Veterinary Parasitology 186 (2012) 38–50

Contents lists available at SciVerse ScienceDirect

Veterinary Parasitology

journal homepage: www.elsevier.com/locate/vetpar

Manipulating small ruminant parasite epidemiology through the combination of nutritional strategies

Jos G.M. Houdijk[a,*], Ilias Kyriazakis[b], Alemayehu Kidane[a,c], Spiridoula Athanasiadou[a]

[a] Disease Systems, SAC, Edinburgh, EH9 3JG, UK
[b] School of Agriculture, Food and Rural Development, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK
[c] Department of Animal & Range Sciences, Hawassa University, Awassa, Ethiopia

ARTICLE INFO

Keywords:
Nutrition
Protein
Plant secondary metabolites
Epidemiology
Parasites
Nematodes
Small ruminants

ABSTRACT

It is increasingly being recognized that non-chemical parasite control strategies may need to be combined to control more effectively gastrointestinal parasitism, result in resilient production systems and reduce reliance on anthelmintics. Here, we consider if and how metabolizable protein (MP) supplementation and anti-parasitic plant secondary metabolites (PSM) may modulate parasite epidemiology through intervention in pasture contamination, development of infection on pasture and larval challenge as target processes. We then propose that combining two or more non-chemical parasite control strategies may have additive effects on host resistance, especially if the individual strategies target different drivers of parasite epidemiology, different processes in the parasite life cycle or different phases of acquired immunity to parasites. This epidemiological framework is used to review recent findings on combining maternal MP supplementation and grazing the PSM-rich bioactive forage chicory as an example of combining nutritional treatments to manipulate parasite epidemiology in a temperate production system. In the absence of available data for combined nutritional strategies in tropical production systems, we make predictions on the consequences of combining such strategies in these systems. We conclude that currently published studies on combining nutritional strategies under temperate conditions show potential to improve additively host resilience and reduce reliance on anthelmintics; however, effects on epidemiology have to date not shown the additive results hypothesized. The framework developed may assist further in evaluating combined (nutritional) strategies to manipulate parasite epidemiology.

1. Introduction

It has long been known, or at least suspected, that improved host nutrition may detrimentally affect gastrointestinal nematodes (Clunies-Ross and Gordon, 1933; Taylor, 1935; Gibson, 1963). Such anti-parasitic activity has been considered to arise from indirect nutritional effects, i.e. those mediated through nutritional modulation of host immune responses, or direct nutritional effects, i.e. those arising from ingestion of anti-parasitic plant secondary metabolites, PSM (Coop and Kyriazakis, 2001; Houdijk and Athanasiadou, 2003). For other possibilities of how host nutrition may affect parasites, including the modulation of gut environment and allowing for a reduction in the nutrients available to parasites, we refer to Houdijk and Athanasiadou (2003). The above indirect and direct effects of host nutrition on gastrointestinal nematodes form the basis for the use of immunonutrition and bioactive forage consumption, respectively, as potential non-chemical parasite control strategies. Although these strategies have largely been developed independently and their underlying mechanisms are usually considered in isolation, it is

* Corresponding author.
E-mail address: jos.houdijk@sac.ac.uk (J.G.M. Houdijk).

0304-4017/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.vetpar.2011.11.044

increasingly being concluded that such indirect and direct nutritional effects may need to be combined to achieve the most effective, sustainable parasite control (Coop and Kyriazakis, 2001; Houdijk and Athanasiadou, 2003; Torres-Acosta and Hoste, 2008; Athanasiadou et al., 2008).

This review focuses on the possibility of using metabolizable protein (MP) supplementation and PSM-rich bioactive plants to modulate the epidemiology of gastrointestinal nematode infections in sheep, although we will occasionally refer to other host–parasite systems where appropriate. We focus on MP because it is often scarce for growing and reproducing sheep, for example, due to consumption of low-quality forages or restricted feeding, at times of high MP requirements for growth and periparturient reproductive functions (AFRC, 1993). Parasitism further increases MP requirements for maintenance, arising from parasite-induced repair of damaged host tissue (Coop and Kyriazakis, 1999), and for production of the proteinaceous immune response components involved in regulating worm establishment, fecundity and survival (Balic et al., 2000; Coop and Holmes, 1996). MP supplementation may improve resistance to parasites, observed as reduced worm burdens and FEC, because in its absence, the allocation of scarce MP would be prioritized to maintenance and productive functions rather than expression of immune functions (Coop and Kyriazakis, 1999).

Plants with anti-parasitic properties indigenous to many parts of the world have regularly been reported in the literature, including the anti-parasitic efficacy of their extracts and/or purified PSM (Hammond et al., 1997; Schlage et al., 2000; Houdijk and Athanasiadou, 2003; Sori et al., 2004; Githiori et al., 2006; Hoste et al., 2006). Recent studies have confirmed and extended these reports, demonstrating anti-parasitic activity from bioactive forages such as chicory (*Cichorium intybus*), birdsfoot trefoil (*Lotus corniculatus*), sainfoin (*Onobrychis viciifolia*) (Heckendorn et al., 2007) and sericea lespedeza (*Lespedeza cuneata*) (Lange et al., 2006), but also from tropical plants such as acacia (*Acacia cyanophylla*) foliage (Akkari et al., 2008), *Ziziphus nummularia* bark and *Acacia nilotica* fruit (Bachaya et al., 2009), *Chenopodium album* and *Caesalpinia crista* (Jabbar et al., 2007), falcon's claw acacia (*Acacia polacantha*) (Max et al., 2007), *Coriandrum sativum* (Eguale et al., 2007) and ginger (*Zingiber officinale*) (Iqbal et al., 2006). Although more than 100,000 PSM have been described (Acamovic and Brooker, 2005), anti-parasitic properties have so far been reported for a few PSM, including lactones (Molan et al., 2003a), alkaloids (Satou et al., 2002), glycosides (Akhtar and Ahmad, 1992) and tannins (Athanasiadou et al., 2001a; Molan et al., 2003b).

In this paper, we first describe the main facets of gastrointestinal nematode epidemiology and review evidence to identify whether MP nutrition and PSM can impact on selected processes in the parasite life cycle as drivers for parasite epidemiology. Whilst we do this for MP nutrition and PSM separately for the sake of clarity, PSM effects on parasitism may to some extent arise from improved MP supply; for example, the anti-parasitic PSM condensed tannins (CT) may bind to dietary protein, resulting in reduced protein degradation in the rumen and thus potentially providing increased intestinal MP supply (Barry and Manley, 1984). Likewise, protein feed ingredients like peas, beans and lupins contain a wide range of PSM (Jezierny et al., 2010), with known or unknown anti-parasitic activities. It should also be noted that additional MP supply may arise from improved fermentable energy intake, as the latter may limit rumen MP supply. Indeed, recent studies have demonstrated improved resistance and resilience to gastrointestinal parasites in goats browsing protein rich fodder trees following supplementation with fermentable energy sources (Knox et al., 2006; Hoste et al., 2008).

The second part of the review considers the combination of nutritional strategies to affect parasite epidemiology. We first develop a framework to assess the potential benefits of combining nutritional strategies on parasite epidemiology. We then describe our recent experience with combining maternal MP supplementation and chicory grazing as an example of combining indirect and direct nutritional parasite control strategies in temperate sheep production systems. We then extend these principles to tropical production systems, although to our knowledge, combining (MP) supplementation with bioactive forage feeding has not (yet) been experimentally tested under these conditions. Therefore, this part of the review is more speculative and, almost by necessity, centres on the dual consequences of supplementation with bioactive forages, i.e. additional nutrient supply and provision of anti-parasitic PSM. The review concludes with suggestions for further research and implications for non-chemical, nutritionally based parasite control strategies.

2. Epidemiology of gastrointestinal nematode infections

Adult parasites within the gastrointestinal tract produce eggs, which are excreted via the faeces onto the pasture (contamination), where over time eggs develop into infective larvae, L_3 (development). The infective larvae vertically migrate onto forage, and are ingested by sheep through grazing (challenge) to develop into adult parasites within the sheep gastrointestinal tract. Controlling (reducing) gastrointestinal nematode infections in grazing animals can be seen as disrupting this cycle, through controlling (1) the source of infection to reduce contamination of the pasture, (2) egg hatchability and L_3 appearance to reduce the development of infection on the pasture, and (3) L_3 uptake to reduce challenge from the pasture (Fig. 1).

The main sources of infectivity early in the season are overwintering larvae and infected periparturient ewes, whilst subsequent pasture infectivity also derives from patent lambs. At less than 0.5%, translation (i.e. number of worms as a percentage of number of eggs deposited) for winter deposition of *Teladorsagia circumcincta* eggs is low but significant (Bailey et al., 2009), and thus puts periparturient ewes at risk of infection (Waller et al., 2004; Makovcová et al., 2009). The elevated ewe FEC, which may also in part result from resumed development of inhibited larvae (Sargison et al., 2007; Waller et al., 2004), arises from periparturient relaxation of immunity (PPRI) to parasites (Barger, 1993; Beasley et al., 2010). The seasonal reproductive cycle further assist epidemiology especially under temperate conditions, as worm eggs excreted by