

GASTROINTESTINAL NEMATODE INFECTIONS IN GRAZING DOMESTIC RUMINANTS

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Abstract

World wide gastrointestinal nematode infections impair production of ruminants. Particularly in small ruminants control of these infections is seriously hampered by the development of resistance of the parasites against anthelmintic drugs. This implies that alternative control measures have to be implemented in order to maintain a sustainable ruminant industry. In this paper the various possibilities to achieve this are briefly discussed. The possibilities discussed include grazing management, vaccination, selective breeding, biological control, nutrition and the use of bioactive forages such as for instance plants containing condensed tannins. At the end it is concluded that combinations of these options should preferably be used in addition to a more selective way of anthelmintic usage in order to maintain a sustainable ruminant industry.

Keywords: Gastrointestinal nematodes, cattle, sheep, epidemiology, control

Introduction

The most important internal parasites of ruminants are the trichostrongylids, nematodes from the abomasum or the small intestine with a direct life cycle. Ruminants are infected by ingestion of the infective third stage larvae (L3). Depending on species development to the adult stage occurs either in the abomasum or in the small intestine after two moults. For most species development to the adult stage takes between 2 and 3 weeks. Development may also be interrupted at a specific parasitic stage, usually the early fourth stage (EL4). This 'inhibited' or 'arrested' development or 'hypobiosis' is a complex phenomenon. In a number of species, but particularly in *Haemonchus*, it represents a seasonal phenomenon, enabling the parasite to survive unfavourable conditions such as winter or a dry season. However, inhibited development may also be associated with host resistance (Michel, 1974; Eysker, 1993). Adult worms produce eggs that are passed to pasture in the faeces. Under favourable conditions the eggs will hatch and the first and second stage larvae feed on bacteria in the faeces until finally the infective third stage (L3) is reached. This development to L3 is temperature dependent and may be as rapidly as 3 days under tropical conditions (Sani et al., 1995). To become available for the host the L3 has to reach the herbage. This is a separate step and the faeces can act as a reservoir of L3. Moist conditions are needed for this process. Not only development and 'translation' to the herbage depend on the weather conditions but also survival. In general warm and moist temperatures are favourable for a rapid development, whereas cool and moist conditions are favourable for survival (Michel, 1969; 1976).

Parasitic gastroenteritis (pge) mainly occurs in young ruminants. However, production losses also occur later. In cattle in The Netherlands a reduction in milk yield is for instance by far the most important economical aspect of pge (Ploeger, 1989). Nematode infections in cattle result in high production losses through poor weight gain and reduced milk yield but

mortality rates are usually low. In contrast high mortality can occur in goats and sheep, particularly in *Haemonchus contortus* endemic regions (Barger, 1993).

Nematode control has to be based on the epidemiological pattern of the important nematode species. It is necessary to know the annual pattern of these species under the local management conditions before rational control measures can be designed. This implies several years of epidemiological studies before measures can be implemented (Hansen and Perry, 1994).

The nematode species present, their annual population dynamics and their importance for animal production mainly depend on the climate and on grazing management. It is impossible to avoid production losses without applying nematode control, particularly under intensive grazing conditions. So far nematode control mainly depends on the application of anthelmintics. Particularly in small ruminant parasites this has resulted in the emergence of anthelmintic resistance as a rapidly increasing problem (Waller, 1997). In some areas, particularly in the major sheep regions in the southern hemisphere including Southern Latin America, nematode populations resistant against all groups of anthelmintics are becoming more and more prevalent, endangering a sustainable small ruminant industry (van Wyk, 1990; Jackson et al., 1992; Eddi et al., 1996; Echevarria et al., 1996; Maciel et al., 1996; Nari et al., 1996; Waller, 1997). In cattle parasites anthelmintic resistance starts to emerge as a problem, particularly in New Zealand (McKenna, 1991; 1996; Vermunt et al., 1995; Watson et al., 1995). This already includes multiresistance of *Cooperia* against benzimidazoles and ivermectin/moxidectin (Vermunt et al., 1995; Watson et al., 1995). Ivermectin resistance in *Cooperia oncophora* has also been observed in the UK (Coles et al., 1998). Although, *Cooperia* spp are not considered to be major pathogens in cattle cases of anthelmintic resistance can be associated with poor performance of calves (Vermunt et al., 1995; Coles et al., 1998). Therefore, a major challenge for parasitologists, nutritionists, grassland scientists and veterinarians in the future will be to develop sustainable alternative nematode control strategies. The need for this is enhanced by the fact that it is unlikely that new classes of anthelmintics will become available during the next decade. Alternatives include avoiding high pasture infectivity level such as in evasive grazing systems, aiming at increasing the ability of the host's ability to cope with infection (vaccination, selective breeding, improved nutrition) and aiming at alternative methods to kill the parasites, such as for instance mowing and the use of nematophagous fungi. Some of these alternatives will be discussed with emphasis on grazing management.

Grazing Management

The use of grazing management for parasite control is only possible when suitable data are available on transmission patterns. In particular it is important to know how long a 'clean' pasture can be grazed before high pasture infectivity levels develop and how long infective larvae survive on pasture. This mainly depends on the local weather conditions and data relevant for one area cannot be used for other regions. Different options of grazing management are possible.

Evasive Grazing

In the Netherlands there is a long tradition of recommending evasive moves of calves to mown pastures every 2-3 weeks (Oostendorp and Harmsen, 1968). Although most farmers cannot maintain this strategy throughout the first grazing season they have appreciated the advantages of it. Therefore, approximately 70% of Dutch dairy farmers start the first grazing season by turning out their calves on mown pasture after the middle of May. Considering that

pasture infectivity decreases rapidly in spring and that mowing adds to this decrease (Borgsteede, 1977), this implies a much better start of the grazing season than in other countries in Western Europe. Recently Eysker et al. (1998b) demonstrated that high pasture infectivity levels will not develop in The Netherlands until infected calves have been grazed for at least four weeks. This longer period compared to the 2-3 weeks of Oostendorp and Harmsen (1968) implies a higher feasibility of the use of evasive grazing throughout the grazing season. A flow scheme that integrates evasive grazing with other options for nematode control is now used in the Netherlands to determine at farm level which control measures are needed (National Working Group Endo- and Ectoparasites, 2000). Probably the information on evasive grazing in the Netherlands is also relevant for other areas in Northwest Europe like Scandinavia and the UK. However, a safe grazing period of 4 weeks may not be valid for Southern Germany and France, considering the slightly higher summer temperatures. That a safe grazing period for cattle can be extended to at least four weeks in the Netherlands does not imply that such period is also safe for sheep. In a preliminary study on the use of a 4-week interval in sheep 7 out of 13 lambs had to be treated with an anthelmintic in order to prevent mortality to haemonchosis (C. Vergouw and M. Eysker, unpublished results 1999).

Another example for the use of evasive grazing is on the control of haemonchosis in small ruminants in the wet tropics. In Fiji high pasture infectivity on goat pastures develops within a week but the large majority of the larvae dies within one or two months (Barger et al., 1994). This was used in a rotational grazing system using 10 paddocks that were grazed for 3.5 days and then spelled for 31.5 days. However, this is not necessarily valid in other areas in the wet tropics because development and survival rates of infective larvae may vary. In Malaysia for instance development of L3 of *Haemonchus contortus* was observed in 3-3.5 days on open pastures and of 5 days under rubber trees, whereas pasture infectivity levels decreased below detectable levels in 5-6 weeks on open and 6-7 weeks under shaded conditions (Sani et al., 1995). In conjunction with this strategy for the wet tropics a warning against rotational grazing as control measure for pge should be given. Only when, as in the case of *Haemonchus* in the tropics, pasture infectivity decreases rapidly, rotational grazing is a suitable option. In temperate regions it usually takes more than a grazing season before a decrease in pasture infectivity to safe levels can be expected.

Mowing

As mentioned before the system of Oostendorp and Harmsen (1968) was based on the consequent moves of calves to mown pastures every 2-3 weeks. This suggests an effect of mowing on pasture infectivity. The explanation of this effect could be i) a direct removal of larvae with the herbage and/or ii) a higher exposure of preparasitic stages to adverse conditions, such as ultraviolet light, dry conditions and hot conditions. Studies by Borgsteede (1977) clearly demonstrated an effect of mowing at the beginning of the grazing season, because mean faecal egg counts were lower in calf herds turned out at the same time on a mown than a non-mown pasture. However, data on an effect of mowing during the grazing season were not available, although the recommendation of Oostendorp and Harmsen (1968) also implied that calves could return to mown pastures grazed earlier in the grazing season. Preliminary studies carried out in Utrecht demonstrate that indeed mowing during the grazing season results in a reduction of pasture infectivity levels of 55 to 80% for *Ostertagia ostertagi* and *Cooperia oncophora* (C. Vergouw and M. Eysker, unpublished results 1999). Although such decrease is significant it is possibly not sufficient. Nansen et al. (1995) working on the effect of biological control through the nematode trapping fungus *Duddingtonia flagrans* indicated that the reduction of pasture infectivity should be well over 90%. Nevertheless, it is

obvious that there is a substantial effect of mowing that should be quantified better, not only under temperate, but also under tropical conditions.

Alternate grazing

Alternate or mixed grazing of different host species can be used as control measure against parasitic gastroenteritis. Mixed grazing represents a dilutive strategy and will be discussed later, whereas alternate grazing is in fact a form of evasive grazing. Both methods are only effective if the nematode species of the different domestic ruminants are host specific. This is partially true. Sheep and goats share their nematode species but in cattle other species are found.

The degree of host specificity varies between species. In the temperate region sheep and goats are virtually refractory for *Ostertagia ostertagi*, by far the most important cattle nematode, while *Teladorsagia (Ostertagia) circumcincta*, of sheep/goats does not establish well in cattle (Michel, 1976; Eysker and Jansen, 1982).

In the (sub)tropics *Haemonchus* spp are more important, predominantly *Haemonchus placei* in cattle and *H. contortus* in small ruminants. The latter species also causes serious problems in small ruminants in temperate regions such as The Netherlands. Cross transmission of these species to the alternate host can occur but usually does not lead to major production losses, particularly not in cattle infected with *H. contortus*. However, this may be different in some regions, such as The Gambia, where cattle are claimed to be infected with *H. contortus* and not *H. placei* (Kaufmann and Pfister, 1990; Zinnstag et al., 1997; 2000). When this is indeed true, transmission of *Haemonchus* infection from cattle to small ruminants may be more important than elsewhere.

Cross transmission from cattle to small ruminants and/or vice versa may easily occur for *Cooperia* spp., *Ostertagia leptospicularis*, *Nematodirus battus* and *Trichostrongylus axei*. Cross transmission of *Cooperia* infections will not have a major impact on production of the alternate host. On the other hand cross transmission implies that alternate grazing programs may be less effective than expected. However, despite high faecal egg counts for *C. oncophora* in sheep in an annual alternate grazing schedule, transmission of this parasite to its natural bovine host in the next year was not prominent (Bairden et al., 1995).

O. leptospicularis is a parasite from deer with a low host specificity. While cross transmission of the 'sheep' and 'cattle' Ostertagiinae failed in an alternate grazing experiment in the Netherlands, *O. leptospicularis* could build up to substantial levels in sheep (Eysker and Jansen, 1982). Considering that this species may be more pathogenic in cattle than *O. ostertagi* (Al Saqur et al., 1983; 1984) this may be of some relevance for the temperate region.

In Scotland outbreaks of nematodiosis, caused by *Nematodirus battus*, have been observed despite alternate grazing of sheep and calves on an annual basis (Bairden and Armour, 1987; Armour et al., 1988; Coop et al., 1988). Considering the occurrence of such outbreaks it is probably better to recommend a three year cycle of alternate grazing (cattle-sheep-rest) than a two-year cycle (cattle-sheep) in the UK. However, this system implies a set stocked scheme within a grazing season (Bairden et al., 1995). Considering the build up of high infections following very low initial infections (Eysker et al., 1998c; 2000) it is not surprising that such a set stocked scheme may occasionally fail, despite a start with low initial infections.

Trichostrongylus axei establishes well in sheep and cattle and even in equids. However, although cross infection occurs and clinical problems have been described (Abbott and McFarland, 1991) it usually does not lead to major production losses.

This relative host specificity of the most important nematodes of cattle on one, and of small ruminants on the other hand may be exploited in various alternate or mixed grazing systems. Such schemes may not always result in a reduction in faecal egg counts. *H. contortus* infections in calves and *C. oncophora* infections in lambs may result in high faecal egg counts without any clinical implications (Eysker and Jansen, 1982).

Dilusive strategies

As mentioned above mixed grazing can be considered as a dilusive strategy for the control of nematode infections. This, however, does not necessarily imply reduced infections and increased production. Jordan et al. (1988) observed that mixed grazing of beef cattle and sheep resulted in reduced infections and higher weight gains than in single species grazing in lambs but not in calves. Mixed grazing with pigs has recently been investigated as a control measure of pge in calves in an organic farming setting (Thamsborg et al., 1999). The results look promising as a reduction in nematode infections in calves was observed. An important reason for this reduction is that pigs graze the heavily contaminated areas around faecal pats and the characteristic ‘bushes’ on cattle pastures don’t develop. Obviously pigs should have nose rings in order to prevent rooting.

Compared with calves of dairy cattle the cow-suckling calf situation also represents a form of dilusive grazing considering that faecal egg output in cows is low. Therefore, clinical pge is rare in suckling calves and major production losses in beef calves usually start after weaning.

A dilusive system developed in the UK is the leader-follower system (Leaver, 1970). This implies a rotational grazing system of a group of calves and a group of older animals with a higher grass consumption. The calves are the leaders and the older cattle the followers. Calves are moved to the next plot and the older animals to the ‘calf’ plot when the older animals have finished the grass on their plot. The consequence is that calves always have access to a good quality of grass and they are not forced to graze the heavily contaminated bushes surrounding faecal pats. A drawback of this system is that the older animals may be exposed to high pasture infectivity and subsequently may build up high worm burdens (See Armour in Barger, 1997, p. 505).

Dose and Move

The dose and move system for the prevention of pge in dairy calves has been recommended for a long time (Michel 1969; 1976). Michel started to recommend this after he had demonstrated that it takes until July before high pasture infectivity will develop on calf pastures. A move in July to aftermath combined with anthelmintic treatment will result in evasion of high pasture infectivity levels and will prevent immediate contamination of the ‘clean’ second pasture. During the last two decades the push of drug companies towards using early season anthelmintic treatment schemes for the control of pge in calves in Europe has decreased the use of this system. Nevertheless, Nansen et al. (1989) claimed that dose and move is the best system for control of pge in Denmark. Furthermore, a recent series of experiments in The Netherlands confirmed that it is a highly effective system (Eysker et al., 1998a). Care should be taken to avoid early outbreaks caused by immediate exposure to high overwintered pasture infectivity levels (Tharaldsen and Helle, 1984; Jacobs et al., 1987; Nansen et al., 1989). This can easily be achieved by avoiding a very early turnout on pasture heavily contaminated in the previous year, although this may be less easy in Northern Scandinavia (Tharaldsen and Helle, 1984).

In sheep anthelmintic treatment combined with a move to clean pasture has been recommended at weaning (Boag and Thomas, 1973). Furthermore, the dose and move strategy should be adapted to the local situation. In almost any setting where the population dynamical patterns of the major nematode species has been sorted out it will be possible to reduce the number of anthelmintic treatments needed by combining anthelmintic treatments with moves to clean pasture. In New South Wales Smeal et al. (1980) recommended a dose and move system with the aim to avoid the late winter early spring peak of pasture infectivity on calf pastures.

A comment that should be made on the dose and move system is that although it is a method that will reduce the numbers of anthelmintic treatments it does not necessarily imply a low selection pressure for anthelmintic resistance. The fact that treatment is combined with a move to clean pasture implies that survivors of the treatment are the contaminators of the clean pasture.

Vaccination

The development of vaccines against nematodes in general has not been successful. Attenuated vaccines against the lungworms *Dictyocaulus viviparus* in cattle and *D. filaria* in sheep are commercially available. A similar vaccine was developed for dog hookworms but this product failed commercially (Miller, 1971). Development of attenuated vaccines for gastrointestinal nematodes in ruminants has failed. In sheep the main problem is the unresponsiveness of young lambs; they fail to develop protective immunity against the most important nematodes during the first 5-6 months of their life. In cattle development of immunity against *O. ostertagi* infections takes much more time than against lungworm. A problem for developing vaccines is also that producers would aim for a vaccine effective against the whole range of important species. For the moment this is far away.

Developing a successful vaccine requires identification of protective native proteins. Then, these have to be expressed in a suitable expression system that allows appropriate folding and glycosilation of the recombinant protein. The selection of the right expression system often will be a matter of trial and error, but is possible for parasites as it has been done for the tick *Boophilus microplus* (Willadsen et al., 1995). It is difficult to select the suitable protective proteins. It is even more difficult when a candidate recombinant protein appears to be one of a series of related proteins expressed by a gene family. Even when the combined native proteins are protective this is not necessarily true for all the related proteins in it. Furthermore, not all of them may be recognised by all hosts.

The most promising vaccine candidates are the so-called 'concealed' or 'hidden' antigens identified in *Haemonchus contortus*. These are proteins from the surface of the epithelium of the parasite's digestive tract. Therefore, the host is normally not exposed to them and does not recognise them. The mode of action of the vaccine is that the antibodies produced in the host react with the gut proteins in the blood sucking nematode and damage the worm. Thus, the protection has nothing to do with a build up of immunity of the host against the parasite. Therefore, young lambs that cannot yet build up a natural immunity against this parasite, can be protected with a vaccine based on such hidden antigens. So far this strategy seems to work primarily in blood sucking parasites (Smith et al., 1994; Munn, 1997; Newton, 1995). However, some success also has been achieved with related proteins of *Teladorsagia circumcincta* (Smith, 1999).

Other potential candidate proteins include surface proteins and excretory/secretory products of the nematodes. These are often proteases or other enzymes (Knox et al., 1993; Schallig et al., 1994). Although protection has been recorded with some of these when used as native proteins, there is no record of them being effective as recombinant proteins. Moreover,

it seems unlikely that these proteins will protect young lambs or calves, considering that animals are naturally exposed to these proteins and are not able to develop immunity against them.

A possible problem for development of a vaccine against gastrointestinal nematodes is that even in very good trials an efficacy of 80-90% is rarely observed. Such efficacy would be unacceptable for any bacterial or viral vaccine and also looks poor compared to the efficacy of anthelmintic drugs. This may hamper commercial development of such vaccine candidates. However, Barnes et al. (1995) examined the efficacy needed for a vaccine on sheep production using a simulation model. Their results indicate that an efficacy of 60% in 80% of the flock would be enough. Thus, vaccine development does not have to aim for a virtually 100% efficacy. However, a lot of explanation may be needed to the users when a vaccine with a relatively low efficacy would become commercially available.

Selective breeding

Between breed and within breed variation in the level of 'resistance' and 'resilience' against worm infections can be observed in domestic ruminants. Resistance should then be defined as 'initiation and maintenance of responses provoked in the host to suppress the establishment of parasites and/or eliminate the parasite load' and resilience as 'the ability of the host to maintain a relatively undepressed production level under parasite challenge' (Baker, 1995, 1998). Breeds of sheep that are well known to have a high resistance and/or resilience to nematodes, in particular *H. contortus* include among others the Red Maasai and Djallonke from Africa, the St. Croix and Barbados Blackbelly from the Caribbean, the Florida Native and Louisiana Native from the US. Goats are usually more susceptible to nematode infections than sheep but again some indigenous African breeds, such as the West African Dwarf and the Small East African goats seem to be more resistant (Baker, 1995). It is interesting to note that this relative resistance and resilience of the Djallonke sheep and the West African Dwarf goats coincides with trypanotolerance in these breeds (Goossens et al., 1997; Osaer et al., 2000), thus enabling the host to cope with the two most important causes of blood loss in their environment. The trypanotolerant N'Dama breed also seems relatively resistant against *Haemonchus* infections (Kaufmann et al., 1992). In general these breeds are small and not highly productive. Therefore, studies are carried out at ILRI whether marker assisted breeding programmes can be used to improve production of sheep with maintenance of the resistance in the Red Maasai (van Arendonk et al., 1999).

Within breeds skewed distributions of nematodes and faecal egg counts are also seen. In part this depends on the reproductive status and age. Young animals still have to build up immunity and during late pregnancy and lactation ewes, goats and cows show a periparturient rise in faecal worm egg counts, as a result a relaxation of immunity. However, part of the variation represents differences in ability between animals to cope with nematode infections. These have been shown to be highly heritable (Albers, 1981; Kloosterman et al., 1992; Gray, 1997).

Programmes are implemented in Australia (Anon, 1994) and New Zealand (McEwan et al., 1995) to breed against susceptibility in sheep. Faecal egg counts are the most important trait to select animals in these programmes. Basically, rams with high faecal egg counts in comparison with flock members of the same cohort are eliminated for further breeding.

This within-breed variation in cattle has not yet been exploited for selection against susceptibility for nematode infections. Considering that artificial breeding and embryo transfer technology is widely used in breeding programmes in dairy cattle it may be feasible to include selection against susceptibility for worms. However, before that it would be necessary to link molecular markers to susceptibility for worms and elimination of this trait in

breeding programmes should neither interfere with important production parameters nor with resistance against other diseases.

Biological control

During the last decade the possible use of nematophagous fungi has been an important issue in veterinary parasitology (Grønvold et al., 1993; Larsen et al., 1997). The most successful concept was the use of the nematode trapping fungus *Duddingtonia flagrans* and field experiments have been carried out in many parts of the world (Fernandez et al., 1999; Larsen et al., 1997; Saumell et al., 1999; Waller et al., 1994). These studies demonstrated that *D. flagrans* can reduce transmission of gastrointestinal larvae by 60-90% under field conditions. However, to be effective the fungus has to be fed to the animals throughout the period that suppression of transmission is needed. This implies that the logistics to commercialise the use of nematophagous fungi are not easy to cope with. At first cheap methods of mass cultivation of a constant good quality of spores are required; spores should be able to survive during passage of the digestive tract and they should have good trapping characteristics. In addition the spores as well as the delivery device, supplementary feed or otherwise, should be available at low costs. Moreover, the efficacy is less than the use of anthelmintics and there is general consensus that it has to be used in conjunction with other methods of control (Larsen et al., 1997). Thus, despite the promising results it is not certain that biological control will be commercially available in the future.

Nutrition

A theoretical basis on the nutrition-parasite interaction has been given recently in the excellent review of Coop and Kyriazakis (1999). They view this interaction in a framework that accounts for the allocation of scarce nutrient resources, such as energy and protein, between the various competing body functions of the host. In growing animals they distinguish an 'acquisition phase of immunity' in the youngest age category and an 'expression phase' in older animals. As possible ordering of priorities (1 highest to 4 lowest) for these and for reproducing animals when partitioning a scarce food resource they indicate for animals in the acquisition phase: 1) maintenance of body protein, 2) acquisition of immunity, 3) protein gain, 4) maintenance and gain of body lipid; for animals in the expression phase: 1) maintenance of body protein, 2) protein gain, 3) expression of immunity, 4) maintenance and gain of body lipid and for reproducing animals: 1) maintenance of body protein, 2) reproductive effort (pregnancy/lactation), 3) expression of immunity, 4) maintenance of desired fatness (Coop and Kyriazakis, 1999). The indicated priorities indeed are based on a vast body of experiments on the effect of nutrition on performance of animals and severity of nematode infections. In principle it implies that maintenance of body fat has the lowest priority and the maintenance of body proteins, including repair, replacement and reaction to damaged tissue, has the highest priority.

An important aspect of the negative effect of nematode infections on productivity is that they generate a depression in appetite. This really depends on the presence of the worms because Kyriazakis et al. (1996) demonstrated that appetite returns to normal within days after anthelmintic treatment.

Host protein and energy nutrition can effect the expression of immunity of ruminants against gastrointestinal nematodes. Supplementation with a high protein diet can result in an earlier expulsion of worms (van Houtert et al., 1995) or a decrease of worm fecundity (Wallace et al., 1995). Also the periparturient rise in faecal egg counts can be explained by this nutritional hypothesis. Obviously, lactating animals are under great nutritional stress. The

relaxation of immunity appears to depend on the numbers of lambs (O'Sullivan and Donald, 1973; Donaldson et al., 1998) and termination of pregnancy or weaning of lambs leads to an immediate termination of the periparturient rise (Salisbury and Arundel, 1970; O'Sullivan and Donald, 1973).

Although it is obvious that a high quality diet should be given to ruminants to optimise productivity it is less easy to translate this into practical recommendations. It will be no problem to achieve this in the dairy industry in Europe and the US, but it is much more difficult in tropical regions with poor soils. Particularly, during the dry season it will be very hard to provide the animals with adequate feeding.

Condensed tannins

Recently it has been demonstrated that plants containing condensed tannins increase resilience of small ruminants against nematode infections (Niezen et al., 1995). It is not yet clear whether this is an anthelmintic effect or whether it involves other factors. The use of plants containing tannins for nematode control is only possible when these plants can maintain themselves on pastures with grazing ruminants. Furthermore, the tannins in the plant should have a chemical composition that is effective against nematodes and should not be too toxic for the host.

Integrated control

Nematode control in the future should be directed towards a sustainable animal husbandry that relies much less on anthelmintics. Probably it will include a combination of the large majority of the strategies discussed above, in conjunction with a far more selective use of anthelmintics. By itself each of these methods is usually not enough but in combination they will do the job. It should be clear though that optimising parasite control starts with a good assessment of the effects of grazing management, including feasible improvements in the use of pastures.

It has to be realised that each control measure has its own life span. Considering the genetic flexibility of the parasites as demonstrated by development of resistance against antiparasitic drugs, they may also be able to develop resistance against other strategies. Perhaps evasive grazing systems may result in selecting for nematode genotypes that either develop more rapidly, enabling infection before animals are moved or may result in genotypes that allow a longer survival (Barger, 1997). Considering the threat posed by anthelmintic resistance on survival of, in particular the small ruminant industry, it is necessary to maintain expertise on these parasites. Baseline data on the population dynamics of nematode infections and on the impact of control measures are still needed. Considering this need another threat for the development of sustainable parasite control is that nowadays applied clinical veterinary parasitologists are retiring, without being replaced.

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