able to formulate and compare rations so that farmers could plan for housed winter feeding of animals. Hence, various systems were developed, for example, starch equivalents, and nearly every country has developed some form of energy-based system by which to formulate and compare rations for a particular target level of production. All use the same principles established on the laws of thermodynamics, but the equations differ markedly, being based largely on empirical relationships. For example, the net energy and metabolisable energy systems have the same basis for energy use and partitioning by an animal, but calculate requirements and supply by two different mathematical means. Often the mathematical basis of the system was set by the capacity for arithmetic calculation at the time, which in today's computer age is not a constraint. Perhaps the basis of these empirical equations needs revisiting, but for this to be of value they must be first shown to have deficiencies. More on this will be discussed later.

The quantitative values of energy transformation were often developed using very few animals. Despite this, the principles of energy metabolism were firmly established by these earlier studies, and subsequent research over the past 50 years has only served to improve the precision of the various energy use equations. This is a very useful approach and not to be discredited, but it serves to illustrate that there have been few major advances in this field since. The history of energy metabolism provides us with a paradigm for the development of nutritional science in that key nutritional principles were established very early followed by a large body of work verifying the principles and improving the precision of predictions.

The development of principles of protein, carbohydrate, fat, mineral and vitamin metabolism mirrored the approach used in energy metabolism. The principles of nutrient use and requirements for co-factors for metabolism were quickly established and then a huge body of work set about quantifying these principles in many different circumstances, including physiological state of the animal, feed type and region. Underwood (1981) established the concept of essential minerals and their quantitative requirements for animals. The key defining approach used by Underwood was to have a robust problem animal model, which was an important economic and practical issue of the day, the resolution of which led to important economic benefits to livestock producers. Today, we have poor definition of problem models and the main ones centred around growth and reproduction have been largely discarded as being old problems while the search goes on for the application of new technology (e.g. genomic studies) to a problem. It is quite clear that achieving high rates of growth, reproduction, and milk and fibre production are still the major issues facing the livestock

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industries. The requirements for specific market products (e.g. meat, milk and fibre characteristics) pose further challenges to change the nutrition and genetics of the animals within these systems. The solutions are simple, namely to feed more high quality feeds, but the economic solutions, that is, reducing the cost of the feed and the search for low cost alternatives, are not simple and are basically not researched any more. For example, agronomic research in northern Australia has virtually ceased, with no meaningful funding by any agency in terms of staff or operating funds. There needs to be a clearer focus on two main areas; the search for new principles underpinning growth, development, reproduction and milk and fibre production by animals, and the search for nutritional solutions to practical problems. An example of the former is the role of the *trans*-10, *cis*-12 conjugated linoleic acid (CLA) in depressing milk fatty acid synthesis (Bauman *et al.* 2008) and of the latter is the marked increase in lamb growth to provision of Na and Mg based on established principles of mineral requirement (Dove and McMullen 2009).

The final introductory point is that nutrition is a quantitative science. There are two phases, namely, establishment of a principle of nutrient use, requirement and response, and then the measurement of quantitative response or requirement under various circumstances. The latter approach has been largely based on a factorial method of calculation for the use of energy, protein or mineral. Thus, comparative slaughter and balance experiments involving accurate measurement of intake, excretion and composition of product have been the method of choice, albeit with some differences in the mathematical approach (e.g. using net energy *vs* metabolisable energy), but not in the principles of nutrient use or associated biochemical pathways. Lee Baldwin established the field of modelling within nutrition. This concept did not set out to establish new principles, but rather to use established biochemical principles and new methods of arithmetic formulation to test our knowledge and understanding of the principles (Ferrell and Oltjen 2008). Our knowledge was found wanting in that model output quite often did not match expected or measured biological output. The use of models is still the best way to collate information and apply principles, and they allow less experienced nutritionists to investigate practical situations. The poor output of such models in some circumstances, for example, northern Australia, has led to their rejection, but on what basis? We have recently shown that the basic equations of energy and protein use are robust in principle, but that there are quantitative differences between observed and computed output applying to growing *Bos indicus* steers on low protein diets (<7% crude protein; CP) associated with maintenance energy requirements, recycling of N to the rumen and composition of gain or loss, all of which are old issues but issues that are obviously not resolved satisfactorily when applied to cattle in northern Australia (McLennan 2005). So the question is: ‘is the approach wrong or is our knowledge of the mechanisms limiting?’ We contend it is the latter.

In this paper we set out two areas of nutritional research that should drive our research efforts in the next decade or so. We believe we first need a program of work on the application and testing of existing knowledge within clearly defined problem models, and second on developing new principles and mechanisms that will similarly be based on clearly defined problem models, some of which may be identified in the first scientific pursuit. We set out some examples but, by necessity, limit these to issues largely facing the beef industry in northern Australia. Similar issues occur in Mediterranean temperate regions of Australia.

Application and testing of existing knowledge

Models

It is counter-productive to effectively ‘reinvent the wheel’, but we are in danger of doing that with current nutritional research. In the present day, when existing knowledge is assumed to be only that which is retrievable in an electronic search of journals, it would be wise for students (young and mature) to read *Bioenergetics and growth* (Brody 1945), *The rumen and its microbes* (Hungate 1966) and *The mineral nutrition of livestock* (Underwood 1981) where the principles of nutrient use by animal tissues and by rumen microbes were clearly elucidated some 30–60 years ago. All subsequent research and reviews have by and large simply added more and more data around these established principles, but until recently, the collation of this plethora of data has had to wait until national organisations have collated them and used them to modify existing empirical relationships within national feeding standards. The time for this process to occur, arising from national and international reviews of this nature, has been growing longer, reflecting more the shortage of scientists willing and with the knowledge to take on this task rather than the need for continual update and assessment. For example, it has taken 18 years for the Australian feeding standards to be updated (CSIRO 2007). The recent application of meta-analysis and other modelling approaches, and the willingness of journals to publish such analyses has been welcome and timely because it has provided a means of rigorous statistical analysis of large numbers of studies with the potential to derive new problem models for research or, at the very least, identify gaps and weaknesses in current knowledge (St-Pierre 2001; Ellis *et al.* 2009). This endeavour must be encouraged at regular intervals.

The most obvious way to derive new knowledge or to find where the application of existing knowledge is limiting is to continually test the animal model using new datasets. An example of this is the application of the knowledge of nutrient use, as encompassed within the feeding standards, to cattle growth in northern Australia. This may be tested within simple ‘feed them and weigh them’ experiments and the evaluation of the outputs against those predicted using equations within any international feeding standard or associated models. This was carried out in a series of reports by McLennan (1997, 2004, 2005) examining the responses of young cattle to various supplement types. The response curves so generated were useful but limited in their application to specific circumstances and were not expected to yield new principles. They were based on applied experiments designed for a specific purpose. However, it was recognised that the datasets could be used for a more important purpose, that of evaluating the equations used in two models [Cornell Net Carbohydrate and Protein System (Fox *et al*. 2004) and GRAZFEED (Freer *et al*. 1997)]. Another objective was to counter the assertions that the feeding standards do not apply to animals in tropical environments, an untenable suggestion that somehow the laws of thermodynamics are invalid in this region.

We showed some time ago that the metabolisable energy system applied to cattle in the tropics and that the alternative means of mathematical expression of energy use based on gross energy was misleading (Poppi and McLennan 1995). The dataset, including six feeding experiments (240 individually fed steers), where intake, digestibility, microbial protein production and liveweight gain in weaner steers consuming tropical forages with various supplements were measured, provided the means to test the equations. There were several outcomes, some of which cannot be covered here. However, there was general agreement between predicted and observed liveweight gain or intake depending on which way the equations were used, but there was wide variation around the $y=x$ linear regression relationship. This is a problem in the practical application of any set of equations and leads to dissatisfaction with the feeding standards, especially within tropical feeding systems where the problem is partly associated with the application of empirical relationships set up primarily using temperate forage data. Some of the notable areas of deficiency were in estimating ME content of the diet, maintenance energy requirements, the efficiency of use of energy and in the composition of the gain.

Growth rate and growth paths at pasture

The important practical issue for the cattle industry of northern Australia is to increase the growth rate of animals at pasture. Low productivity is largely due to the low protein content (<7% CP) and low digestibility (~50%) of the diet during the dry winter/spring period. The issue in temperate environments during this period is more about feed supply (low pasture growth under low temperatures) than low diet quality. The solution for the tropical environment is simple and has been demonstrated many times, that is, feeding a protein meal supplement, such as cottonseed meal, will stimulate intake and liveweight gain of cattle to acceptable levels of moderate growth (up to 0.5–1 kg/d). However, because of the cost, this strategy is hardly ever followed, except in the survival feeding of weaners. The research question is obvious. It is not about determining the response to protein meal, but how to identify and supply an inexpensive protein source to rangeland cattle. It seems futile to expect that some day protein meals will decline in cost. Instead, it seems more realistic to start a program of work on how a source of protein could be generated close to the location of the cattle. We know of no current program addressing this issue, yet it was previously the cornerstone of most agronomic research in northern Australia. Similarly, our experience would suggest that large scale replacement of the existing pasture base is difficult and not desirable, but the development of specialised pasture systems close to the extensive rangelands or the development of novel protein sources (e.g. algae grown on property) are different ways to address this issue (Panjaitan *et al*. 2010).

There are no doubt other solutions, but they require some imagination focussed clearly on the research question of how to get more protein to these rangeland cattle consuming low protein diets (around 4–5% CP for up to 8 months of the year). It took ~20 years for urea feeding to be an accepted industry practice and given the current cost of urea, many producers are now looking at ways to reduce their reliance on such supplements. This poses new research questions centred around enhancing N recycling to the rumen and capitalising on compensatory growth in growing cattle or stimulating fat deposition in cows during lactation. The underlying biology is known, but the quantitative manipulation within these unique circumstances is not. The current models suggest that cows on northern tropical pastures should be dying within a few months of consuming these low quality diets and yet they can produce a calf each year if the principles of nutrition are judiciously aligned against animal requirements. They appear to be doing some things more effectively, for example, lowering maintenance requirements or increasing N recycling to the rumen, than is the accepted paradigm within most feeding standards. Therein lies an interesting biological research question that was a feature of much research in the 1960s and 1970s but needs revisiting. The recent application of new methodology to measure N recycling to the digestive tract has led to new quantitative relationships (not new principles), which can be exploited to reduce the cost of supplementation (Reynolds and Kristensen 2008).

The possible development of new production systems in the future raises questions in relation to dry season supplementation and the application of existing knowledge to this area. Will the production systems in 25 years time be the same as those of today? Northern Australia has seen a revolution in the systems of production over the past 30–40 years. Why should we not expect similar changes in the next 30–40 years? Where are the novel systems being tried? The issues around growth path from birth to slaughter and weight for age at slaughter are very important in determining market access and meat quality, for instance, as defined by Meat Standards Australia. Tomkins *et al*. (2006) and Schutt *et al*.(2009) have shown that weight for age and feedlot finishing are the most important factors affecting meat quality with no effect of Brahman crossbred (up to 75% Brahman) compared with *Bos taurus* breeds, but a detrimental effect of the straightbred Brahman. Pasture finishing at young ages had some effects on meat quality in some studies, but none in others compared with feedlot finishing. Most issues around low meat quality (except for marbling) in cattle in northern Australia would disappear if a finished carcass was achieved at 2–2.5 years of age. In targeting higher meat quality, we strongly believe there has been a disproportionate emphasis on genetic selection using molecular markers relative to the development of novel growth paths that allow animals to be marketed younger. Selection of animals based on genetic markers will not finish an animal at 2–2.5 years on most current production systems in northern Australia, however, it will improve productivity to some extent and result in a more consistent and competitive end product. It took some 50 years for leucaena to find a niche in northern production systems, despite the technology and benefits being largely known, as it was not until markets demanded younger finished animals that there was wide scale adoption. Examples of other novel production systems are available. Taylor *et al*. (1985) highlighted the efficiency of a once-bred heifer system whereby a heifer is mated to calve at 2 years of age, after which the calf is weaned and the cow finished for slaughter. This system was much more efficient [g of lean tissue/MJ metabolisable energy (ME)] than traditional beef production systems. Advances in sexing of semen combined with artificial insemination and the use of irrigated pasture-based production systems means that such unconventional practices are now feasible.

Pasture production

A knowledge and understanding of plants on which to base new production systems has largely been lost and there is an urgent need to increase the number and capacity of agronomic scientists to address this issue. The solution to poor nutrition in northern Australia may also come from other novel sources, such as the use of cultured algae, but the issue is to start the imaginative process now. Any new production systems in northern Australia will need to address animal welfare concerns of long distance transport to feedlots or live export, the high cost of fuel and transport to move supplements and cattle, methane emissions from livestock, and the carbon cost of production. Depending on the regulations that emerge, these may place intolerable burdens on current production systems and change them in much the same way that the Brucellosis eradication scheme previously altered beef production systems in the north. Utilising more of what is grown, which underpins the New Zealand production systems, has huge potential to affect the economic returns and production/area. This is not new work, but rather is the application of established principles of grazing management and, in the process, key research questions arise. Another example of this is dairying in subtropical Queensland. The huge potential for pasture DM production within this environment has never been exploited. Thus, the New Zealand and temperate Victorian systems are held in esteem for their production capacity. Within these systems, some 10–15 t of DM is harvested annually by grazing compared with ~7 t DM/ha within the subtropical systems (D. Barber, pers. comm.). The New Zealand industry, with typical imagination, has been steadily raising this threshold to ~18 t DM/ha annually through pasture management and has targeted 30–35 t DM/ha with cropping (Glassey 2007). Currently, some innovative young scientists in Queensland have set the target in the subtropics of cropping 50 t DM/ha or grazing 20 t DM/ha annually (M. Callow and D. Barber, pers. comm.). In this, they have succeeded, but in so doing have raised questions about water use, fertiliser requirements and environmental issues. Nevertheless, using existing knowledge, they have challenged current systems, devised new ones and developed new research questions positioning developments in the subtropical dairy industry for the next 10–20 years. Where are similar innovations in the beef industry?

Managing nutrient requirements

Applying established principles of nutrient demand during pregnancy and lactation has led to new management strategies, in particular, early weaning of calves (Boorman and Hosegood 1986), which have changed the northern beef industry. This has reduced cow mortality and increased calving percentage. In low input systems, this is by far the most cost-effective strategy to follow, especially relative to the use of expensive supplements. Using the same principles, all aspects of the annual cow nutrient requirements to produce a calf and also to feed that calf post-weaning to some sale weight should be investigated to ascertain where management of cow requirements might be fruitfully targeted. In order to do this, good data are needed on cow requirement, nutrient supply and the probability of rainfall events. All these principles are known, but what is required is more specific experimentation and modelling to develop the reliable quantitative relationships.

Quality data are vital to make correct management decisions in any business model and in the past the lack of such information has limited application of nutritional principles. In grazing systems today, we have the ability to gather some of this data, the application of which will alter production systems within the next 20 years. Faecal near infrared reflectance spectroscopy (NIRS) has for the first time given us a tool to define the nutritional status of grazing animals, in terms of CP content, DM digestibility and C3/C4 plant ratio, with sufficient accuracy to make informed management decisions (Coates 2000). Its wider application and mapping within region, soil type and season will provide generic changes in nutrition by region and season. The combination of faecal NIRS with satellite imagery and pasture growth models will enable management decisions to be made on stocking rate and likely animal performance and, together with probability forecasts of future rainfall events, will facilitate more forward planning. Cropping farmers use this approach now and there is no reason why livestock producers should not be able to capitalise on the same technology.

Management decisions on the cow (weaning and mating) and also segregation of cows based on fetal age enable the nutrient requirement to more closely match the nutrient supply according to well established principles. The application of automatic drafting and weighing provides a tool to achieve production targets and to be able to address special requirements of supplements or feed supply for specific groups of animals. The research questions relate to developing robust management systems, quantifying the outcomes and ascertaining that the biology does indeed follow current principles. This can only be done by applying the technology widely within a systems context and examining the response of the animal to these manipulations. The Hill Farming Research Organisation (1979) used this approach to develop systems of sheep, beef and deer production in the Scottish highlands. Good science underpinned the component parts of system models providing a basis for ecological, agronomic and nutritional aspects to be integrated. The 'Pigeon Hole' Project in northern Australia provided a similar example of a systems approach on a large enough scale to be practically relevant, but yielded data that were a consequence of the scale of operation as much as the biology of the process (Petty *et al*. 2007). Here, management options on large paddocks (>25 km^2) investigated pasture utilisation rate and wet season spelling with associated studies in biodiversity, plant dynamics and grazing behaviour. The derived combination of wet season spelling, utilisation of ~20% of pasture grown and increased watering points to better distribute grazing across the landscape represented a sustainable production system with a higher stocking rate than is currently in place across this class of country.

New knowledge or blue sky science

So what of the future of nutritional research and where is it headed? We have argued to this point that nutrition is a mature science and that few new principles have been discovered since the early work up to the 1960s. This may well continue to be the case. However, there are still some old problem models that require elucidation from a different angle and some exceptions to the accepted paradigm that might yield new concepts or certainly new ways of accommodating the quantitative discrepancies that occur from the accepted paradigms. There are several issues emerging for which nutrition is a fundamental element. These include: greenhouse gas emissions, meat quality, functional foods, water use, carbon balance of enterprises, remote sensing and management, and the nutrition × genome interaction. Some of the information that contributes solutions to these issues comes from published nutritional literature. For instance, Ellis *et al*. (2009) have collated and presented rigorous equations for methane emission based on published data largely arising from classical calorimetric studies. The above issues will not be discussed further, but they are very topical. There are several issues that still define animal productivity and their sustainability. These are: growth rate, milk production, reproductive and weaning rates, and fibre growth and quality.

Whilst increasing production does not have high support in various sectors of public administration or research organisations, it is still the most important aspect that we have to address. We need to be firm in putting this at centre stage. A profitable enterprise needs biological targets of the highest order to be reached within a realistic cost structure. Without a profitable enterprise, the system will collapse regardless of its other contributions. Measures aimed at improved environmental outcomes are discarded in non-profitable enterprises. High production targets are also associated with lower methane emissions, fertiliser and water use/unit product so the two are not mutually exclusive. World demand for animal products is increasing, yet the land and food resources for animals are decreasing. Ruminants offer the unique ability to use forage and resources unsuitable for other ventures, and convert cellulosic material into high quality protein. The biological solution to many issues around increased and sustainable production is often simple, and obvious in most cases, but an economic solution is not. So, we have an opportunity to use principles established on science, but we need the imagination to provide the solution. An example is the previously discussed case of providing a low cost source of protein for weaner cattle grazing low quality tropical forages, close to the location of the cattle, in an economic environment where the cost of protein by-products is continually rising.

The methods that we use in nutritional studies will alter. We will always need to measure production parameters (liveweight gain, milk and fibre production, reproduction rate), but we will need to use techniques that will give us new insights into underlying mechanisms. From such knowledge, novel solutions arise. Traditionally, biochemical methods provided understanding of mechanisms of quantitative nutrient transfer that underpins all nutrition. These processes enabled the whole body changes in energy metabolism to be interpreted, for example, fractional synthesis rates of protein in various tissues summed to give whole body energy expenditure. Increasingly, we are looking to molecular methods to provide a better understanding, but as in any new field there has been an emphasis more on the method than the application. Cassar-Malek *et al*. (2008) outlined some of these issues. The advantages of the molecular methods are that they are getting faster (though not necessarily more accurate than the old methods), a wider range of enzyme steps can be screened, the samples are easier to take in the field and a bigger and different picture of metabolic pathway coordination may arise. If this is coupled with proteomic work and functional studies, then new insights into the animal response may also eventuate.

Nutritional research has shifted from defining requirements (which is still useful) to understanding the response to nutrients as exemplified by the ARC reviews on the response to energy and protein (AFRC 1990, 1992). Underlying the responses are biochemical pathways, long established, that define how nutrients are metabolised. The physiological and biochemical approach of quantifying those transactions have led to our understanding of the inefficiencies of metabolism and the nutritional means by which to alter them. Examples of these are the rates of protein synthesis and degradation quantified by Oddy (1993) and the various physiological and nutritional factors that alter these and ultimately the growth rate of the animal. Another example was how the supply of cobalt affected vitamin B_{12} production and contributed to the elimination of coast disease or wasting disease (Underwood 1981). However, with knowledge of the genome and molecular methods of gene expression, there was much promise of new knowledge.

The current approach of using microarrays, based as they are on expression of mRNA of known proteins (enzymes or other functional proteins or products of interest), can only examine known pathways and their up- or downregulation. How will we find new pathways (if they exist) or new control points if all we look for are proteins already known to us? It is possible that previously unknown pathways might be discovered based on the coordinated expression of known genes that were not previously thought to be linked or involved in a particular biochemical/enzymatic process or the expression of anonymous genes or those with an unknown function in a tissue under investigation. Proteomics offers the most promising way of finding new principles within nutrient use and metabolism (Lippolis and Reinhardt 2008). Gene expression provides an approach to look for the control networks or coordination of metabolic pathways as they respond to nutritional manipulation. Thus, in a study of weight loss and re-alimentation, Lehnert *et al*. (2006) identified a range of steps that were upregulated or downregulated in response to a decline or increase in the level of nutrition and identified that they were associated with muscle structural proteins, muscle metabolic enzymes, extracellular matrix proteins (e.g. collagen) and fatty acid metabolism. Perhaps the most interesting result was identifying through microscopic histological examination that there was a larger reduction in glycolytic fast-twitch fibres than the oxidative fibres in undernutrition and that this information coupled with the gene expression work provided a more complete picture of what was happening to animals under weight loss and compensatory growth (Greenwood *et al*. 2009). Furthermore, Hood and Thornton (1980) using sheep under similar weight loss and compensatory growth models showed with tissue slices and their incorporation of ^{14}C-labelled acetate that acetate metabolism to fatty acid declined precipitously in conditions of weight loss and increased markedly in conditions of weight gain. So how did gene expression advance our knowledge of weight loss and compensatory growth over that derived from the simple tissue slice metabolism? Similarly, with real-time PCR of specific gene expression, all that is measured is whether a defined step has increased or decreased in response to the nutritional treatment. Whether this is a more precise method or more illuminating method than, for example, measuring plasma concentration of the metabolite or fractional rates of protein synthesis is debatable. What the methodology does provide is the ability to screen a wide range of known, largely enzymatic steps to define the activity and coordination of pathways (Cassar-Malek *et al*. 2008). Patterns of gene expression associated with different nutritional states will be important to understand how the animal responds to nutrient supply (e.g. protein, energy and minerals), nutrient × parasite interaction and environmental stressors (e.g. heat). Bioinformatics is an essential process to be able to elucidate these patterns and poor access to such statistical techniques limits the application of gene expression to our problem models. Therefore, molecular methodology in its various forms of application has an important role in elucidating the response to various livestock model problems, but at present the literature appears to be driven more by the methodology than by the application to the problem model.

In this next section we outline some problem models the understanding of which, we believe, will require a concerted effort using a variety of approaches of which molecular based methods are but one.

Issues worthy of investigation

Skeletal growth

Growth is allometric, by which we mean that, irrespective of the growth rate (kg/day), the proportions of protein, fat and ash stay in relatively constant proportions defined by a generic growth curve. Nutrient limitation or excess can shift the tissue proportions from these allometric relationships in the short term, but the values soon return to the long-term pattern. Muscle growth responds to skeletal elongation and so it follows that we need to understand processes of skeletal elongation (Young and Sykes 1987). However, selection for growth (eye muscle depth or liveweight gain) was not correlated with skeletal elongation but with bone hypotrophry (Gilbert *et al*. 1993; Cake *et al*. 2006). But does this apply to compensatory growth? It may be speculated that compensatory growth would be enhanced if the realimenting muscle (and more specifically, the muscle fibre type) was associated with a greater bone length on which to rebuild rather than relying on a commensurate increase in bone length. To date, it appears difficult to alter bone dimensions independent of muscle growth within an animal and the nutrients that drive muscle growth also drive bone elongation and may have similar endocrine signals in growth hormone, IGF-1, and testosterone (Kertz *et al*. 1998). From a problem model perspective within weaner nutrition, an ideal scenario would be to increase bone length of weaners in the dry season, whilst maintaining or losing total weight of protein and fat. This would prime weaners for significant compensatory growth in the wet season. Some evidence for this is apparent in results from Swans Lagoon Research Station near Townsville. Kidd and McLennan (1998) showed that the extent of wet season growth (kg/day) depended on the percentage weight loss of weaners over the preceding dry season. Since the skeletal dimensions cannot decrease with loss of weight, it follows that the allometric relationship was altered in that there was much less muscle weight/length of bone in animals that had lost most weight and these animals showed the greater rate of subsequent wet season weight gain. A recent review has also linked the skeleton to energy metabolism in mice based on the role of osteocalcin (in particular the uncarboxylated form released from osteoblasts) and leptin (Wolf 2008). All of these studies demonstrate that we have an interesting and very old problem model in compensatory growth and frame size, which has been studied for a very long time, but new ideas of metabolism combined with new molecular based methodology could be usefully employed to understand how to manipulate this.

Parasites

Animals are exposed to parasites and environmental stressors that affect growth. Of these, internal parasites and their effects on efficiency of use of nutrients have been most studied. Bown *et al*. (1991) showed that there was an extra requirement for amino acids by parasitised animals and that the inefficiencies of use of energy and protein could be explained by the animal diverting nutrients away from the synthetic pathways of muscle and fat deposition to repair of the digestive tract, replacement of lost plasma and mucous proteins, and mounting of an immune response. The extent of the nutrient demand for this latter purpose was not appreciated until Greer *et al*. (2005) showed that suppressing the immune response reversed many of the effects of the internal parasite, especially the depression in food intake. If food intake could be maintained in parasitised animals, growth rate could also be maintained. The immune axis related to cytokines and the production of this molecular cascade require more specific amino acids, such as aromatic amino acids, and this provides a basis for the interaction of nutrition and the immune response, which needs to be explored more closely (Colditz 2004).

Fatty acid isomers and lipid synthesis

Milk fat depression has long been an issue in the dairy industry. Recently Bauman *et al.* (2008) have reviewed the role of specific fatty acid isomers (e.g. *trans*-10, *cis*-12 CLA) in causing a marked depression in milk fat synthesis. This is an excellent example of a nutrient × gene expression interaction whereby the isomer appears to specifically act on the expression of the lipogenic enzymes and hence fatty acid synthesis through the action of the sterol response element-binding protein (SREBP) family and Spot 14 gene. Quantitatively, such a mechanism is impossible to detect by standard nutritional experimentation directed at determining the efficiency of nutrient transfer as the isomer quantities are so small, although infusion-response relationships were necessary to initially identify the issue. These isomers can only be detected with sophisticated gas–liquid chromatography and mass spectrometry methods, and the range of such isomers in our pasture-based systems has not yet been described. A practical outcome would be the use of this technology to manipulate changes in the body condition score of lactating cows. The problem model thus centres around accumulation of fat in cows during the wet season, whilst cows are lactating and drawing on this body fat for reproduction and reserves for survival during the subsequent dry season. Do we know how efficiently fat is accumulated during this wet season period in terms of the efficiency of use of energy for retention as fat, or in energetic terms, the k_f? Do we thus have a problem model involving the rate of fat deposition in cows under diets leading to high acetate content in absorbed products (Pethick *et al*. 2004), pasture systems with a range of CLA isomers (Bauman *et al*. 2008), variable fatty acid profiles of the microbial ecosystem (Or-Rashid *et al*. 2007) or different fatty acid profiles in *Bos indicus vs Bos taurus* breed types (O'Kelly and Spiers 1992)? The feeding standards use a high value for energy gain for lactating cows (e.g. k_f of 0.6, CSIRO 2007) but, on the basis of the ME content for tropical forages in the wet season (7.6–8.6 MJ ME/kg DM), the estimated k_f would be 0.33–0.37 (CSIRO 2007). What opportunities are there to manipulate energy gain of the lactating cow in the wet season? Isomers of specific fatty acids may also play a role in determining rates of total fat accumulation, although at present the data suggest that the effect is predominantly isolated to the mammary gland and not other fat depots. However, Smith *et al*. (2009) have outlined a role for Vitamin A and D, and *trans*-10, *cis*-12 CLA in intramuscular fat deposition. Longer chain n-3 fatty acids (docosahexaenoic acid), provided during the last trimester of pregnancy from sources of fish oil and algae, have improved suckling behaviour and lamb vigour at birth, indicating other effects of small amounts of specific fatty acids (Pickard *et al*. 2008).

Adaptation to low crude protein forages

Results from faecal NIRS analyses have shown that cows in northern Australia cope with low protein diets (~4% CP) for up to 8 months of the year, and moderate rates in the range of 7–10% CP for the remainder of the year. Yet despite this, these cows maintain weight or nearly so on an annual basis (providing the pasture utilisation rate is maintained at around 25%) and 80% weaning rates are achievable. This suggests, with some confidence, that some physiological adaptive mechanisms are operating under conditions of long-term dietary protein deficiency, based on the early work on N recycling to the rumen (McDonald 1946; Norton *et al*. 1979), yet the feeding standards would suggest that the cows could not survive. N recycling occurs, but there has been limited study into the quantitative values in these circumstances (Norton *et al*. 1979). Other contributing factors may be changes in the rumen microbial population, leading to more efficient rumens in terms of microbial protein production and/or shifts in tissue metabolism associated with fat and protein metabolism, and in maintenance. Simpler methods are now available for studying N recycling than before (Reynolds and Kristensen 2008) and, supported by gene expression studies, may elucidate the nature of the adaptive mechanisms. In this pursuit, one would not expect to establish new principles, as McDonald did when detailing the use of ammonia-N in the rumen, but the interest is in the quantitative nature of the changes and in discovering the pathways that can be manipulated to improve animal performance under low protein diets.

Microbial protein production in the rumen linked to microbial genetic population profiles

Microbial crude protein (MCP) provides most of the metabolisable protein for ruminants, especially where low protein forages are grazed. The MCP production within the rumen varies markedly with diet and the feeding standards show that the efficiency of MCP production (EMCP) varies with N supply, feeding level (dilution rate), and the supply of peptides and amino acids. N supply (expressed as rumen degradable protein or rumen degradable N) has the greatest effect, but the range in EMCP values across the combined literature is very wide. With adequate N, the feeding standards combined show a range of 9–11 g MCP/MJ fermentable ME or 130–170 g MCP/kg digestible organic matter (DOM). Feeding urea can increase EMCP to ~130 g MCP/kg DOM, but it has proved difficult to achieve values higher than this with urea alone. There is a vast amount of literature from the 1960s and 1970s describing the factors that affect EMCP, but the problem model is how to increase EMCP in ruminants on low protein diets to the high values recorded with temperate forage, as such an increase would lead to significant increases in liveweight gain (Poppi and McLennan 1995). Obviously, factors other than increasing rumen degradable N supply as urea need to be manipulated, but are these higher targets for EMCP achievable? A precursor to achieving this would be to have a better understanding of the rumen microbial ecology, that is, the population of microbes that occur under these low nutrient conditions and constitute the MCP supply of the animal. Mackie *et al*. (2002) have estimated that only 15% of the microbial population have been grown in culture. Thus, our knowledge of the conditions that affect microbial growth comes from isolated cultures of species that may not be the dominant species within the rumen. Denaturing gradient gel electrophoresis, PCR and DNA sequence analyses are methods used to identify these microbial populations. Bacteria, protozoa, fungi and archaea can be studied separately. Some examples of the application of these techniques are provided by Larue *et al*. (2005) and Harper *et al*. (2010), where the population of dominant bacteria have been outlined and largely shown to be uncharacterised species. Harper *et al*. (2010) have identified a large increase in scavenging bacterial species (uncultured rumen bacterium from the order Bacteroidales) most probably in response to a rapid decrease in dietary N. Further, animals selected into groups on the basis of liveweight gain post-weaning had microbial population matrices that could be grouped as similar on the basis of groups of individual animals, but not within the post-weaning growth rate groups (E. Martinez, pers. comm.). Whether or not these distinct populations are established at or soon after birth or respond to the physiological adaptation of the host to varying nutrient supply (e.g. N recycling to the rumen) is not known. All this emphasises is that we do not have a good understanding of the rumen microbial ecology and its response to dietary manipulation. Further advances using high-throughput next generation DNA sequencing (e.g. 454 pyrosequencing, Shendure and Ji 2008) have markedly increased the speed with which ruminal microbes can be sequenced and that data analysed. Using rumen samples from an algal supplementation experiment (Harper *et al*. 2010), L-M Gulino (pers. comm.) has shown that cattle supplemented with large amounts of algae had ruminal populations of bacteria from the SR1 phylum, bacteria not seen in other cattle examined. The same group, using a similar approach, showed that cattle fed high grain diets for 50 days had rumens dominated by bacteria from the Proteobacteria phylum, whereas cattle at pasture, irrespective of supplementation, had rumens dominated by the phyla Bacteroidetes and Firmicutes. Pyrosequencing results for methanogen populations (archaea) have supported previous work (Ouwerkerk *et al.* 2008) and shown that in cattle fed a variety of diets, the genus *Methanobrevibacter* dominated methanogen populations, averaging 86% of the total archaeal community. As these dominant microbes across all the above studies presumably provide the bulk of the MCP flowing from the rumen, it is apparent that we are in the early stages of understanding the populations of microbes in the rumen, their variation with diet and their association with high or low EMCP.

In utero *nutrition*

Epigenetics is an emerging discipline, the application of which has the potential to be a major contributor to the lifetime performance of animals. The grazing ewe and cow are, by and large, subjected to varying nutritional inputs, in terms of energy, protein and mineral intake, before and during pregnancy, with generally unknown consequences for the fetus, for growth and development of the offspring and possibly for future generations. Bell (2006) has outlined some of these *in utero* effects and drawn attention to the observation that there are large amounts of unexplained variation for many productive traits and epigenetic effects may contribute to this variation.

The timing of any imposed *in utero* treatments is important and may need to occur around the time of conception for subsequent effects. Quigley *et al*. (2005) showed that restricting feed intake of ewes in the peri-conception period decreased total muscle fibre number of fetuses at mid-gestation. In a separate study, ewes receiving 0.6, 1.2 and 1.8 × maintenance energy requirements from 89 days before pregnancy to late pregnancy showed maternal, placental and fetal adaptations to maintain fetal survival and development in such a way that only in late pregnancy did the prolonged low maternal intake result in a reduction of fetal growth that was associated with a reduction in fetal IGF-1 concentration (Quigley *et al*. 2008). In cattle, Greenwood and Cafe (2007) indicated that restricted prenatal and pre-weaning growth resulted in smaller cattle that yielded less meat at 30 months of age, with pre-weaning but not prenatal growth retardation resulting in partial compensation in weight gain. Prenatal and pre-weaning growth had no long-term consequences for carcass composition, yield and meat quality characteristics at the same carcass weight, although slower pre-weaning growth resulted in slightly leaner carcasses but similar meat quality. At the same feedlot entry weights, efficiency of nutrient utilisation was not affected by either prenatal or pre-weaning growth (Cafe *et al.*2009). They concluded that in pasture-based systems with variable nutrition, there was little long-term effect of prenatal and/or pre-weaning nutrition on body composition.

The effects of *in utero* nutrition on the development of the reproductive organs and subsequent reproductive performance, neonatal survival and postnatal feed intake may be of more relevance to livestock production than those that are currently of interest from a human health perspective (e.g. insulin resistance), where livestock with a much shorter lifespan provide no opportunity for the effects to arise. Future directions of this area of work will need to move away from a ‘global’ nutrient supply perspective and focus more on individual nutrients relevant to the animal model under investigation. For example, Chadwick *et al*. (2009) showed recently that there was an effect of high NaCl levels *in utero*. Lambs of ewes consuming saltbush or high salt diets showed higher wool production and lower plasma renin activity compared with control lambs from ewes on low salt diets. The lower renin activity enabled them to adapt to high salt diets such that when grazing saltbush they grew faster than lambs from control ewes.

Minerals

Minerals have been extensively researched within Australia (Underwood 1981) and regions mapped. Despite this, mineral deficiencies can arise in production systems (Dove and McMullen 2009). The role of minerals in gene expression and the study of their action by such methods will lead to new developments. Of more immediate concern is the poor adoption of mineral supplementation even with elements known to be widely deficient, for example, P, in northern Australia. Here, the response is well known, but it only occurs in the wet season and the practical difficulty is distributing P to animals in that period. Thus, research is necessary into carry-over effects of supplementation in the dry season to raise P reserves in the body (skeleton) that may be called upon in the wet season.

Conclusions

These examples illustrate that there are many problem models that have nutrition as an underlying basis. Many of them are long term, but the time is now right with new methods available to reexamine them. Understanding the underlying mechanism provides opportunities for manipulation. Feed costs (including the true cost of pasture) continue to rise and the search for new feed sources and their evaluation will continue. Often, the problem model is not clearly identified, and benchmarking and epidemiology studies have a role in identifying the problem and, if nutritional in origin, identifying what needs to be addressed. Some of this may be done by the application of existing knowledge and some of it may need new fundamental research to be carried out. Producers will still need to increase production and reduce costs of production if they are to be profitable, but at the same time, address environmental and welfare concerns about animal production systems.

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