Organic Eprints

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Small Ruminant Research 60 (2005) 141–151

Small Ruminant Research

www.elsevier.com/locate/smallrumres

Interactions between nutrition and gastrointestinal infections with parasitic nematodes in goats☆

H. Hoste[a,*], J.F. Torres-Acosta[b], V. Paolini[a], A. Aguilar-Caballero[b], E. Etter[e], Y. Lefrileux[c], C. Chartier[d], C. Broqua[f]

[a] *UMR 1225 INRA DGER Interactions Hôte Agent Pathogène, Physiopathologie des Maladies, 23 Chemin des Capelles, F31076 Toulouse Cedex, France*

[b] *FMVZ, Universidad Autónoma de Yucatán, Km 15.5 cha. Mérida-Xmatkuil, Mérida, C.P. 97000, Mexico*

[c] *Station du Pradel, Ferme Expérimentale Caprine, F07170 Mirabel, France*

[d] *AFSSA/Laboratoire de Recherches Caprines, 60 rue de Pied-de-Fond, F79012 Niort, France*

[e] *TA 30/G Equipe d Epidemiologie, CIRAD EMVT, F34398 Montpellier, France*

[f] *Institut de l Elevage, Agropole, Mignaloux Beauvoir, F86800 Lusignan, France*

Available online 15 August 2005

Abstract

Parasitic nematodes of the digestive tract remain one of the main constraints to goat production both in temperate and tropical countries. The usual mode of control of these gastrointestinal nematodes (GIN) based on the repeated use of anthelmintics is now strongly questioned because of the increasing development of resistance to these molecules. Among the alternative methods to anthelmintics currently available, the manipulation of host nutrition in order to improve the host resistance and/or resilience to parasitic infections seems to represent one of the most promising options to reduce the dependence on conventional chemotherapy and to favour the sustainable control of gastro intestinal nematode infections. This paper will review the available information on the interactions between nutrition and nematode parasitism in dairy or meat goats both in temperate and tropical conditions. It will refer to quantitative aspects of the diet (influence of the protein and/or energy parts) as well as to qualitative components (effects of plant secondary metabolites on worm biology) and will discuss the specificities of goats in regard of theses interactions.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Goat parasites; Goat health; Goat nutrition; Nematodes

1. Introduction

Parasitic nematodes of the digestive tract remain one of the main constraints to goat production both in temperate and tropical countries. The usual mode of control of these gastrointestinal nematodes (GIN)

☆ This paper is part of the special issue entitled Plenary Papers of the 8th International Conference on Goats, Guest Edited by Professor Norman Casey.

* Corresponding author. Tel.: +33 561 193875; fax: +33 561 193944.
E-mail address: h.hoste@envt.fr (H. Hoste).

0921-4488/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.smallrumres.2005.06.008

remains based on the repeated use of anthelmintics (AHs), either for prevention of infection or to cure the animals. However, the development of anthelmintic resistance in worm populations is now a worldwide phenomenon, in constant expansion, and is particularly prevalent in goats (Jackson and Coop, 2000). This constant increase in AH resistance has stimulated the search for alternative solutions, which is also supported by an enhanced public concern for more sustainable systems of production, less reliant on chemotherapy (Waller, 1999; Jackson, 2000). Among these alternative methods, manipulation of host nutrition in order to improve the host resistance and/or resilience to parasitic infections seems to represent one promising, short-term options. Studies on these aspects of interactions between host nutrition and nematode infections are abundant in sheep (see reviews by Van Houtert and Sykes, 1996; Coop and Kyriazakis, 1999, 2001) but, surprisingly, they still remain few in goats.

The rationale for manipulation of nutrition as a complementary method to control GIN is based on the knowledge of the pathophysiological processes associated with the presence of worms in the gut. Nematode parasitism can be assimilated to a nutritional disease, since the presence of worms usually induces a decrease in appetite, a decreased digestibility of the food and a diversion of nutrients from production sites towards the repair of tissue-damage provoked by the parasites (Hoste et al., 1997; Coop and Holmes, 1996). Therefore, an improvement of the host diet has been associated with two distinct potential benefits. On one side, this can provide the nutrients needed by the increasing demand to raise an immune response against the worms. On the other side, it can contribute to maintain the tissue and/or blood homeostasis and the host production despite the presence of worms. To summarise, an improvement in host nutrition can enhance the host resistance i.e. its aptitude to regulate the worm populations as well as the host resilience, i.e. its ability to withstand the negative effects of nematode infections.

The majority of the pathophysiological studies have underlined the fact that protein metabolism is much more disturbed by the presence of gastrointestinal nematodes than other components of the diet, including energy (Bown et al., 1991). In addition, in temperate conditions, proteins are usually the main limiting factor of the diet. Therefore, most studies have examined the role of an enhancement of dietary protein on the host response. However, some recent studies have underlined the need to consider both the protein and energy components, in particular in tropical conditions. Last, an increasing number of recent studies suggest that some natural compounds of the diet, in particular plant secondary metabolites, could have direct or indirect effects on nematode populations (Athanasiadou et al., 2003; Min et al., 2003; Waghorn and McNabb, 2003).

This paper reviews the available information concerning the manipulation of nutrition in order to reduce the dependence on conventional chemotherapy and to favour the sustainable control of gastro intestinal nematode infections in goats both in temperate and tropical conditions.

2. The role of protein supplementation in the improvement of resistance and/or resilience of dairy goats

Most studies conducted in sheep have examined the interactions between nutrition and nematode parasitism in meat or fibre producing animals. However, lactating ruminants, including dairy goats, represent an unique model to study the interactions between nutrition, GIN infection and the consequences on production, both to assess the negative action of the worms on the nutritional status of the host, and conversely, to investigate the benefits related to manipulation of the host diet. This is due first to the sensitivity of measurement allowed by daily collection of milk but it is also explained by the variability in nutritional requirements associated with lactation, either with time or between individuals within a flock.

In 1999, Coop and Kyriazakis proposed a framework postulating a prioritisation of allocation of nutrients to various body functions in a situation of scarce resource in parasitized animals. In adult, reproducing animals, the framework suggests that the first priority will be given to (1) maintenance of body protein and survival, (2) reproductive efforts, (3) expression of immunity, and (4) attainment of fatness. The functions with higher priority are less likely to be affected by host nutrition. This framework has been mainly validated by results obtained in meat or fibre producing sheep, but far less in goats. According to this framework, it can be postulated that circumstances associated with high milk production, i.e. either peak of lactation and/or high producing goats within a flock should correspond to higher susceptibility to parasitism.

Several results examining directly or indirectly the effects of nematodes in dairy goats tend to support this hypothesis. Within a flock of dairy goats experimentally infected with the abomasal species *Haemonchus contortus*, and the intestinal one *Trichostrongylus colubriformis*, does with the highest level of production were found to be more infected with parasites and more susceptible to their negative effects since they presented higher reduction in milk yield. In addition, these differences were particularly prominent at the peak of lactation (Hoste and Chartier, 1993). Indirectly, it was also observed that the response in milk yield to monthly AH treatments in a flock was significantly better for goats with high potential of milk production than for the low producing ones (Chartier and Hoste, 1994; Hoste et al., 1999). Lastly, epidemiological surveys conducted in naturally infected flocks of dairy goats have shown significant differences in egg excretion, which were repeatedly assessed between high and low producing goats within the flocks (Hoste et al., 1999; Chartier et al., 2000; Hoste et al., 2002). These results confirmed the idea of an inverse relationship between the resistance and resilience status of individual goats and the importance of milk yield excreted and the dependent nutritional requirements.

Conversely, dairy goats provide also a valuable model to measure the positive effects of protein supplementation to improve the host response to nematodes. Again, major modulations were observed according to the nutritional requirements of the does. In a flock of naturally infected goats, a better resistance (measured by the lower levels of faecal nematode egg excretion) and a better resilience (estimated through a higher milk yield and fat contents) were expressed by animals fed with a diet covering 125% of the protein requirements compared to the control diet covering 106% (Chartier et al., 2000). Similarly, some data suggest that an improvement in the level of protein nutrition around kidding could significantly contribute to alleviate the increase in faecal egg excretion, usually described as the “periparturient rise”, generally observed around parturition in small ruminants and which corresponds to a period (end of gestation/start of lactation) of major nutritional demands (Etter et al., 1999). On the other hand, one trial failed to show any improvement of either resilience or resistance of dairy goats to GIN infection when supplemented with specific amino acids in the diet (methionine) (Bouquet et al., 1997).

These relationships between the response to parasitism, the protein nutrition and the host requirements were examined further in details from an indoor study with dairy goats experimentally infected or not with *T. colubriformis,* receiving isoenergetic diets which differed in their protein contents, i.e. covering either 118 or 130% of the requirements. The 130% protein supplementation was associated with a better resistance, indicated by lower levels of parasite egg excretion. In addition, it was also associated with a better resilience, expressed by significant increase in milk production, but exclusively in the high producing goats with the highest requirements. Overall, these results confirm (1) the competition in the allocation of resources to milk or to the response to nematodes; and (2) the exacerbation of the process in a situation of high nutritional requirements (Etter, 2000; Etter et al., 2000).

From an applied point of view, the manipulation of protein nutrition to improve the host response to nematode infection appears an attractive issue to reduce the reliance on chemotherapy to control parasitism. However, one of the main limiting factor to implement the method in farm conditions with dairy goats remains the difficulty to measure precisely the increase in nutritional requirements induced by the presence of worms in the different anatomical segments of the gut. Despite these restrictions, one of the main potential applications appears the possible protein flushing around parturition in order to decrease the periparturient rise, which is recognised as a major phenomenon in the epidemiology of trichostrongylosis in small ruminants. The basic information needed to apply this option are also largely explored and evaluated in sheep production (Houdijk et al., 2001, 2003).

3. The role of supplementary feeding in the improvement of resistance and/or resilience of growing goats

3.1. Defining the role of protein supplementation in growing goats

Changes in protein metabolism as a major consequence of infection with GIN have focused attention on the effects of modifications in protein supply on outcome of infection (Van Houtert et al., 1996). However, the relationships between dietary protein and parasitism have been insufficiently investigated in goats with only a limited number of trials being reported. The first trials investigated interactions between plane of nutrition and *H. contortus* infection (Blackburn et al., 1991, 1992) confirming that a high plane of nutrition can result in improved resilience. However, it did not determine if these differences were the result of protein level or the combined effects of higher energy, protein and voluntary feed intake (VFI).

Thus, the need for an artificial infection pen trial designed to identify the role of dietary protein on the resilience and resistance of growing kids fed iso-energetic diets was evident. Such trial needed to avoid the possible confounding effects between protein level and feed intake, as the latter can be increased when protein level of the diet is increased (Lu and Potchoiba, 1990). A controlled infection trial performed by Torres-Acosta (1999) showed that, although a higher level of metabolizable protein (MP) increased nitrogen (N) retention, the extent of this retention was possibly limited by a lack of any additional energy (Lallo, 1996). Although N retention was increased due to higher protein intake, growth rate was not improved. It is possible that some of the extra N offered to the kids in the high protein (HP) diet group was used as a source of energy for increasing N retention (Van Soest, 1994). Meanwhile, a large proportion of the extra N given to kids was ultimately transformed into urea and this resulted in higher elimination of N in the urine.

Two further trials by Singh et al. (1995), using a source of non-protein nitrogen (NPN) also tended to underline the importance of interactions between protein and energy components in goats. These studies showed that urea supplementation alone, neither reduced the effects of parasitic infection nor improved the productive performance of kids. Only when urea supplementation was accompanied by a cottonseed meal was there any beneficial effect of supplementation (Singh et al., 1995; Knox and Steel, 1996). The lack of response to non protein nitrogen in those experiments suggest that rumen degradable protein supply from the basal diet might not have been limiting and therefore the extra NPN was wasted in the urine (Van Soest, 1994).

These experiments illustrate the problem of separating energy responses from protein responses. The use of protein can be affected by energy metabolism because rumen organisms need energy for protein synthesis. Also, the animal expends energy in protein turnover and deposition as well as recycling and excreting excess urea in urine (Boorman, 1980; Van Soest, 1994). These authors suggest that such interactions between energy and protein are particularly relevant to consider in goats. This was less illustrated from previous trials in sheep, probably because sheep are better able to obtain energy for extra N retention by mobilising their more abundant fat reserves. In addition, in tropical countries, some data suggest that, besides protein, the energy component of the diet could be the scarce resource in some seasons and therefore, should also receive attention (Gutierrez Segura et al., 2002). There is a need to define further protein-energy interactions in infected goats.

3.2. *Browsing trials using combined energy and protein supplementary feeding*

The previous section showed that there is no clear answer to questions about the role of dietary protein supplementation on the resilience and resistance of growing goats against GIN. However, it is possible to adopt a more pragmatic approach in which the role of supplementation on voluntary food intake (VFI), intake of protein, energy and other nutrients are parts of the mechanisms that allow animals to show improved responses against GIN infections. Thus, browsing trials have been used to determine the latter in Criollo goats naturally infected with GIN under tropical conditions.

3.2.1. *Wet season trials*

Two trials during the wet season, i.e. during a period of high parasitic challenge, were designed in order to investigate to what extent a supplementation which represented either a source of combined energy and protein or energy alone might improve the resilience and resistance of Criollo kids against natural GIN infections, in tropical Mexico. Animals browsed native vegetation consisting of a large proportion of shrubs, browsing legumes and tropical grass. In a first trial (Torres-Acosta et al., 2000), supplement was offered daily (100 g/animal) and consisted in 74% sorghum meal and 26% soybean meal. Tracer kids and faecal cultures showed that kids suffered of mixed infections with *H. contortus* (more prevalent from July to September), *T. colubriformis* (more prevalent from October to December) and *O. columbianum*. Supplementary feeding improved resilience of browsing Criollo kids against natural GIN infections and was economically feasible compared to non-infected (AH treated), non-supplemented kids. Improved resistance was also suggested. However, heavy mixed infections overwhelmed resilience and resistance of several supplemented kids. Reduced productivity of infected kids may have resulted from parasite related diarrhoea, decreased appetite, increased endogenous protein loss, reduction in the efficiency of energy utilisation and net movement of retained proteins from production sites to defence functions.

Results of the latter trial were sufficiently encouraging to warrant new browsing trials aimed at producing more information on the role of different supplements that can be sources of dietary protein, energy or both. Another wet season trial thus investigated the possible role of a rumen fermentable energy (RFE) supplement, such as maize, on both resilience and resistance of browsing Criollo kids against natural GIN infection. RFE may improve the efficacy of utilization of dietary protein from the browse, causing a positive impact in the animals. This field trial compared the effect of maize (M) or maize-soybean (MS) supplementation (Gutierrez Segura et al., 2002) in kids that faced natural infections with *H. contortus*, *T. colubriformis* and *O. columbianum*. Both supplements (M or MS) improved resilience (growth rate and blood parameters) of kids against GIN infection and were economically feasible. Resistance was also improved by both supplementation strategies. Kids in both supplemented groups had females with less eggs in utero compared to infected non-supplemented (I-NS) kids and the male:female ratio was also affected (more males than females). Both supplementation groups had lower faecal egg counts compared to I-NS kids. In addition, kids supplemented with M increased their mean peripheral eosinophil counts, had lower *H. contortus* and the female *H. contortus* worms were smaller compared to I-NS kids.

3.2.2. Dry season trial

During the dry season in the tropics the quantity (Rios and Riley, 1985) and/or quality (Collier and Beede, 1985) of forage feed resources deteriorates, thereby increasing the risk of under-nourishment. These environmental conditions also reduce the survival of GIN infective larvae in the vegetation. Thus, nutrition-parasite interactions in browsing goats at this time are complex and needed further investigation. A browsing trial was designed to determine the role of supplementary feeding on the resilience and resistance of Criollo kids against natural GIN infections, when browsing native vegetation during the dry season in tropical Mexico. This trial showed that the distribution of 100 g of the same supplement (74:26 sorghum:soybean meal) used during the wet season trials overrode the effect of the negligible infection found in the dry season. The supplement improved growth rate by almost 30 g/day in both infected and non-infected kids (Torres-Acosta et al., 2000). The supplement could have improved the rumen environment by providing energy that could be used by the microbes to produce more microbial protein. The intended outcome was to increase the availability of MP to the small intestine, not only from the less degradable soybean meal, but also from the increased microbial protein produced in the rumen, as well as the extra energy obtained in the process of fermentation. This trial also showed that, during the dry season, infection with GIN is less important than under-nourishment as a constraint to goat production in central Yucatan.

3.2.3. Long-term effect of supplementary feeding

Recent browsing trials had investigated the existence of “carry-over” effects of supplementary feeding on resilience and resistance against GIN infection from one season to the next. Recent evidences in sheep have suggested that short periods of enhanced post-weaning nutrition can have long-term benefits maintaining higher rates of live-weight gain and lower faecal egg counts (FECs) (Datta et al., 1999). Evidences of such carry-over effects were suggested in a trial with Criollo kids where kids weaned at higher live-weight had lower FECs compared to those weaned at lower live-weight (Santamaría-Colonia et al., 1995). However, results from the wet season trials described above did not show any indication of long-term effect of supplementary feeding. So far, field studies tested the effect of supplementary feeding on resilience and resistance of kids against GIN over periods of 5–7 months, either in the dry or wet seasons. Therefore, the question of “When is it best to offer supplements?” had not been addressed.

For that purpose, Aguilar-Caballero et al. (2002, 2003) designed two field trials aiming to evaluate the effect of short term (dry or wet season) and long term (dry and wet seasons) supplementary feeding (100 g/day, 26:74 soybean/sorghum meal) on the resilience and resistance of Criollo kids to GIN under browsing conditions. In their first trial, Aguilar-Caballero et al. (2002) showed that dry season supplementation did induce a carry-over effect into the wet season. This trial started when kids were weaned during the dry season and finished at the end of the wet season. The only supplementation strategy that gave a considerable increase in resilience, in terms of total live weight gain, was supplementation in both seasons. Moreover, this was proven to be economically feasible. Both short-term supplementation strategies (dry season only or wet season only) also improved resilience of kids but were significantly less efficient. A reduced excretion of nematode eggs was also associated with supplementation.

A second trial aimed at evaluating the effect of wet season supplementation and its possible carry-over effect into the dry season compared to continuous supplementation (Aguilar-Caballero et al., 2003). Again, continuous supplementation (wet and dry seasons) increased resilience of infected kids significantly compared to that of wet season only supplementation. Non-supplemented animals needed salvage treatment at the end of the wet season and did not finish the trial. Both supplementation strategies reduced FECs when compared to non-supplemented animals.

These field trials performed in growing goats showed that supplementary feeding of browsing kids can improve resilience but the effect on resistance was less evident. Clear improvement in resilience is a point that farmers can possibly appreciate without means of laboratory techniques. A promising area of research would thus be to use resilience parameters (growth, PCV, Famacha® indexes, body conditions scores) as selection criteria for future breeding stock in goats as previously suggested in sheep (Morris and Bisset, 1996; Bisset et al., 1996). The rationale behind this approach would be to select those animals that can perform better than the others under infection challenge in farm conditions, irrespective of the faecal egg counts or other parameters by measuring resistance.

4. Secondary metabolites, tannins and tanniferous plants

An increasing number of recent studies indicates that nutrition could affect parasitism not only through quantitative variations of different diet components but also by the presence of some qualitative compounds in plants consumed by herbivores, and particularly secondary metabolites (Athanasiadou et al., 2003). By referring to the feeding behaviour, goat is usually more qualified as a "browser" species compared to sheep, which is usually classified as a "grazer" one (Landau et al., 2000). These behavioural differences are also related to various physiological and metabolic adaptations of goat favouring the ingestion of large amounts of nutritional sources rich in potentially toxic secondary metabolites (Silanikove et al., 1996; Silanikove, 2000). However, despite these main differences between the two small ruminant species and the fact that goats, by comparison to sheep, appears better adapted to exploit rangeland and their vegetation rich in secondary compounds, studies on the interactions between secondary metabolites and nematode infections in goats remain less abundant.

Some indications have been acquired in natural infections under rangeland conditions. Several comparisons between goat breeds or between individuals, within one breed, have shown that when goats consumed a higher proportion of browse species, they were usually less infected with GIN than those exhibiting a grazing behaviour (Hoste et al., 2001). However, browsing conditions are usually associated not only with the presence of higher concentrations of secondary metabolites in the consumed plants but also with lower stocking rates and lower concentration of parasites on pastures as well as a lower probability of contamination of goats with the infective larvae. Due to these confounding factors, it appeared difficult to conclude specifically on the role of secondary compounds on infection through these observations. However, two types of observations appeared more conclusive, supporting the hypothesis of a possible regulation of nematode biology through secondary metabolites collected from the browse.

Firstly, the survey of individual profiles of egg excretion from 25 goats bred under rangeland conditions in two organic farms showed dramatic decreases in egg output in some individual goats, exceeding 95%

reduction. Due to the absence of AH treatment, it was postulated that such dramatic decreases in excretion could be related to the consumption of plants, whose components might affect some traits of life of the nematodes. The precise nature of the compounds responsible for these changes remains undetermined in this case. However, the role of tannin could be more specifically suspected from results acquired in another survey in Uganda. Two groups of Anglo-Nubian goats, bred under rangeland environment, received or not an inhibitor of tannins (PEG) for 6 months. This distribution induced a significant rise in parasite egg excretion suggesting a possible repressive role of tannin on worm fertility (Kabasa et al., 2000). Moreover, the consumption of PEG was also associated with a better growth of the animals.

Besides those observations from natural infections, results from in vivo studies performed in conditions of experimental infections tend to confirm the hypothesis of a possible impact of plant secondary metabolites on worms. Using quebracho, extracted from *Schinopsis* species, as a source of tannins, Paolini et al. (2003a, b) showed that the presence of 5 to 6% of tannins in the diet resulted in significant variations in the biology of nematode populations. Differences in the effect were noticed according to the parasitic stage submitted to the action of quebracho. The main consequence on populations of adult worms was a decrease in female fertility, whereas, concomitant distribution of quebracho with initial infection with larvae provoked severe reduction in the size of the worm populations (Paolini et al., 2003a, b). Some variations were also observed depending on the nematode species since the action of plant secondary compounds appeared more efficient against *T. colubriformis*, an intestinal species, than against the abomasal ones.

Other controlled studies performed under quite different conditions of parasite epidemiology and using various plants as source of tannins have completed these results acquired with quebracho and tend to confirm the possible action of tannins in infected goats. Min et al. (2003) showed recently that a short term consumption of *Sericea lespedeza* (*Lespedeza cuneata*), a forage containing 46 g of extractable tannins per kg DM, induced a rapid and significant reduction in trichostrongyle egg excretion compared to goats ingesting a control forage with only 6 g of extractable tannins per kg DM. In addition, it was also associated with 40% decrease in egg hatching. Similar negative effects on egg excretion, worm burden and parasite development have also been mentioned in Angora goats consuming the same source of tannins. In more temperate conditions, the distribution of sainfoin hay, a legume forage containing 3.2% of tannins, to naturally infected goats was associated with a persistent decrease in egg excretion, a lower contamination of pastures and a better resilience of adult goats (Paolini et al., 2003c). Last, the influence of the consumption of dried leaves from two Acacia species, *A. karoo* and *A. nilotica*, on goats experimentally infected with *H. contortus*, was examined (Kahiya et al., 2003). Significant effects on egg output and the number of worms were related exclusively to the consumption of *A. karoo* whose tannin content was much higher than *A. nilotica*.

Last, some in vitro studies, based on different bioassays, have been performed in order: (1) To identify the possible sources of tannin that can be used; (2) to examine the possible direct effects of plant components on the worms; (3) to underline and confirm the main implication of tannins in these effect by using of specific inhibitors. By this screening of bioactivity, extracts of different species of legume forages (*Lotus pedonculatus*, *L. corniculatus*, *Hedysarum coronarium*, *Onobrychis viciifoliae*) have been shown to represent potential sources of secondary compounds affecting different stages of the parasites (Athanasiadou et al., 2001; Molan et al., 2000a,b, 2002). These in vitro results tended also to confirm in vivo data acquired in sheep and, to a lesser extent, in goats. A recent in vitro study demonstrated that extracts from woody plants (*Rubus fructicosis*, *Quercus robur* and *Corylus avellana*), which are largely ingested by goats in rangeland conditions, also modified the biology of both third stage larvae and adult worms (Paolini et al., 2004).

In some of these studies (Molan et al., 2000a,b; Molan et al., 2002; Paolini et al., 2004), the role of tannins in the observed effects was ascertained through the use of PEG. Addition of this inhibitor of tannins to plant extracts correlated with the concomitant disappearance of negative effects on the nematodes. Moreover, direct effects of various oligomers composed of flavan-3-ols (the monomer unit of condensed tannins) were also demonstrated on the development and the viability of *Trichostrongylus* larvae (Molan et al., 2003).

Two main hypotheses have been proposed to explain the action of tanniferous plants on the parasitic nematodes. Tannins might interfere directly with the biology of various nematode stages. On the other hand, indirectly, tannins could also improve the host nutrition by protecting the diet proteins from ruminal degradations and this could modulate worm biology. Results from the in vitro studies as well as from some in vivo ones, which indicated a rapid response after tannin consumption (Min et al., 2003; Paolini et al., 2003c) are in favour of the direct hypothesis, i.e. potential anthelmintic properties associated with some plant components. Nevertheless, the indirect option cannot be discarded.

Regardless of the mechanisms of action of plant secondary compounds, practical options for agronomical applications of plants containing condensed tannins in grazing systems began to be explored. First results associated with the possibility to use either "anthelmintic" pastures seeded with tanniferous forage (Min and Hart, 2003; Min et al., 2003) or repeated distribution of hay (Paolini et al., 2003c; Shaik et al., 2004; Paolini et al., 2005) or last, possible integrated use of rangelands (Kahiya et al., 2003) have been obtained, underlying the fact that tanniferous plants offer solutions to reduce the use of chemotherapy in various epidemiological situations.

5. Conclusions

Overall, the results presented in this review illustrate how the improvement of host nutrition might contribute to the improvement of the goats' response against worm populations. Therefore, they tend to confirm the bulk of data acquired in sheep. The rationale for this manipulation of the host diet has been provided by the basic information accumulated on the host-parasite relationship in regard of pathophysiological processes. However, some new directions of research can also be identified. From the results acquired on browsing goats, it appears that attention should be given not only to the proteins of the diet but also to the energy/protein balance. Additionally, in many studies, it appeared that the response of goats to supplementary feeding was characterised first by an improvement in resilience, whereas, effects on host resistance were less evident. This can be attributed to the usually acknowledged lower aptitude of goats to develop an efficient immune response against gastro intestinal nematodes (Huntley et al., 1995). However, it might be worth to question and to explore the aptitude of goats to be really "more resilient" than sheep to nematode infections. Furthermore, some field observations suggest that the two small ruminant species might face the nematode infections with different strategies. Whereas, the regulation of infection based on immune mechanisms at infrapopulation levels appeared dominant in sheep, avoidance by feeding behaviour combined with better resilience might be the key processes in goats. Goats represent, therefore, a valuable model for basic research aiming at exploring the mechanisms of the host resilience and the complex interactions between parasitism and the feeding behaviour. Such basic information is clearly needed since this could have major applied implications for nutrition and health of ruminants as well as for the ecology of the grazing and browsing systems (Rook et al., 2004). For example, further work with browsing trials in the tropical areas of Mexico could help to avoid the destruction of the ecosystem by making sustainable use of plants in such land. By doing so, both biodiversity of plants and wildlife animals in such ecosystem will be preserved. In the future, these plants could provide resources not only for alternative anthelmintics (from plant secondary compounds) but also for other drugs with medical use.

Last, some results also suggest that another angle of perception could be worth to investigate basically. Pen studies with kids had shown that animals fed low protein (LP) diets paradoxically presented lower FEC than kids fed HP diets (Blackburn et al., 1991; Torres-Acosta, 1999). A similar situation was found in milking adult goats receiving protected methionine (Bouquet et al., 1997). A possible explanation for this phenomenon has been suggested by Blackburn et al. (1991): worms in environments with no nutritional restriction can develop to their full physiological and reproductive potential; on the other hand, LP diets may provide restricted nutrition for the worms too. As a consequence, they could be less able to fulfil their requirements for physiological and reproductive functions and to express fully their pathogenic potential. Basic studies to understand the nutritive requirements of nematodes are also expected to further improve our knowledge of the host parasite relationship.

From an applied point of view, trials both in temperate or tropical conditions showed that supplementation could not fully override the negative effects of GIN in kids or adult goats. This is especially obvious in the last 3 months of the wet season in tropical conditions (Torres-Acosta et al., 2000; Gutierrez Segura et al., 2002) but can also be observed in high producing dairy goats (Etter et al., 2000). The effects obtained by manipulation of nutrition are far from being negligible but they have to be combined with other alternative solutions, such as grazing management or the rationalised use of treatment. Such an integrated concept should achieve a better and more complete control of GIN infections. For example, further browsing trials with Criollo kids in wet season have investigated the combination of supplementary feeding with anthelmintics or with the use of copper oxide wire particles (COWP). Both strategies aimed at investigating the same principle: to control part of the worm populations at a critical period in order to permit a better use of the supplemented nutrients to improve resilience and resistance of Criollo kids. Results of the two assays indeed confirmed synergistic effects when combining solutions when compared to treatment or supplementation alone (Torres-Acosta et al., 2003; Vargas-Magaña et al., 2003). In temperate situations, this integrated approach of control received also more and more attention and is considered to represent a more sustainable approach by reducing the risk of adaptation of nematodes to one exclusive method (Barger, 1999).

Acknowledgements

The authors would like to thank the financial support from the European Union through the Contract Wormcops (no. QLK5-CT 2001-01843), which is part of a collaboration between Denmark, UK, The Netherlands, Sweden, Spain and France. The experimental work performed in Mexico was financially supported by Conacyt, Mexico (project 25019-B) and PRIORI-UADY, Mexico (project 02-011). In addition, Torres-Acosta, Aguilar-Caballero and Hoste also sincerely acknowledge the financial support from an ECOS-ANUIES project between Mexico and France.

References

Aguilar-Caballero, A.J., Torres-Acosta, J.F., Vera-Ayala, C.E., España-España, E., 2002. Long and short term supplementary feeding and the resilience of browsing Criollo goats to gastrointestinal nematodes. In: Proceedings of the International Conference:“Responding to the increasing global demand for animal products”, British Society of Animal Science, Mérida, México, November 2002, pp. 213–214.

Aguilar-Caballero, A.J., Torres-Acosta, J.F., Sandoval-Castro, C., Vargas-Magaña, J., May-Martínez, M. 2003. Effect of supplementation during wet season on resilience and resistance of Criollo kids naturally infected with GIN in two seasons (wet-dry) in Yucatan, México. Memorias de la XVIII Reunión Nacional sobre Caprinocultura (Electronic Proceedings), Puebla, México, October 2003, Health Section.

Athanasiadou, S., Kyriazakis, I., Jackson, F., 2003. Can plant secondary metabolites have a role in controlling gastro intestinal nematode parasitism in small ruminants? In: Proceedings of the VI International Symposium on the Nutrition of Herbivores, 19–24 October 2003, Merida, Mexico.

Athanasiadou, S., Kyriazakis, I., Jackson, F., Coop, R.L., 2001. Direct anthelmintic effects of condensed tannins towards different gastrointestinal nematodes of sheep in vitro and in vivo studies. Vet. Parasitol. 99, 205–219.

Barger, I.A., 1999. The role of epidemiological knowledge and grazing management for helminth control in small ruminants. Int. J. Parasitol. 29, 41–47.

Bisset, S.A., Morris, C.A., Squire, D.R., Hickey, S.M., 1996. Genetics of resilience to nematode parasites in young Romney sheep – use of weight gain under challenge to assess individual anthelmintic treatment. N.Z. J. Agric. Res. 39, 314–323.

Blackburn, H.D., Rocha, J.L., Figueiredo, E.P., Berne, M.E., Vieira, L.S., Cavalcante, A.R., Rosa, J.S., 1991. Interaction of parasitism and nutrition and their effects on production and clinical parameters in goats. Vet. Parasitol. 40, 99–112.

Blackburn, H.D., Rocha, J.L., Figueiredo, E.P., Berne, M.E., Vieira, L.S., Cavalcante, A.R., Rosa, J.S., 1992. Interaction of parasitism and nutrition in goats: effects on haematological parameters, correlations, and other statistical associations. Vet. Parasitol. 44, 183–197.

Boorman, K.N., 1980. Dietary constraint on nitrogen retention. In: Buttery, B.J., Lindsay, D.B. (Eds.), Protein Deposition in Animals. Butterworths, London, UK, pp. 147–166.

Bown, M.D., Poppi, D.P., Sykes, A.R., 1991. The effect of post ruminal infusion of protein or energy on the pathophysiology of *Trichostrongylus colubriformis* infection and body composition in lambs. Aust. J. Agric. 42, 253–267.

Bouquet, W., Hoste, H., Chartier, C., Coutineau, H., Koch, C., Pors, I., 1997. Effects of dietary supplementation with methionine in dairy goats infected with *Haemonchus contortus* and *Trichostrongylus colubriformis*. The British Society for Parasitology, University of Manchester, Institute of Science and Technology, p. 77.

Chartier, C., Hoste, H., 1994. Anthelmintic treatments against digestive-tract nematodes in grazing dairy goats with high or low levels of milk production. Vet. Res. 25, 450–457.

Chartier, C., Etter, E., Hoste, H., Pors, I., Mallereau, M.P., Broqua, C., Mallet, S., Koch, C., Masse, A., 2000. Effects of the initial level of milk production and of the dietary protein intake on the course of natural nematode infection in dairy goats. Vet. Parasitol. 92, 1–13.

Collier, R.J., Beede, D.K., 1985. Thermal stress as a factor associated with nutrient requirements and interrelationships. In: McDowell, R.L. (Ed.), Nutrition of Grazing Ruminants in Warm Climates. Academic Press, Orlando, FL, USA, pp. 59–71.

Coop, R.L., Holmes, P.H., 1996. Nutrition and parasite interaction. Int. J. Parasitol. 26, 951–962.

Coop, R.L., Kyriazakis, I., 1999. Nutrition-parasite interaction. Vet. Parasitol. 84, 187–204.

Coop, R.L., Kyriazakis, I., 2001. Influence of host nutrition on the development and consequences of nematode parasitism in ruminants. Trends Parasitol. 17, 325–330.

Datta, F.U., Nolan, J.V., Rowe, J.B., Gray, G.D., Crook, B.J., 1999. Long-term effects of short-term provision of protein-enriched diets on resistance to nematode infection, live weight gain and wool growth in sheep. Int. J. Parasitol. 29, 479–488.

Etter, E., Chartier, C., Hoste, H., Pors, I., Bouquet, W., Lefrileux, Y., Borgida, L.P., 1999. The influence of nutrition on the periparturient rise in faecal egg counts in dairy goats: results from a 2-year study. Rev. Méd. Vét. 150, 975–980.

Etter, E., Hoste, H., Chartier, C., Pors, I., Koch, C., Broqua, C., Coutineau, H., 2000. The effect of two levels of dietary protein on resistance and resilience of dairy goats experimentally infected with *Trichostrongylus colubriformis*: comparison between high and low producers. Vet. Res. 31, 247–258.

Etter, E., 2000. Contrôle intégré des strongyloses gastro intestinales en élevage caprin laitier: l'amélioration de la réponse de l'hôte par l'alimentation. Thèse de Doctorat d'Université INA PG.

Gutierrez Segura, I., Torres-Acosta, J.F., Aguilar-Caballero, A., Canul-Ku, I., Lozano-Argaez, I., Cob-Galera, L., 2002. Improving resilience and resistance against nematode infections through maize supplementation in Criollo kids. In: Proceedings of the International Conference: "Responding to the Increasing Global Demand for Animal Products", BSAS, ASAS, Mérida, Yucatán, México, Noviembre 2002, pp. 78–79.

Hoste, H., Leveque, H., Dorchies, P.H., 2001. Comparison of nematode infections of the gastrointestinal tract in Angora and dairy goats in a rangeland environment: relations with the feeding behaviour. Vet. Parasitol. 101, 127–135.

Hoste, H., Chartier, C., 1993. Comparison of the effects on milk production of concurrent infection with *Haemonchus contortus* and *Trichostrongylus colubriformis* in high- and low-producing dairy goats. Am. J. Vet. Res. 54, 1886–1893.

Hoste, H., Huby, F., Mallet, S., 1997. Strongyloses gastrointestinales des ruminants: conséquences physiopathologiques et mécanismes pathogéniques. Le Point Vétérinaire. 28, 53–59.

Hoste, H., Le Frileux, Y., Pommaret, A., Gruner, L., Van Quackebeke, E., Koch, C., 1999. Importance du parasitisme par des strongles gastrointestinaux chez les chèvres laitières dans le Sud Est de la France. INRA Prod. Anim. 12, 377–389.

Hoste, H., Le Frileux, Y., Goudeau, C., Chartier, C., Broqua, C., Pors, I., Bergeaud, J.P., 2002. Distribution and repeatability of nematode faecal egg counts in dairy goats: results from a farm survey and implications for worm control. Res. Vet. Sci. 72, 211–215.

Houdijk, J.G.M., Jessop, N.S., Kyriazakis, I., 2001. Nutrient partitioning between reproductive and immune functions in animals. Proc. Nutr. Soc. 60, 515–525.

Houdijk, J.G.M., Kyriazakis, I., Jackson, F., Huntley, J., Coop, R.L., 2003. Is the allocation of metabolisable protein prioritised to milk production rather than to immune function in *Teladorsagia circumcincta* infected lactating ewes? Int. J. Parasitol. 33, 327–338.

Huntley, J.F., Patterson, M., McKellar, A., Jackson, F., Stevenson, L.M., Coop, R.L., 1995. A comparison of the mast cell and eosinophil responses of sheep and goats to gastrointestinal nematode infections. Res. Vet. Sci. 58, 5–10.

Jackson, F., 2000. Options for the sustainable control of gastrointestinal nematode infections in goat production systems in Europe. In: Proceedings of the Seventh International Conference on Goats, Tours, France, 15–21 May 2000, pp. 789–792.

Jackson, F., Coop, R.L., 2000. The development of anthelmintic resistance in sheep nematodes. Parasitology 120, 95–107.

Kabasa, J.D., Opuda-Asibo, J., Ter Meulen, U., 2000. The effect of oral administration of polyethylene glycol on faecal helminth egg counts in pregnant goats grazed on browse containing condensed tannins. Trop. Anim. Health Prod. 32, 73–86.

Kahiya, C., Mukaratirwa, S., Thamsborg, S.M., 2003. Effects of *Acacia nilotica* and *A. karoo* diets on *Haemonchus contortus* infection in goats. Vet. Parasitol. 115, 265–274.

Knox, M., Steel, J., 1996. Nutritional enhancement of parasite control in small ruminant production systems in developing countries of Southeast Asia and the Pacific. Int. J. Parasitol. 26, 963–970.

Lallo, C.H.O., 1996. Feed intake and nitrogen utilisation by growing goats fed by-product based diets of different protein, and energy levels. Small Rum. Res. 22, 193–204.

Landau, S., Provenza, F., Silanikove, N., 2000. Feeding behaviour and utilization of vegetation by goats under extensive systems. In: Gruner, L., Chabert, Y. (Eds.), Proceedings of the VII International Conference on Goats (Tome I). Tours 15–18 May 2000, Poitiers 19–21 May 2000, pp. 47–52.

Lu, C.D., Potchoiba, M.J., 1990. Feed intake and weight gain of growing goats feed diets of various energy and protein levels. J. Anim. Sci. 68, 1751–1759.

Min, B.R., Hart, S.P., 2003. Tannins for suppression of internal parasites. J. Anim. Sci. 81 (Suppl. 2), E102–E109.

Min, B.R., Pomroy, W.E., Hart, S.P., Sahlu, T., 2003. The effect of short-term consumption of a forage containing condensed tannins on gastro-intestinal nematode parasite infections in grazing whether goats. Small Rum. Res. 51, 279–283.

Molan, A.L., Waghorn, G.C., Min, B.R., McNabb, W.C., 2000a. The effect of condensed tannins from seven herbages on *Trichostrongylus colubriformis* larval migration in vitro. Folia Parasitol. 47, 39–44.

Molan, A.L., Alexander, R.A., Brookes, I.M., Mc Nabb, W.C., 2000b. Effect of an extract from Sulla (*Hedysarum coronarium*) containing condensed tannins on the migration of three sheep gastrointestinal nematodes in vitro. Proc. N.Z. Soc. Anim. Prod. 60, 21–25.

Molan, A.L., Waghorn, G.C., McNabb, W.C., 2002. Effect of condensed tannins on egg hatching and larval development of

Trichostrongylus colubriformis in vitro. Vet. Rec. 150, 65–69.

Molan, A.L., Meagher, L.P., Spencer, P.A., Sivakumaran, S., 2003. Effect of flavan-3-ol on in vitro egg hatching, larval development and viability of infective larvae of *Trichostrongylus colubriformis*. Int. J. Parasitol. 33, 1691–1698.

Morris, C.A., Bisset, S.A., 1996. Progress on genetic studies of resilience to nematode parasites in sheep. Proc. N.Z. Soc. Anim. Prod. 56, 91–93.

Paolini, V., De La Farge, F., Prevot, F., Dorchies, Ph., Hoste, H., 2005. Effects of the repeated distribution of sainfoin hay on the resistance and the resilience of goats naturally infected with gastrointestinal nematodes. Vet. Parasitol. 127, 277–283.

Paolini, V., Frayssines, A., De La Farge, F., Dorchies, P.H., Hoste, H., 2003a. Efficacy of condensed tannins on established populations and on incoming larvae of *Trichostrongylus colubriformis* and *Teladorsagia circumcincta* in goats. Vet. Res. 34, 331–339.

Paolini, V., Bergeaud, J.P., Grisez, C., Prevot, F., Dorchies, P.H., Hoste, H., 2003b. Effects of condensed tannins on goats experimentally infected with *Haemonchus contortus*. Vet. Parasitol. 113, 253–261.

Paolini, V., Dorchies, P.H., Hoste, H., 2003c. Effects of sainfoin hay on gastrointestinal nematode infections in goats. Vet. Rec. 152, 600–601.

Paolini, V., Fouraste, I., Hoste, H., 2004. In vitro effects of three woody plant and sainfoin extract on third-stage larvae and adult worms of three gastrointestinal nematodes. Parasitology 129, 69–77.

Rios, G., Riley, J., 1985. Estudios preliminares sobre la produccion caprina con dietas a base de ramoneo en monte bajo en la zona henequenera de Yucatan. 1. Seleccion y valor nutritivo de plants nativas. Trop. Anim. Prod. 10, 1–11.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., Wallis DeVries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biol. Conserv. 119, 137–150.

Santamaría-Colonia, N., Torres Acosta, J.F., Rodriguez-Vivas, R.L., 1995. Efecto del peso al destete sobre el parasitismo gastrointestinal de cabritos en clima tropical. Rev. Bioméd. 6, 143–150.

Shaik, S.A., Terrill, T.H., Miller, J.E., Kouakou, B., Kannan, G., Kallu, R.K., Mosjidis, J.A., 2004. Effects of feeding *Sericea lespedeza* hay to goats infected with *Haemonchus contortus*. S. Afr. J. Anim. Sci. 34, 234–237.

Silanikove, N., Gilboa, N., Perevolotsky, A., Nitsan, Z., 1996. Goats fed tannin-containing leaves do not exhibit toxic syndromes. Small Rum. Res. 21, 195–201.

Silanikove, N., 2000. The physiological basis of adaptation in goats to harsh environments. Small Rum. Res. 35, 181–193.

Singh, R., Knox, M.R., Leng, R.A., Nolan, J.V., 1995. Aspects of parasite management in goats. In: Program and abstract handbook of a conference held at the University of New England on Novel Approaches to the control of Helminth parasites of livestock, Armidale, Australia, April 1995.

Torres-Acosta, J.F.J., 1999. Supplementary feeding and the control of gastro intestinal nematodes of goats in Yucatan Mexico PhD Thesis. Royal Veterinary College, University of London.

Torres-Acosta, J.F.J., Jacobs, D.E., Aguilar-Caballero, A.J., 2000. Effect of supplementary feeding on the resilience of Criollo kids browsing under tropical condition. Round table 6. Integrated control of nematode parasites. In: Proceedings of the Seventh International Conference on Goats, 14–20 May 2000, Tours, France, p. 807.

Torres-Acosta, J.F.J., Aguilar-Caballero, A., Canul-Ku, H.L., Cob-Galera, L., Vargas-Magaña, J., 2003. Supplementation and/or single anthelmintic (AH) treatment of browsing kids naturally infected with gastrointestinal nematodes (GIN) during the wet season in tropical México. In: Proceedings of the 19th International Conference of the WAAVP, New Orleans, LO, USA, p. 191.

Van Houtert, M.F.J., Sykes, A.R., 1996. Implications of nutrition for the ability to withstand gastrointestinal nematode infections. Int. J. Parasitol. 26, 1151–1168.

Van Houtert, M.F.J., Barger, I.A., Steel, J.W., 1996. Supplementary feeding and gastrointestinal nematode parasitism in young grazing sheep. Proc N.Z. Soc. Anim. Prod 56, 94–98.

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant, 2nd ed. Cornell University Press, Ithaca, N.Y., USA.

Vargas-Magaña, J.J., Torres-Acosta, J.F.J., Aguilar-Caballero, A.J., Canul-Ku, H.L., Cob-Galera, L., May-Martinez, M., 2003. Uso de la suplementacion y las agujas de cobre en el control de nematodos gastrointestinales de cabritos criollos. XVIII Reunion Nacional sobre Caprinocultura 8–10 de Octobre (Electronic Proceedings), Puebla, Mexcio, Health Section.

Waghorn, G.C., McNabb, W.C., 2003. Consequences of plant phenolic compounds for productivity and health of ruminants. Proc. Nutr. Soc. 62, 383–392.

Waller, P.J., 1999. International approaches to the concept of integrated control of nematode parasites of livestock. Int. J. Parasitol. 29, 155–164.