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# Sustainable nematode parasite control strategies for ruminant livestock by grazing management and biological control☆

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**Abstract**

Internal parasitism constitutes one of the greatest disease problems in grazing livestock worldwide. Control of these parasites is now becoming a serious concern, particularly in the small ruminant industries, due to the widespread and rapid development of resistance to chemotherapy. The broad-spectrum drugs (anthelmintics) used in the control of nematode parasites fall into just three classes *viz.* the benzimidazoles, imidothiazoles and macrocyclic lactones. Resistance to all three drug classes now occurs in the major nematode parasites of sheep and goats throughout the world. This is largely the result of a more-or-less complete reliance on anthelmintics for worm control. By analogy then, any specific parasite control method may be unsustainable when used in isolation. The more choices and the greater variety of controls used in combination, rather than relying almost solely on anthelmintics, the longer effective worm control can be expected. Grazing management strategies and biological control offer two non-chemical methods of parasite control, which have proven effectiveness. These should form part of integrated nematode parasite control programmes for grazing livestock with the objective of maintaining long-term sustainability.


*Keywords:* Nematode parasites; Livestock; Grazing management; Biological control

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## 1. Introduction

In contrast to microbial infections, where replication of organisms occurs entirely within host, the important nematode parasites of livestock have an obligatory free-living stage on pasture. Thus pastures provide the link between the free-living and parasitic phases of gastrointestinal parasites of grazing livestock and every nematode parasite present within the host has been separately acquired by the ingestion of an infective larval stage from pasture.

Another important contrast between microbial and metazoan parasite infections is the time required for the completion of the within host phase of the life cycle — a matter of hours for microbes (bacteria and viruses), but several weeks for nematodes. A minimum, or threshold, level of antigenic information must be produced by nematode parasite burdens before immunological recognition and mobilization of host responses affecting nematode survival in the host occurs (Dineen et al., 1965). As a consequence, microbial infections characteristically induce prompt and aggressive immune reactions by the host, whereas nematodes induce varying forms of immunological tolerance to permit their longer survival (Dineen, 1963, 1978; Maizels and Lawrence, 1991). The development of immunity to helminth parasites is dependent of sufficient numbers being present in the host to exceed the required threshold, thus it generally develops slowly, is dependent upon a good nutritional state and is abrogated by any form of stress experienced by the animal. Consequently, parasites are ubiquitous wherever grazing livestock are kept and impose a constant and often high infectious pressure on animals (Waller, 1999).

Although there are many different species of nematode parasites that infect ruminant livestock, there are only relatively few parasite species that cause major problems, notably *Haemonchus*, *Ostertagia*/*Teladorsagia*, *Trichostrongylus*, *Nematodirus* and *Cooperia* spp. (Urquhart et al., 1996). However, nematode infections in grazing livestock are almost always a mixture of species. All have deleterious effects and collectively they lead to chronic ill-thrift. Economic evaluations consistently show that the major losses due to parasites are on animal production, rather than on mortality (Hawkins, 1993; McLeod, 1995; Perry and Randolph, 1999; Perry et al., 2002).

Conventional methods of controlling nematode parasites of grazing livestock have been with the use of synthetic chemotherapeutic drugs (anthelmintics). Largely because of the remarkable developments in these products in terms of efficacy, safety, spectrum of activity and remaining relatively inexpensive, livestock producers have relied almost exclusively on their use (Morley and Donald, 1980; Waller, 1993). However, the spectre of resistance to all the major groups of broad-spectrum anthelmintics now looms large in the control of nematode parasites, particularly for the small ruminant industry, throughout the world (for review see Waller, 1997).

In recent years there has been an increasing demand by consumers that agricultural products should be both “clean” and “green”. Impetus for “clean” livestock products has followed adverse publicity surrounding purported agro-chemical induced effects on human health, and the development of super-resistant human microbial pathogens, caused by the use of antibiotics in intensive livestock production systems. The threat of adverse effects on the environment from the use of any chemicals in agricultural production has also driven this agenda (Donald, 1994).

The term “green”, as it applies to livestock products, are those produced by animals raised under outdoor conditions, in contrast to those produced in intensive, “factory farming” systems. Ruminant livestock in Europe are now spending more time on pasture, due to both economic and animal welfare reasons, and with this is their greater exposure to pasture-borne parasites. This has been accompanied by the rapid increase in popularity of organic farming. Countries in Europe lead the world in the move towards organically produced livestock products (Thamsborg et al., 1999). For example in Sweden, there is an active government policy to foster organic farming and the country is aiming to have 20% of its agricultural commodities organically produced by 2005 (Dimander et al., 2003). Standards, which define organic production systems, specifically state that the prophylactic use of drugs, including of course anthelmintics, is prohibited.

Assessments of animal health issues associated with organic farming are often based on farmer’s perceptions, rather than detailed veterinary investigation (for review see Hovi et al., 2003). However, as stated above, the most profound effects of parasitism is on sub-clinical production loss (Hawkins, 1993; McLeod, 1995) and farmers – or their advisers – are unlikely be aware of this. A graphic example to illustrate this point comes from studies over several years in Sweden, where organically reared, but set-stocked, first-year grazing cattle showed weight gain penalties exceeding 60 kg at the end of the season due to parasites, although from their general appearance as well as faecal egg count monitoring throughout the year, worm infections would generally be considered to be low (Dimander et al., 2003). As a consequence, new and serious animal welfare issues are likely to emerge throughout Europe caused by distress suffered by animals due to uncontrolled parasite infections.

Therefore these two quite contrasting issues, namely anthelmintic resistance in conventional farming practice and the trend towards greater organic farming, have brought the matter of maintaining effective parasite control to the forefront of grazing livestock management enterprises throughout the world. Two important, non-chemical, means towards achieving this objective are through grazing management strategies and biological control.

## 2. Parasite control by grazing management

Environments favourable for the establishment and maintenance of improved pasture species also favour the development, survival and transmission of nematode parasites of ruminant livestock. The distribution and abundance of nematode parasites varies considerably within and between species, with the principle determinant being the prevailing weather conditions — most importantly rainfall and temperature. As a broad generalisation, *Haemonchus* and *Cooperia* spp. are most important in sub-tropical/tropical environments, *Ostertagia* and *Nematodirus* spp. in the temperate regions and *Trichostrongylus* spp. well represented throughout. Obviously, within regions the mix will vary and some other parasite species may well be more important locally.

The degree of nematode infection acquired by the grazing animal is determined by a number of factors, which are to some extent inter-related. These include the direct and indirect effect of seasonal conditions, which determine the availability of both infection and pasture, grazing behaviour, previous experience of infection and physiological state of the animal. The effects of parasite infection may be modified by nutrition but are nevertheless directly related to the number of parasites present, which since each worm must be separately ingested, broadly reflects the number of infective larvae on pasture. The impact of parasitism on pasture utilization is therefore influenced by the effects on the physiological and metabolic processes in the infected animals, and secondly by management decisions taken by farmers to reduce the degree of infection on pasture.

### 2.1. Grazing management strategies to control parasite infection

Michel (1985) classified grazing management strategies aimed at controlling nematode parasite infections in ruminant livestock as:

- *Preventive*: These are strategies that rely on putting worm-free animals onto a clean pasture, or by suppressing worm egg output by anthelmintic treatment in the early part of the grazing season until the initial population of infective larvae on pasture has declined to safe levels.
- *Evasive*: These strategies do not attempt to restrict contamination of the pasture with parasite eggs, but rely on movement of livestock to another pasture just before the larvae resulting from this contamination are likely to appear in significant numbers on the original pasture.
- *Diluting*: Strategies that exploit the concurrent grazing of susceptible animals with a greater population of animals with acquired natural resistance to parasites of the same livestock species (generally dry adult stock), or different livestock species, in order to reduce the herbage infestation resulting from their combined faecal output of worm eggs.

Up until relatively recently, the combination of anthelmintic treatment with all of these grazing management strategies was highly recommended. This was based on the sensible interpretation of drug efficacy *vis a vis* parasite epidemiology, whereby "clean animals go onto clean pasture". By doing so, re-infection rates are extremely low and the suppressive effect of anthelmintic treatment on nematode egg output is prolonged for several months, rather than for a few weeks as seen on contaminated pastures (Waller et al., 1995). Unfortunately, although such combination strategies were very highly effective at controlling parasite infections, they have also proved (at least in the sheep industry in Australia) to select potently for anthelmintic resistance (Besier, 1999). This is due to the fact that any parasites that survive anthelmintic treatment – although exceedingly few in the first instance – carry resistance genes. They have an enormous survival advantage, given that following a move to parasite-free pastures there will be very little pickup of nematode larvae that escaped anthelmintic selection, thus the resident worm populations will make a disproportionate contribution to the anthelmintic resistance status of forthcoming parasite generations (Barnes et al., 1995).

In the temperate regions of the world considerable benefits have been achieved in worm control for both sheep and cattle parasites by interchange grazing between these two species of livestock. Such grazing management strategies exploit host specificity, whereby parasite species that are pathogenic in one host species either do not infect the alternative host, or are less pathogenic and prolific. Typical procedures involve alternation of the separate host species at intervals from 2 to 6 months (Barger and Southcott, 1978; Donald et al., 1987), with anthelmintic usually, but not always given (Donald et al., 1987), at times of alternation. These management strategies proved to be very successful, with parasitism and production of young sheep given only one or two drenches annually being equivalent to that of suppressively treated (12–24 times/year) sheep over a 3 years period. However, there is a need for caution in relying heavily on sheep/cattle interchange grazing in the longer term, as there is some evidence that parasites primarily of cattle, may show increased ability to infect sheep and cause clinical disease (for review see Barger, 1997).

In comparison with the temperate regions of the world, there are relatively few examples of grazing management schemes in the tropics/sub-tropics, even though in this region their potential may be even greater. This is because, despite the fact that development of the free-living stages of parasites is generally faster and more successful than in the temperate regions, their longevity is much shorter. Studies in wet tropical climates showed that peak larval concentrations of *H. contortus* and *Trichostrongylus* spp. occurred on pasture about 1 week after contamination but fell to barely detectable levels within 4–6 weeks (Banks et al., 1990; Barger et al., 1994; Sani and Chandrawathani, 1996; Sani et al., 1996). A grazing system was developed to exploit these findings for the control of parasites in small ruminants. It consisted of 10 paddocks, easily, cheaply and effectively established by using solar powered fencing. Each paddock was grazed in sequence for 3.5 days then spelled for 31.5 days because parasite larvae die within this period. This grazing period had to be less than 1 week to prevent auto-infestation and 3.5 rather than 4 days was chosen so that the stock movements were made at the same times and the same days each week (Barger et al., 1994). Egg counts of goats which grazed in the rotational system were less than half those of similar goats that were set-stocked on an adjacent area. In addition, the set-stocked goats required nearly four times more anthelmintic treatments than the rotationally grazed animals, over the course of a year. But most dramatically, there were indications that it may have been possible to dispense with anthelmintic treatment entirely in the rotational grazing system.

These excellent examples of practical parasite control systems readily lend themselves to adoption in many areas throughout the tropics/sub-tropics. However, a cautionary note must be heeded for those designing schemes for environments, which are cooler and/or dryer than the above. Development and survival times of the free-living stages of these parasites are almost certain to be longer. Before launching into similar rotational grazing schemes, it is important to have a good understanding of the local ecology of the free-living stages.

Care must also be exercised in adopting breed interchange (sheep/cattle) schemes in the tropics and the sub-tropics. Similar benefits may result from alternate grazing, but the grazing intervals almost certainly need to be shorter. Furthermore, control of *H. contortus* may prove difficult. In the more temperate regions this species can cycle in calves, but they rapidly acquire natural immunity to become refractory to infection by 12 months of age (Southcott and Barger, 1975). In the tropics this age resistance is slower to develop, or may never occur. For example, in Paraguay there was no indication that cattle had acquired significant immunity to *H. contortus* after 2 years of grazing (Benitez-Usher et al., 1984).

### *2.2. The effect of stocking rate on parasite infection*

Increasing stocking rate must of course be accompanied by providing more feed to the animals for them to remain productive. In the conventional ruminant livestock systems, such as cattle, sheep and goat production, this is generally achieved by improving pasture production (better pasture plants), often providing fertilizer and additional watering (irrigation) to improve pasture growth. However, enhanced productivity of pasture following application of fertilizer often fails to improve overall animal production (Speedy, 1980), and a commonly held view is that increasing stocking rate leads to increasing levels of parasitism in grazing livestock. This has prompted a number of studies to investigate such a relationship, particularly with sheep in the temperate countries of the world, with mixed results. Although there was no positive correlation between stocking rate and parasitism in a number of investigations (Cameron and Gibbs, 1966; Downey and Conway, 1968; Spedding et al., 1964; Waller et al., 1987), these were based on assessments of performance in young lambs up to weaning or marketing at around 3–4 months of age when the effects of parasites would have been too early to have any marked effect. However, equally a number of studies have shown a direct relationship between increasing stocking rate and increasing parasitism of livestock (Beveridge et al., 1985; Brown et al., 1985; Downey, 1969; Southcott et al., 1967, 1970; Thamsborg et al., 1996; Zimmerman, 1965).

### *2.3. Direct effects of plants on parasite infection*

Anthelmintic medication has its origin in the use of plant preparations. These included various extracts from jallop, quassia, areca nut, cloves, aloes, garlic, cucurbit seeds, castor oil, male fern and chenopodium. In general, these were hazardous concoctions with low anthelmintic efficacy, especially in ruminant species, and they rapidly disappeared from veterinary use with the synthetic anthelmintic compounds (for review see Waller et al., 2001c).

Although there is a large and diverse range of herbal de-wormers used throughout the world, particularly in the Asian and African countries, generally there is a lack of scientific validation of the purported anthelmintic effects of these products. However, there is considerable and apparently expanding interest worldwide in traditional health practices in both the industrialised and developing countries of the world (Schillhorn van Veen, 1997), including herbal de-wormers (Hammond et al., 1997). Studies are now underway to evaluate some of the "best candidates", used as livestock de-worming preparations by pastoralist communities in east Africa (Githiori et al., 2002, 2003, 2004).

The possible use of specialised crops to control nematode infections in grazing ruminants has attracted considerable research interest in recent years. Bioactive plants or forages with secondary metabolites, particularly legumes with a high content of proanthocyanidins (condensed tannins) *e.g. Hedysarum coronarium* and *Lotus pedunculatus* have been reported to reduce worm burdens in grazing lambs by up to 50% (Niezen et al., 1995). An *in vivo* anthelmintic effect has also been observed using quebracho, a condensed tannins extract, as a single high dose against sheep nematodes (Athanasiadou et al., 1999) and the capacity of purified condensed tannins from legumes grown in Denmark to kill nematode larvae *in vitro* has been demonstrated (Kahiya et al., 1999). However, in several field studies it has been difficult to relate anti-parasitic effects to the actual amounts of condensed tannins (*e.g.* Niezen et al., 1998). A complicating factor is that condensed tannins are a poorly defined group of compounds (basically polymers capable of covalently binding protein) making standardised determinations in plant material difficult.

It has been postulated that the beneficial effects of tanniferous plants against internal parasites could be due to one, or a combination, of the following factors. Firstly, tannins may form non-biodegradable complexes with protein in the rumen, which dissociate at low pH in the abomasum, to release more protein for metabolism in the small intestine of ruminants. In other words, “natures protected protein”. This indirectly improves host resistance and resilience to nematode parasite infections. Secondly, tannins may have a direct anthelmintic effect on resident worm populations in animals and thirdly, tannins and/or metabolites in dung may have a direct effect on the viability of the free-living stages (development of eggs to infective larval stages). Although there is some evidence to support each of these above claims (Kahn and Diaz-Hernandez, 1999), the anthelmintic effects of tanniferous plants remains equivocal.

## 3. Biological control of nematode parasites of livestock

In contrast to virtually all other methods of nematode parasite control in livestock, which are directed at the parasitic stage within the host, biological control is targeted at the free-living stages on pasture. Biological control for any target pest organism is aimed at exploiting their natural enemies so as to reduce the number of the pests in the environment to a level less than what would have occurred in the absence of the biological control organism(s). So it is with helminth parasites. For more than 50 years, natural enemies to nematode parasites have been reported in the literature and some attempts had been made to control worm parasites of man and livestock by these organisms (for review see Grønvold et al., 1996; Waller and Faedo, 1996; Waller and Larsen, 1993).

However in the broadest sense, any means by which animals are separated from their faeces (thus the free-living stages of parasites) constitutes a form of biological control. Thus it could be argued that man’s manipulation of livestock movement and numbers could be classified as a form of biological control. Evasive parasite control brought about by movement of animals so as to avoid the peak periods of larval pick-up from pasture is an excellent, albeit indirect form of biological control. Likewise the sale, often of young susceptible livestock to the slaughterhouse deprives parasites of susceptible hosts in which they may readily complete their life cycle. Without such intervention by man, parasite numbers would be higher in set-stocked animals. On the other hand, it could be argued that man’s influence in the domestication and intensificaton of livestock, has tipped the balance in favor of the parasite in the first instance. One activity of man, which could be more justifiably called biological control, is the practice of dung collection in the developing world for the use as fuel, building material, etc., thus breaking the life cycle of parasites. However, in regions of the world where this custom is practiced, it is generally restricted to bovine dung, weather conditions are often hot and dry and malnutrition rather than parasitism is the major cause of loss in livestock productivity.

Certain birds seek out coprophilous arthropods as a source of food (McCracken, 1993). In doing this they can break open and scatter large deposits of cattle and horse faeces, thus allowing much quicker desiccation of the faecal material than would otherwise occur in the intact pads. Dung pats have been shown to provide an important buffering capacity against both extremes of temperature and moisture, which enhances the development and survival of parasite free-living stages in the faecal pat (Barger et al., 1984). Except in very isolated situations as mentioned by McCracken (1993), the number of birds involved in this activity are unlikely to be sufficiently large enough to have a measurable and consistent effect on parasite numbers on pasture.

With regards to invertebrates, a lot of interest has been shown in the role of dung beetles and earthworms on the free-living stages of nematode parasites on pasture. Dung beetles are ubiquitous and are often capable of rapid and complete dung removal and thus are indirectly responsible for significant reductions in the number of free-living stages of parasites (for review see Waller and Faedo, 1996). However, such dung dispersal activity by beetles is notoriously labile, being dependent on ideal weather conditions, therefore little opportunity exists to exploit these organisms in attempts to achieve cost-effective and reliable biological control of nematode parasites.

Earthworms take over the role of dung beetles in the cool, moist regions of the world, although coprophilic flies and small dung beetles also contribute to dung degradation (Holter, 1979). In northern Europe for example, earthworms play an important and often dominating role in removal of cattle dung from pastures and can be responsible for significant reduction of infective larvae on pasture (Grønvold, 1987).

A number of micro-organisms have been identified that exploit the free-living stages of parasites as a food source. These include viruses, protozoa, predacious nematodes, predacious mites, bacteria and fungi (for review see Grønvold et al., 1996; Waller and Faedo, 1996; Waller and Larsen, 1993). Although all are of intrinsic interest, it is within the latter group of organisms that an effective and commercially acceptable biological control agent for nematode parasites is likely to be found. Fungi that exhibit anti-nematode properties have been known for a long time. They consist of a great variety of species, which include nematode-trapping (predacious) fungi, endoparasitic fungi, fungi that invade nematode eggs and fungi that produce metabolites that are toxic to nematodes (for review see Barron, 1977).

Currently, the work on biological control of nematode parasites of livestock is almost exclusively associated the nematode-destroying microfungus, *Duddingtonia flagrans.* The reason for this is that it has three very important attributes, namely the ability to survive gut passage of livestock, a propensity to grow rapidly in freshly deposited dung and it possesses a voracious nematophagous capacity (for review see Larsen, 1999). Control is effected by the fungus capturing the infective larval stages before they migrate from dung to pasture to complete their life cycle following ingestion by grazing animals. Field evaluation of this concept for a range of livestock species (sheep, goats, cattle, horses, pigs), in a variety of geo-climatic regions, has been underway for the last decade (for review see Anonymous, 1998, 2002; Larsen, 1999). At the same time, a number of potential stumbling blocks on the path towards product registration have largely been overcome. Firstly scaling-up of production of *D. flagrans* to produce commercial quantities of spore material is possible (Gillespie, 2002). Secondly, using *D. flagrans* as a nematode control agent has no adverse effects on the environment (Faedo et al., 2002; Knox et al., 2002; Waller et al., 2005; Yeates et al., 1997, 2002, 2003). Thirdly, it has been established that *D. flagrans* is ubiquitous and that very close genetic similarity exists between isolates from widely separated localities (Faedo, 2001; Skipp et al., 2002), suggesting a clonal population worldwide.

The commonly used means of deployment of *D. flagrans* spore material is by a feed additive. To achieve optimal results, the fungal spores need to be continuously shed in the dung of animals at the same time that contamination of pasture with parasite eggs occurs. Thus daily supplementation of fungal material is recommended; during the predetermined period of time that biological control is to be effected (for review see Waller, 2003). Clearly, much greater opportunities for this innovation would occur if effective methods of *D. flagrans* depot delivery were available. Although work has been conducted aimed at developing fungal feed blocks (Chandrawathani et al., 2002, 2003; Waller et al., 2001a), and fungal controlled release devices (Waller et al., 2001b), at this stage none of these prototype devices provide the effective parasite control (continuous spore release) for the minimum required time of at least 2 months.

However, the “near commercialisation” of this non-chemical approach to nematode parasite control is attracting ever-increasing interest, which is driven by the anthelmintic resistance and the organic farming agenda. The current opportunities, as well as the limitations, in the use of biological control under a variety of livestock grazing systems has recently been reviewed (Waller, 2003).

## 4. Conclusion

For the vast majority of grazing livestock industries, anthelmintics will always remain the cornerstone of effective parasite control programmes. Also there is the necessity for organic livestock producers to have a chemotherapeutic “safety net” in situations where their animals become exposed to high levels of parasite infection which affects their productivity and particularly where this becomes an animal welfare issue. However, the issue of anthelmintic resistance in nematode parasites, particularly in small ruminants, is becoming an increasingly urgent problem. The use of grazing management strategies, combined with anthelmintic treatment, may well result in better parasite control at less cost, but may not reduce significantly the selection pressure for the development of resistance. It has been argued that the selection for resistance in any control strategy involving anthelmintics, will be more closely related to the degree of success of the control strategy than to the frequency of treatment it entails (Barger, 1995). Accepting that even the most efficacious anthelmintic drug will not be 100% effective, against 100% of parasites, in 100% of the treated animals, in 100% of times that it is used, then this literally means that the only parasite control strategy that does not select for resistance does not entail the use of anthelmintics.

Development of anthelmintic resistance is testimony to the remarkable biological plasticity of nematode parasites. Just as strains of parasites have evolved to survive one type of selection pressure (*e.g.* anthelmintics), then they are perfectly capable of doing the same with others. This could well apply to say host interchange grazing strategies and biological control. There are several documented cases of failure of sheep–cattle alternate grazing strategies despite initial success of this strategy (for review see Barger, 1997). Biological control is not sufficiently advanced to have been extensively used in long-term field trials for this to emerge, but it is reasonable to assume that strains of parasites could be selected whose free-living stages could avoid capture by *D. flagrans.* Thus it is important to recognise that any specific worm control strategy, whether it is chemotherapeutic or non-chemotherapeutic, will be unsustainable when used in isolation.

Parasite control schemes that integrate as many different control methods that are practically, financially and economically feasible are the only way to ensure long-term sustainability. Within this objective, grazing management strategies and biological control are important components for future parasite control schemes in grazing livestock enterprises throughout the world.

## References


Anonymous (1998). Biological control of gastro-intestinal nematodes of ruminants using predacious fungi. FAO Animal Production and Health Paper, No.: 141, pp. 94.

Anonymous (2002). Biological control of nematode parasites of small ruminants in Asia. FAO Animal Production and Health Paper, pp. 104.

Athanasiadou, S., Kyriazakis, I., Coop, R.L., Jackson, F., 1999. Evidence for direct anthelmintic effect of condensed tannins. In: Proceedings of the WAAVP Conference, Copenhagen, f.5.04.

Banks, D.J.D., Singh, R., Barger, I.A., Pratap, B., Le Jambre, L.F., 1990. Development and survival of infective larvae of *Haemonchus contortus* and *Trichostrongylus colubriformis* in a tropical environment. Int. J. Parasitol. 20, 155–160.

Barger, I.A., 1995. Control strategies minimising the use of anthelmintics. In: Petersen, G. (Ed.), Proceedings of the 25th Sheep and Beef Cattle Seminar, Publication No. 165. Veterinary Continuing Education, Massey University, Palmerston North, New Zealand, pp. 59–66.

Barger, I.A., 1997. Control by management. Vet. Parasitol. 72, 493–506.

Barger, I.A., Southcott, W.H., 1978. Parasitism and production in weaner sheep grazing alternately with cattle. Aust. J. Exp. Agric. Anim. Husb. 18, 340–346.

Barger, I.A., Lewis, R.J., Brown, G.F., 1984. Survival of infective larvae of nematode parasites of cattle during drought. Vet. Parasitol. 14, 143–152.

Barger, I.A., Siale, K., Banks, D.J.D., LeJambre, L.F., 1994. Rotational grazing for control of gastrointestinal nematodes of goats in a wet tropical environment. Vet. Parasitol. 53, 109–116.

Barnes, E.H., Dobson, R.J., Barger, I.A., 1995. Worm control and anthelmintic resistance: adventures with a model. Parasitol. Today 11, 56–63.

Barron, G.L., 1977. Observations on predatory fungi. Can. J. Botany 57, 187–193.

Benitez-Usher, C., Maciel, S., Rebollo, C., Armour, J., 1984. A study of bovine parasitic gastro-enteritis in Paraguay. Prev. Vet. Med. 2, 295–308.

Besier, R.B., 1999. New strategies to reduce selection for macrocyclic lactone resistance in sheep nematodes. In: Proceedings of the Australian Sheep Veterinary Society Conference, Indooroopilly, Australian Veterinary Association, pp. 16–22.

Beveridge, I., Brown, T.H., Fitzsimons, S.M., Ford, G.E., Judson, G.J., Martin, R.R., Miller, D.W., 1985. Mortality of weaner sheep in South Australia under different regimes of anthelmintic treatment. Aust. J. Agric. Res. 36, 857–865.

Brown, T.H., Ford, G.E., Miller, D.W., Beveridge, I., 1985. Effect of anthelmintic treatment and stocking rate on the productivity of weaner sheep in a Mediterranean climate environment. Aust. J. Agric. Res. 36, 845–855.

Cameron, C.D.T., Gibbs, H.C., 1966. Effect of stocking rate and flock management on internal parasitism in lambs. Can. J. Anim. Sci. 46, 121–124.

Chandrawathani, P., Omar, J., Waller, P.J., Höglund, J., Larsen, M., Zahari, W.M., 2002. Nematophagous fungi as a biological control agent for nematode parasites of small ruminants in Malaysia: a special emphasis on *Duddingtonia flagrans*. Vet. Res. 33, 685–696.

Chandrawathani, P., Jamnah, O., Waller, P.J., Larsen, M., Gillespie, A.T., Zahari, W.M., 2003. Biological control of nematode parasites of small ruminants in Malaysia using the nematophagous fungus *Duddingtonia flagrans*. Vet. Parasitol. 117, 173–183.

Dimander, S.O., Höglund, J., Uggla, A., Spörndly, E., Waller, P.J., 2003. Evaluation of gastro-intestinal nematode parasite control strategies for first-season grazing cattle in Sweden. Vet. Parasitol. 111, 193–209.

Dineen, J.K., 1963. Immunological aspects of parasitism. Nature (London) 197, 268–269.

Dineen, J.K., 1978. The nature and role of immunological control in gastrointestinal helminthiasis. In: Donald, A.D., Southcott, W.H., Dineen, J.K. (Eds.), The Epidemiology and Control of Gastrointestinal Parasites of Sheep in Australia. CSIRO, Academic Press, Sydney, pp. 121–135.

Dineen, J.K., Donald, A.D., Wagland, B.M., Turner, J.H., 1965. The dynamics of the host–parasite relationship. Part II. The response of sheep to primary and secondary infection with *Nematodirus spathiger*. Parasitology 55, 163–171.

Donald, A.D., 1994. Parasites, production and sustainable development. Vet. Parasitol. 54, 27–47.

Donald, A.D., Morley, F.H.W., Axelsen, A., Donnelly, J.B., Waller, P.J., 1987. Integration of grazing management and anthelmintic treatment for the control of nematode infections in young sheep. In: Wheeler, J.L., Pearson, C.J., Robards, G.E. (Eds.), Temperate Pastures, their Production, Use and Management. Australian Wool Corporation/CSIRO, Melbourne, Australia, pp. 567–569.

Downey, N.E., 1969. Grazing management in relation to trichostrongylid infestation in lambs. Level of infestation associated with increased stocking rate and its effects on the host. Irish J. Agric. Res. 8, 375–395.

Downey, N.E., Conway, A., 1968. Grazing management in relation to trichostrongylid infestation in lambs. Influence of stocking rate on the level of infection. Irish J. Agric. Res. 7, 343–362.

Faedo M. (2001). Growth, trapping and genetic diversity of *Duddingtonia flagrans* — a biological control agent of free-living larval stages of ruminant parasitic nematodes. Ph.D. Thesis, The Royal Veterinary and Agricultural University, Copenhagen. Denmark.

Faedo, M., Larsen, M., Dimander, S.O., Yeates, G.W., Höglund, J.H., Waller, P.J., 2002. Growth of the fungus *Duddingtonia flagrans* in soil surrounding feces deposited by cattle or sheep fed the fungus to control nematode parasites. Biol. Control 23, 64–70.

Gillespie, A. (2002). *Duddingtonia flagrans* for control of parasites in farm animals: a commercial perspective, in: Biological Control of Nematode Parasites of Small Ruminants in Asia. FAO Animal Production and Health Paper, p. 19.

Githiori, J.B., Höglund, J., Waller, P.J., Baker, R.L., 2002. Anthelmintic activity of preparations derived from *Myrsine africana* and *Rapanea melanophloeos* against the nematode parasite *Haemonchus contortus* of sheep. J. Ethnophamacol. 80, 187–191.

Githiori, J.B., Höglund, J., Waller, P.J., Baker, R.L., 2003. The anthelmintic efficacy of the plant, *Albizia anthelmintica*, against the nematode parasites *Haemonchus contortus* of sheep and *Heligmosomoides polygyrus* of mice. Vet. Parasitol. 116, 23–34.

Githiori, J.B., Höglund, J., Waller, P.J., Baker, R.L. (2004). Evaluation of anthelmintic properties of some plants used as livestock dewormers against *Haemonchus contortus* infections in sheep. Parasitol. 129 (2).

Grønvold, J., 1987. Field experiment on the ability of earthworms (Lumbricidae) to reduce the transmission of infective larvae of *Cooperia oncophora* (Trichostrongylidae) from cow pats to grass. J. Parasitol. 73, 1133–1137.

Grønvold, J., Henriksen, S.Aa., Larsen, M., Nansen, P., Wolstrup, J., 1996. Biological control. Aspects of biological control — with special reference to arthropods, protozoans and helminths of domesticated animals. Vet Parasitol. 64, 47–64.

Hammond, J.A., Fielding, D., Bishop, S.C., 1997. Prospects for plant anthelmintics in tropical veterinary medicine. Vet. Res. Comm. 21, 213–228.

Hawkins, J.A., 1993. Economic benefits of parasite control in cattle. Vet. Parasitol. 46, 159–173.

Holter, P., 1979. Effect of dung beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. Oikos 32, 393–402.

Hovi, M., Sundrum, A., Thamsborg, S.M., 2003. Animal health and welfare in organic livestock production in Europe — current state and future challenges. Livest. Prod. Sci. 80, 41–53.

Kahiya, C.J., Mukaratirwa, S., Thamsborg, S.M., Ndlovo, L.R., 1999. Anthelmintic effects of proanthocyanidins and related polyphenolics. In: Proceedings of the WAAVP Conference, Copenhagen, g 6.86.

Kahn, L.P., Diaz-Hernandez, A., 1999. Tannins with anthelmintic properties. In: International Workshop on Tannins in Livestock and Human Nutrition, ACIAR Proceedings No. 92, Waite Campus, University of Adelaide, pp. 130–139.

Knox, M.R., Josh, P.F., Anderson, L.J., 2002. Deployment of *Duddingtonia flagrans* in an improved pasture system: dispersal, persistence, and effects on free-living soil nematodes and microarthropods. Biol. Control 24, 176–182.

Larsen, M., 1999. Biological control of helminths. Int. J. Parasitol. 29, 139–146.

Maizels, R.M., Lawrence, R.A., 1991. Immunological tolerance: the key feature in human filariasis? Parasitol. Today 7, 271–276.

McLeod, R.S., 1995. Costs of major parasites to the Australian livestock industries. Int. J. Parasitol. 25, 1363–1367.

McCracken, D.I., 1993. The potential for avermectins to affect wildlife. Vet. Parasitol. 48, 273–280.

Morley, F.H.W., Donald, A.D., 1980. Farm management and systems of helminth control. Vet. Parasitol. 6, 105–134.

Michel, J.F., 1985. Strategies for the use of anthelmintics in livestock and their implications for the development of drug resistance. Parasitology 90, 621–628.

Niezen, J.H., Waghorn, G.C., Charleston, W.A.G., 1998. Establishment and fecundity of *Ostertagia circumcincta* and *Trichostrongylus colubriformis* in lambs fed lotus (*Lotus pedunculatus*) or perennial ryegrass (*Lolium perenne*). Vet. Parasitol. 78, 13–21.

Niezen, J.H., Waghorn, T.S., Charleston, W.A.G., Waghorn, G.C., 1995. Growth and gastrointestinal nematode parasitism in lambs grazing either lucerne (*Medicago sativa*) or sulla (*Hedysarum coronarium*) which contains condensed tannins. J. Agric. Sci. Camb. 125, 281–289.

Perry, B.D., Randolph, T.F., 1999. Improving the assessment of the economic impact of parasitic diseases and of their control in production animals. Vet. Parasitol. 84, 145–168.

Perry, B.D., Randolph, T.F., McDermott, J.J., Sones, K.R., Thornton, P.K., 2002. Investing in Animal Health Research to Alleviate Poverty. International Livestock Research Institute (ILRI), Nairobi, Kenya, p. 148.

Sani, R.A., Chandrawathani, P., 1996. Gastrointestinal parasitism in small ruminants in Malaysia. In: Le Jambre, L.F., Knox, M.R. (Eds.), Sustainable Parasite Control in Small Ruminants, Proceedings No. 74. Australian Centre for International Agricultural Research (ACIAR), pp. 98–100.

Sani, R.A., Mazila, M., Zaki, M., Chong, D.T., Tajuddin, I., 1996. Grazing management for worm control in sheep–rubber integrated systems. In: Proceedings of the 18th Malaysian Society for Animal Production Annual Conference, 28–31 May 1996, Sarawak.

Schillhorn van Veen, T.W., 1997. Sense or nonsense? Traditional methods of animal parasitic disease control. Vet. Parasitol. 71, 177–194.

Skipp, R.A., Yeates, G.W., Chen, L.Y., Glare, T.R., 2002. Occurrence, morphological characteristics and ribotyping of New Zealand isolates of *Duddingtonia flagrans*, a candidate for biocontrol of animal parasitic nematodes. N.Z. J. Agric. Res. 45, 187–196.

Southcott, W.H., Barger, I.A., 1975. Control of nematode parasites by grazing management. Part 2. Decontamination of sheep and cattle pastures by varying periods of grazing with the alternative host. Int. J. Parasitol. 5, 45–48.

Southcott, W.H., Heath, D.D., Langlands, J.P., 1967. Relationship of nematode infection to efficiency of wool production. J. Br. Grassland Soc. 22, 117–120.

Southcott, W.H., Langlands, J.P., Heath, D.D., 1970. Stocking intensity and nematode infection of grazing sheep. In: Norman, M.J.T. (Ed.), Proceedings of the 11th International Grassland Congress. Queensland University Press, St. Lucia, Queensland, Australia, pp. 888–890.

Speedy, A.W., 1980. Sheep Production: Science into Practice. Longman, London.

Spedding, C.R.W., Brown, T.H., Large, R.V., 1964. The interaction of internal parasites and nutrition in the utilization of grassland by sheep. J. Agric. Sci. 63, 421–426.

Thamsborg, S.M., Jørgensen, R.J., Waller, P.J., Nansen, P., 1996. The influence of stocking rate on gastrointestinal nematode infections of sheep over a 2-year grazing period. Vet. Parasitol. 67, 207–224.

Thamsborg, S.M., Roepstorff, A., Larsen, M., 1999. Integrated and biological control in organic and conventional production systems. Vet. Parasitol. 84, 169–186.

Urquhart, G.M., Armour, J., Duncan, J.L., Dunn, A.M., Jennings, F.W., 1996. Veterinary Parasitology, 2nd ed. Blackwell Science, United Kingdom.

Waller, P.J., 1993. Towards sustainable nematode control of livestock. Vet. Parasitol. 48, 295–309.

Waller, P.J., 1997. Anthelmintic resistance. Vet. Parasitol. 72, 391–412.

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

Waller, P.J., 2003. Global perspectives on nematode parasite control in ruminant livestock: the need to adopt alternatives to chemotherapy, with the special emphasis on biological control. Anim. Health Rev. 4, 35–43.

Waller, P.J., Larsen, M., 1993. The role of nematophagous fungi in the biological control of nematode parasites of livestock. Int. J. Parasitol. 23, 539–546.

Waller, P.J., Faedo, M., 1996. The prospects for biological control of the free-living stages of nematode parasites of livestock. Int. J. Parasitol. 26, 915–925.

Waller, P.J., Axelsen, A., Donald, A.D., Morley, F.H.W., Donnelly, J.R., Dobson, R.J., 1987. Effects of helminth infection on the pre-weaning production of ewes and lambs: comparison between safe and contaminated pasture. Aust. Vet. J. 64, 357–362.

Waller, P.J., Knox, M.R., Faedo, M., 2001a. The potential of nematophagous fungi to control the free living stages of nematode parasites of sheep: feeding and block studies with *Duddingtonia flagrans*. Vet. Parasitol. 102, 321–330.

Waller, P.J., Faedo, M., Ellis, K., 2001b. The potential of nematophagous fungi to control the free living stages of nematode parasites of sheep: towards the development of a fungal controlled release device. Vet. Parasitol. 102, 321–330.

Waller, P.J., Bernes, G., Thamsborg, S.M., Sukura, A., Richter, S.H., Ingebrigsten, K., Höglund, J., 2001c. Plants as de-worming agents of livestock in the Nordic countries: historical perspective, popular beliefs and prospects for the future. Acta. Vet. Scand. 42, 31–44.

Waller, P.J., Dash, K.M., Barger, I.A., Le Jambre, L.F., Plant, J., 1995. Anthelmintic resistance in nematode parasites of sheep: learning from the Australian experience. Vet. Rec. 136, 411–413.

Waller, P.J., Schwan, O., Ljungström, B.L., Rydzik, A., Yeates, G.W., 2005. Evaluation of biological control of sheep parasites using *Duddingtonia flagrans* under commercial farming conditions on the island of Gotland, Sweden. Vet. Parasitol. 126, 299–315.

Yeates, G.W., Waller, P.J., King, K.L., 1997. Soil nematodes as indicators of the effect of management on grasslands in the New England Tablelands (NSW): effect of measures for control of parasites of sheep. Pedobiologia 41, 537–548.

Yeates, G.W., Dimander, S.O., Waller, P.J., Höglund, J., 2002. Environmental impact on soil nematodes following the use of either ivermectin sustained release boluses or the nematophagous fungus *Duddingtonia flagrans* to control nematode parasites of cattle in Sweden. Acta Agric. Scand. Sec. A: Anim. Sci. 52, 233–242.

Yeates, G.W., Dimander, S.O., Waller, P.J., Höglund, J., 2003. Soil nematode populations beneath faecal pats from grazing cattle treated with the ivermectin sustained-release bolus or fed the nematophagous fungus *Duddingtonia flagrans* to control nematode parasites. Acta Agric. Scand. Sec. A: Anim. Sci. 53, 197–206.

Zimmerman, W.J., 1965. The role of selected management systems in the control of sheep parasites. J. Am. Vet. Med. Assoc. 147, 499–505.