

# Nutrition—parasite interactions in sheep: future research priorities

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## Summary

The increasing problem of resistance of parasitic nematodes to anthelmintic chemicals has stimulated renewed interest in nutritional approaches to enhance immunity and resilience of sheep to infection. This paper summarises the key issues raised during a comprehensive review of this subject and suggests priority areas for future research. After detailing the context of the review, sections are devoted to outlining how nematode infections affect the nutrient economy and partitioning in the host, how pre-natal and post-natal nutrition can program later life productivity and ability to cope with infection, how nutrition can affect the development and expression of immunity and how nutritional supplementation has been shown to enhance resistance and resilience to infection in experimental studies. Some general principles for the testing and application of nutritional management strategies in the field are discussed together with priorities for further research to better understand mechanisms underlying the response of animals to parasites and the interactions with nutrient supply.

**Keywords:** sheep, nematodes, nutrition, interactions, research priorities

## Introduction

There is abundant evidence that resistance (immunity) of sheep to nematode parasites of the gastrointestinal tract and the ability to withstand their pathogenic effects (resilience) can be markedly influenced by nutritional factors. Numerous experiments have demonstrated that the effectiveness of immunity to worm infections can be manipulated by altering the protein content of rations, and in the field producers have long recognised that sheep in poor condition have a poor tolerance to parasites. Trace minerals have also been shown to have a role.

These observations suggest that improved nutrition, using available forage or specific nutritional supplements at critical periods in the host–parasite

epidemiological cycle, will assist maximal expression of resistance in lambing ewes and in young growing sheep, thereby reducing the need for chemical treatment and minimising production losses.

These matters are given much attention by the Australian Sheep Industry Cooperative Research Centre (CRC). This CRC, based at the FD McMaster Laboratory — Chiswick, Armidale, has the support and collaboration of CSIRO, Universities, State Departments of Agriculture, and organizations for the production and processing of wool and meat, including research–funding agencies (for details of structure and research programs see [www.sheep.crc.org.au](http://www.sheep.crc.org.au)). In its program of research on minimising dependence on chemicals in parasite management the use of nutrition is considered complementary to other sustainable approaches being investigated, including novel diagnostic aids, breeding for enhanced resistance, and the use of biological control agents. In order to establish priorities for research on nutritional management to enhance resistance and resilience to parasites in sheep production systems focussed on both wool and meat, the CRC held a workshop in October 2002 with the following objectives:

- to ascertain how nematode parasites can affect the nutrient economy of sheep;
- to evaluate the evidence for the enhancement of resistance/resilience to infection by strategic nutritional supplements;
- to establish research priorities to extend this knowledge and provide practical solutions for application to Australia's sheep industries and reduce current reliance on anthelmintic chemicals.

The workshop was attended by 25 invited experts drawn from the CRC collaborating organizations, and AgResearch Ltd and Lincoln University, New Zealand. The outcomes were a series of scientific reviews that will be published in full (see References), and a series of recommendations for immediate extension and

definition of research needed to further clarify practical aspects of nutritional management of parasites.

This paper summarises the main elements of the scientific reviews and the group discussion of these, and concludes with the recommendations of the workshop.

## Context

In his introduction to the workshop, Rowe (2003) emphasised the overriding dual focus of the CRC to optimise the returns from both meat and wool through moving from flock to individual sheep management. This in turn would enable meaningful changes and new opportunities for managing parasites and re-evaluation of nutritional strategies for improving sheep production in light of the possibility of making good profits from both commodities. Although previous nutritional strategies applied to whole flocks or whole age groups have rarely proved to be economically attractive, on-farm introduction of electronic data capture and automatic drafting would enable segmentation of flocks for differential nutritional management of animals most likely to respond in terms of improved parasite control.

Further context for the workshop was given by Besier and Love (2003) who reviewed the problem of anthelmintic resistance and the need for new approaches to the control of sheep nematodes in Australia. Current control of the most important roundworms, namely *Haemonchus contortus*, *Trichostrongylus* spp. and *Ostertagia (Teladorsagia) circumcincta*, depends heavily on chemotherapy and the prevalence and severity of resistance on Australian sheep farms continues to rise to the extent that it threatens profitability in some areas. Field studies in Western Australia (WA) indicated that significant production loss and increased clinical parasitism were negatively correlated with drench effectiveness; for example, when a drench was only 65% effective 10% less wool was produced and there was a threefold increase in mortality and scouring. The resistance on the majority of Australian sheep properties is such that the efficacy of benzimidazole and levamisole drenches is below that required for effective worm control. Avermectin resistance is common in *H. contortus* endemic areas and closantel resistance also threatens control of this parasite. In WA, ivermectin resistance in *O. circumcincta* is present on 19% of farms. Early signs of moxidectin resistance have also emerged in several locations in all three nematode species.

It is estimated that present trends in anthelmintic resistance could increase the cost of worm control in the sheep industry to \$700 million annually in the absence of new sustainable strategies and technologies. There is a need to focus on integrated management of these tools and not rely on complete suppression of parasites using anthelmintics. Such fundamental changes in approach will place greater emphasis on planning parasite control in relation to other sheep management

imperatives aimed at optimising production. Besier and Love (2003) concluded that, in the shorter term, the strategies of choice are likely to involve grazing management, avoidance of excessive drench exposure of the worm population, and strategically targeted nutritional regimes to promote optimal immunity and minimise pathogenic effects.

## Nutrient economy and partitioning

In this session, fundamental knowledge of the metabolic and physiological effects of parasitism and of the known and potential influences on the utilisation of nutrients was reviewed from various perspectives in four papers.

Sykes and Greer (2003) considered research on the effects of parasitism on the nutrient economy of sheep and concluded that, while 25 years of work had significantly improved understanding, it was still not possible to provide a quantitatively precise answer within the 'industry' context of the workshop. This reflected the complex and dynamic relationship between larval challenge and immune response together with the difficulty of quantifying nutrient utilisation and worm exposure and burden under field situations. Nevertheless estimates of 35% reduction in growth rate under well-controlled farmlet conditions show that effects of parasitism under field conditions are not dissimilar to those recorded under controlled, monospecific infections in pens. There is good evidence that once immunity is acquired productivity returns to normal although reports of reduced wool growth in 'immune' sheep under challenge suggests acquired immunity may have a nutritional cost. Impaired immunity of ewes in the peri-partum period and its moderation by improved protein nutrition suggests competition between the immune system and the udder for nutrients.

Whilst reduced feed intake of up to 50% in infected, naïve lambs is a major factor underlying impaired performance, there is compelling evidence that infections of the abomasum and small intestine induce a protein deficiency additional to the reduced supply through appetite depression. This is attributable principally to increased losses of endogenous proteins, from plasma, gut secretions and epithelial cells, into the gastrointestinal tract rather than an impaired digestive and absorptive function *per se*. Sykes and Greer (2003) highlighted the apparent linkage between these physiological events and the activation and maintenance of host immunity, suggesting that the major influence on the nutritional economy was the actual demands of the acquisition phase of the immune response, which may also be implicated in the characteristic appetite depression. They concluded a need to assess specific amino acid demand of the immune response to parasitism and the ability of grazing animals to supply this post-ruminally.

Adams and Liu (2003) reviewed the principles of nutrient partitioning in relation to the physiological demands for body and wool growth, pregnancy and

lactation and their implications for immune responsiveness to nematode parasitism. Nutrient flow is not determined by competition among tissues and is co-ordinated by hormones in a process termed homeorhesis. For example, muscle growth is under active control by growth hormone, androgens, insulin-like growth factor-1 (IGF-1), insulin, and other hormones. Total flow of nutrients from feed intake and body reserves is more important than specific partitioning mechanisms and, because of seasonal interactions, partitioning to growth or reproduction is normally confounded with the availability of nutrients from pasture.

Large changes in amino acid metabolism in late pregnancy precede the perturbations in parasite immunity that are most evident in early lactation when the main partitioning focus is on energy metabolism. Ewes fed below protein maintenance mobilise amino acids from muscle and skin, but not visceral tissue, to support foetal growth and a sparing effect on the gut could explain why faecal egg count does not rise until the peri-parturient period. Although parasite resistance appears mostly influenced by protein metabolism, and closely relates to wool growth rate which depends on amino acid supply, energy availability also affects resistance through effects on availability of amino acids for uses other than growth. Despite there being no simple explanation relating partitioning with changes in faecal egg count in the field, Adams and Liu (2003) concluded that management practices that match pasture protein supplies with periods of susceptibility would improve parasite resistance cost-effectively.

Liu, Masters and Adams (2003) quantified the demands placed by various physiological states on protein supply, to demonstrate why this is a key determinant of strong immunity-associated responses to gastrointestinal parasites. In fast growing lambs, ewes in late pregnancy and in early lactation, metabolizable protein requirements are respectively increased 1.4, 0.7 and 2.5 fold above maintenance. Infestation with internal parasites may result in a total net protein loss of about 12 g/d, of which about 50% is loss from the gastrointestinal tract and 50% through increased amino acid oxidation in various body tissues. Additional metabolizable protein of 17 g/d to meet this loss from the infection is equivalent to about 57, 71, 14 and 77% of the protein requirements respectively for growth, pregnancy, lactation and wool production. This activation of immunity-associated responses thereby creates strong competition for protein and diminishes nutrient status in late pregnancy and particularly in early lactation. Pastures in Mediterranean environments cannot meet the total demands for protein during the reproductive season. The immunity-associated response requires more protein rather than energy and therefore parasite infection has a more severe effect on wool- than meat-producing sheep. Body condition of sheep could also be a predominant factor in determining immune status.

In their consideration of the influence of nematodes on nutrient partitioning Roy *et al.* (2003) concentrated particularly on associations between protein metabolism and amino acid utilisation and oxidation in the gastrointestinal tract and liver and activation of the immune system in sheep exposed to *T. colubriformis* infection of the small intestine. The very high metabolic requirements of the gut, particularly for protein synthesis and energy expenditure in the small intestine, account for 20–50% of whole body protein turnover and energy expenditure even in the absence of parasite challenge. Following infection, metabolic changes in the gastrointestinal tract disrupt partitioning of amino acids to other tissues such as the liver, muscle and skin. Although fractional protein synthesis rate of the small intestine is not affected proximally, various studies have shown it may be increased or decreased in the terminal section. As a result of increased plasma flow across mesenteric-drained viscera, inflow of total plasma amino acids was increased 27–48% with parasite infection. However, net apparent absorption of total, essential, branched chain and sulphur amino acids was unaffected indicating a significant proportion of inflowing amino acids are used in the small intestine of parasite-infected sheep as substrates for protein synthesis. Net uptake of plasma amino acids by the liver tends also to increase, presumably to support increased synthesis of enzymes, acute phase proteins and export proteins such as albumin production.

### Key points of discussion of research needs

- Role of immune response in pathogenesis of nematode infections—are the apparent differences between pen and field studies attributable to nutrition?
- Importance of feed intake in resistance expression—need to examine axes between feed intake/nutrition and pro-inflammatory cytokines and Th2 vs Th1 response.
- Need to define total protein supply—or even essential amino acid supply—from pasture.
- Protein partitioning—need to examine genotype effects, role of liver, hormonal and growth factors (e.g. IGF1) in response to parasitism.
- Significance of elevated mucin production in determining additional amino acid requirements in response to parasites—cysteine, threonine seem important.
- Need for further work on efficiency of ME utilization in different nematode infections.

### Nutritional programming

In recent times, studies on the longer-term effects of human foetal and infant malnutrition on metabolism,

growth and ability to resist disease have generated considerable interest. This session focused on evidence suggesting that nutritional programming of young sheep could impact on lifetime productivity, reproductive performance and ability to respond to parasitic and other diseases.

Cronje (2003) reviewed the evidence that nutrition and stress during gestation can programme gene expression of the immune system and the hypothalamic–pituitary–adrenal (HPA) axis in the developing foetus, and that these effects have lifetime persistence. Foetal programming of these axes may cause reduced immune competence since low protein diets and stress during gestation result in blunted acute phase responses, reduced thymic and splenic lymphocyte proliferation and decreased splenic natural killer cell activity in the progeny. These effects appear linked to increased incidence of asthma in adolescent humans and increased pre-weaning morbidity and mortality in piglets. Low protein diets and stress during gestation also alter the HPA axis of the progeny with resultant increased basal corticosteroid blood concentrations and an exaggerated response to stress. These effects have been linked to increased pre-weaning mortality and slower wound healing in piglets. Few studies have been conducted with ruminants and none have examined the impact of foetal programming on susceptibility to parasites. Nutritional manipulation of foetal development of the immune system may therefore enable long-term, improved resistance of sheep to parasites, since the supply of dietary protein and S-containing amino acids available to the pregnant sheep is typically sub-optimal in most farming systems.

Evidence that nutritional programming of young sheep could improve later-life liveweight, wool production, reproductive performance, and resistance to nematode parasites was presented by Knox, Deng and Nolan (2003). The greatest impacts of supplementation are achieved under circumstances where nutrient availability is substantially below that required for normal growth and development. Nutritional deprivation whether caused by seasonal influences on pasture growth or by the negative effects of gastrointestinal nematode parasitism, appears to be a particular problem for young sheep and may affect their lifetime production unless corrective measures are taken to alleviate the problem. Achievement of 40% of mature liveweight before suffering growth impairment is thought to be critical to avoid permanent detrimental effects on growth and body composition. If this is also the case for wool growth, reproductive performance and ability to resist infection with nematode parasites, particular attention needs to be given to ensuring nutritional needs are met and negative impacts of nematode parasitism are minimised during lactation and around weaning in sheep production systems. Further research to better define nutritional requirements of periparturient ewes and growing sheep during exposure to nematode parasites should assist in this regard.

## Key points of discussion of research needs

Induction of immune competence during foetal development:

- need to establish role of protein, specifically methionine, and fatty acids, effect of feeding during each trimester of pregnancy, and the differences elicited by single and twin lambs;
- does pre-partum feeding influence immediate post-natal development of the immune systems and parasite resistance in the lamb?;
- to what extent are the above factors influenced by the known ability of the ewe to buffer changes in nutrition to the foetus?

Long-term influence of post-weaning supplementation on resilience:

- uncertain how long benefit persists and important to define nutrient supply from pasture and window of opportunity for supplementation strategies;
- effect only applies if sheep have low growth rates at that time;
- pen and pasture experiments apparently give different results and energy effects may explain differences between pasture experiments.

## Nutritional influences on immune function

Inflammation and other immune responses occur locally and systemically as a result of the presence of, and damage caused by, gastrointestinal parasites. These responses can represent a significant drain on the nutritional resources available to the host and redirection of protein away from normal body processes may result. This session concentrates on influences of nutrition on the expression of immunity in sheep.

Colditz (2003) reviewed current evidence for metabolic effects of immune activation from studies on the acute phase response (APR) in mastitis, fly strike, wool growth in high and low staple strength genotypes and during parasitic infection. Part of the APR is a change in priorities for nutrient utilisation, when the pro-inflammatory cytokines, IL-1 $\alpha/\beta$ , TNF $\alpha$ , IL-6 and IFN $\alpha/\beta$  override normal hypothalamic–somatotrophic control. These cytokines reduce synthesis and increase catabolism of muscle protein, induce hepatic synthesis of APR proteins, and decrease *de novo* fatty acid synthesis and increase lipolysis in adipose tissue. In the CNS there is induction of fever, which increases metabolic rate, and induction of sickness behaviour. Although there are few studies on the APR during

gastrointestinal nematode infection in sheep, IL-6 message is present in mucosa during *T. colubriformis* infection and mast cells involved in parasite immunity contain preformed TNF $\alpha$ . Changes in appetite, growth and nitrogen metabolism during parasitism in sheep accord with the systemic effects of the APR.

Colditz (2003) suggested that modified capacity of tissues to take up amino acids during pro-inflammatory cytokine perturbation of nutrient utilisation may limit amelioration of the cost of immune activation by dietary supplementation. Genetic variation in production of, or tissue sensitivity to pro-inflammatory cytokines during nematode infection may provide a basis for selection for resilience.

Influences of nutrition on expression of genotypic resistance to gastrointestinal nematodes were reviewed by Walkden-Brown and Eady (2003). Differences in faecal egg count between genotypes appear greatest when nutrient availability is low, and under such conditions both resistant and susceptible genotypes generally respond to supplemental protein by reducing egg count. However, under moderate to good nutritional conditions, responses to additional protein tend to be observed only in susceptible genotypes. While host genetic resistance is associated with reliable, moderate to large reductions in egg count, nutritional intervention seems less reliable and induces smaller reductions. The converse situation applies with host resilience to infection; increased genotypic resistance is rarely associated with improved growth or production during the period of infection, whereas nutritional supplementation reliably increased host productivity irrespective of infection status and prevailing nutritional conditions. Overall the review suggests complementary roles for resistance selection and strategic nutritional intervention in integrated management of parasites. The former will contribute primarily to disease epidemiology by reducing pasture contamination over a wide range of conditions, reducing host challenge and frequency of treatment. The latter will boost resilience to infection, with lesser effects on resistance.

The role of mineral nutrition in gastrointestinal immune function was addressed by McClure (2003) who showed that, in addition to more specific functions, both major and trace elements have wide-ranging roles in activity of enzyme systems, thereby potentially affecting immunity by several pathways. There is little reported work on effects of minerals on mucosal immunity of ruminants, but effects of dietary deficiencies of the trace elements selenium, cobalt and molybdenum on protective immunity to worms have received some attention. Selenium supplementation of deficient diets appears not to affect worm resistance whereas cobalt and molybdenum deficiency impedes immune responses. Importantly, optimal protective immunity was found at higher dietary molybdenum concentrations than the recommended nutritional maximum, and there is evidence that for both molybdenum and selenium the dose response curve is not linear.

McClure (2003) concluded that minerals, particularly trace elements, are an under-rated and little-understood influencer of immunity to internal parasites in grazing ruminants. Better understanding of their role and requirements would provide an immediate, easily applied strategy of defined duration with potential to cost-effectively improve long-term resistance.

### Key points of discussion of research needs

- Can measurement of acute phase response parameters provide a sensitive index of changes in tissue protein metabolism and nutrient utilization during infection, and how do these interact with nutrient supply?
- Is host-induced pathology a necessary pre-requisite for acquired immunity and is it possible to differentiate between the costs of both?
- Does genetic selection for resistance lead to change in Th1 and Th2 type responses?
- Why don't genetically resistant animals express an increased production? How important are hypersensitivity effects on production? Longer-term benefits accruing from reduced pasture larval contamination may need to be examined.

### Supplementation to enhance resistance and resilience

Numerous studies have shown that increasing the supply of protein for intestinal absorption can alleviate the detrimental effects of nematode parasites on production and can also result in improved protective immunological responses to infection. In some situations the practical implementation of such a strategy for improved nematode parasite control is hampered by the high cost and/or unavailability of high quality protein sources for use as ruminant livestock feed. The provision of non-protein nitrogen (NPN) in the diet can compensate for nitrogen deficiencies of roughage based diets and enable increased productivity from this feed resource.

Knox (2003) presented evidence from studies with young sheep to demonstrate that supplementation with urea can achieve similar qualitative benefits in reducing the effects and level of infection with parasitic nematodes to that achieved with protein supplements. Experimental evidence shows that the use of urea-molasses blocks (UMB), a popular low-cost means of delivering NPN, can have a beneficial impact on enhancing the resilience and resistance of sheep to infection with nematode parasites. Consistent with other nutritional studies, urea appeared to confer greater benefits with increasing supplement intake as shown by reduced pathological effects, parasite numbers and faecal egg output. Application of these findings in

Australian pasture systems may require revision of current delivery practices for NPN supplements to ensure adequate urea consumption occurs.

Influences of dietary supply of metabolizable protein (MP), on immunocompetence and on resilience to pathogenic effects during continuous exposure of young sheep to infective larvae were reviewed by Steel (2003) for the most important abomasal and small intestinal nematodes present in Australian grazing systems. In lambs infected with *H. contortus* supplementary protein improves both development of immunity and resilience in breeds of sheep which are susceptible to haemonchosis. Increased protein requirements of Merino weaners parasitised by *H. contortus* would be met by diets containing about 19% crude protein, depending on the rumen degradability of the dietary protein source. Evidence exists for an enhanced immune response to *O. circumcincta* in lambs receiving an increased supply of protein at the intestines. Response to protein supplementation of lambs infected with *T. colubriformis* depends on the MP content of the basal diet and on the period of exposure to incoming larvae. Where the basal diet only meets requirements for maintenance or low growth rates, increased supply of rumen undegradable protein enhances immune expression in terms of reducing faecal egg count and expelling adult worms, but does not appear to limit the initial establishment of incoming larvae. Effects on growth rate and wool production are most pronounced during the period of worm expulsion, indicating that this phase of the immune response competes with production when nutrient resources, and particularly protein, are limited.

Supplementation of Merino weaners exposed to natural infection from pasture with protein meals can reduce faecal egg count and improve resilience in terms of both growth rate and wool production.

Kahn (2003) examined the role of dietary supplementation in regulation of resistance and resilience during the periparturient phase of the reproductive cycle when ewes experience a temporary loss, or diminution, of immunity to gastrointestinal parasites. The periparturient ewe experiences an increased requirement for MP which predisposes it to an 'increased MP pressure'. Increased MP supply in housed and grazing periparturient ewes significantly improves resistance to infection. This is attributable to positive gut immune responses and countering of the combined pathological consequences of infection *per se* and the host's immune response, namely a net loss of amino acids. It is proposed that the priorities for use of MP which predispose the ewe to nematode infection are altered following infection to favour a gut immune response. Despite being influenced by both MP supply and genotypic resistance, loss of immunity during the periparturient period cannot be fully restored by either approach, suggesting involvement of other unidentified factors. Maternal weight loss and, more precisely, body protein mass may be good indicators of

the likely immuno-responsiveness of periparturient ewes to increased MP supply.

Resilience to gastrointestinal nematodes is responsive to both ME and MP supply. The practice of supplementing periparturient ewes with MP and ME to enhance resistance and resilience to parasites, is gaining favour with graziers in some regions. Other benefits e.g. increased reproductive rates, arising from such strategies improve their cost-effectiveness.

### Key points of discussion of research needs

- Major effect of urea-N mediated through stimulation of feed intake.
- Response to urea dependent on background nutrition and very difficult to obtain in Australian conditions where any green feed available.
- Economics of block delivery compared to protein meals not attractive.
- Need to define growth rate required for animals to cope with parasites—does this depend on production genotype?
- Economic analysis required to determine whether supplementation justifiable on improved parasite control alone or in conjunction with improved liveweight gain, wool growth and reproductive performance.
- Need to determine the importance of protein quality and differences in 'metabolizable protein pressure' in different production systems—periparturient ewes, prime lambs and weaner replacements.
- Mechanisms involved in the periparturient relaxation of immunity require elucidation e.g. role of prolactin, leptin, corticosteroids.

### Conclusion and recommendations

The workshop concluded that nutritional management strategies that aim to maximise the acquisition of effective immune expression and to concurrently minimise the impact of these effector mechanisms on productivity both in young growing sheep and in reproductive ewes must be considered within the context of the particular production system, its economics, and the climatic environment in which such strategies are to be applied. A major benefit of effective strategies would be to reduce the requirement for anthelmintic treatment, and hence minimise the development of resistance by worms to drenches. Some general principles for testing and application in the field were agreed together with priorities for further research to better understand mechanisms underlying the response of animals to parasites and the interactions with nutrient supply:

- Level of nutrition required for more effective management of the effects of worms in susceptible sheep may not differ from that usually considered optimal for production anyway. The essential criteria may be the same generally accepted benchmarks for growth rate of weaners or weight gain over the last trimester of pregnancy of ewes in a 'good' production system.
- Nutritional composition and availability of the feedbase through the year is available for most Australian sheep production systems. This information should be mapped to the epidemiology and population dynamics of the principal parasite species in the particular system and with animal requirements. This will facilitate identification of optimal times for strategic nutritional manipulation which match the need for extra metabolizable protein to support full expression of naturally acquired immunity without compromising productivity.
- Practical application of this information may require more intensive monitoring of faecal egg count in susceptible stock on a flock basis so that cost-effective grazing management or supplementation strategies are implemented at the most appropriate time relative to host need for protein in particular. Integration of models of worm epidemiology with decision support tools for managing forage supply to meet animal feed requirements is considered a high priority.
- Extension to farmers may require integrated communication on feeding for better worm management with other nutritional messages for optimising utilisation of the feedbase to meet animal performance requirements. Messages targeted only on worm control will not have high impact without a clear indication of economic and sustainability benefits, since for most producers this is not their highest management priority.
- There is a need to better identify the benefits of animals selected for parasite resistance within the context of their apparent requirements for extra metabolizable protein during expression of presumably a more effective immune response. Is it possible to shift random-bred animals towards the immuno-responsiveness of resistant genotypes using nutritional manipulation?
- Nutritional research being conducted in other areas could be applied to the management of resistance and resilience to worms, including methods to enhance microbial protein flow to the intestines, the influence of specific nutritional components on immune gene expression, or conditioning of the gut environment to inhibit worm establishment or enhance worm expulsion. There is presently little evidence that nutritional strategies can shorten the time for acquisition of immunity to worms. Basic research to define physiological and metabolic factors involved in immune acquisition may be required to determine appropriate strategies for manipulation or optimisation of the response.
- Within any particular production system it will be important to determine whether nutritional management to improve immunity is best targeted at the peri-parturient ewe or the growing weaner (or both).
- Any research on nutritional manipulation for enhanced parasite resistance and/or resilience should, wherever possible, include measurements to define the impact on lifetime productivity (wool, meat and reproductive performance). Long-term economic benefits of short-term supplementation strategies will be a critical determinant of the acceptance of recommendations by producers.

## References

- Adams, N.R. and Liu, S.M. (2003). Principles of nutrient partitioning for wool, growth and reproduction: implications for nematode parasitism. *Australian Journal of Experimental Agriculture* 43, in press.
- Besier, R.B. and Love, S.C.J. (2003). Anthelmintic resistance in sheep nematodes in Australia: the need for new approaches. *Australian Journal of Experimental Agriculture* 43, in press.
- Colditz, I.G. (2003). Metabolic effects of immune activation during gastrointestinal parasitism in sheep. *Australian Journal of Experimental Agriculture* 43, in press.
- Cronje, P.B. (2003). Foetal programming of immune competence. *Australian Journal of Experimental Agriculture* 43, in press.
- Kahn, L.P. (2003). Regulation of the resistance and resilience of periparturient ewes to infection with gastrointestinal nematode parasites by dietary supplementation. *Australian Journal of Experimental Agriculture* 43, in press.
- Knox, M.R. (2003). The impact of non-protein nitrogen supplements on nematode infected sheep. *Australian Journal of Experimental Agriculture* 43, in press.
- Knox, M.R., Deng, K.D and Nolan, J.V. (2003). Nutritional programming of young sheep to improve later-life production and resistance to nematode parasites. *Australian Journal of Experimental Agriculture* 43, in press.
- Liu, S.M., Masters, D.G and Adams, N.R. (2003). Potential impact of nematode parasitism on nutrient partitioning for wool production, growth and reproduction. *Australian Journal of Experimental Agriculture* 43, in press.
- McClure, S.J. (2003). Mineral nutrition and effects on gastrointestinal immune function of sheep. *Australian Journal of Experimental Agriculture* 43, in press.

- Rowe, J.B. (2003). Nutrition and parasite management — introduction. *Australian Journal of Experimental Agriculture* 43, in press.
- Roy, N.C., Bermingham, E.N., Sutherland, I.A. and McNabb, W.C. (2003). Nematodes and nutrient partitioning. *Australian Journal of Experimental Agriculture* 43, in press.
- Steel, J.W. (2003). Effects of protein supplementation of young sheep on resistance development and resilience to parasitic nematodes. *Australian Journal of Experimental Agriculture* 43, in press.
- Sykes, A.R. and Greer, A.W. (2003). Effects of parasitism on the nutrient economy of sheep. *Australian Journal of Experimental Agriculture* 43, in press.
- Walkden-Brown, S.W. and Eady, S.J. (2003). Nutritional influences on the expression of genotypic resistance to gastrointestinal nematode infection in sheep. *Australian Journal of Experimental Agriculture* 43, in press.