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Elevated temperatures and long drought periods have a negative impact on survival and fitness of strongylid third stage larvae

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ABSTRACT

In grazing cattle, infections with gastrointestinal nematodes pose some of the most important health threats and subclinical infections result in considerable production losses. While there is little doubt that climate change will affect grazing ruminants directly, mean temperature increases of ~3 °C and longer drought stress periods in summer may also influence the free-living stages of parasitic nematodes. Hostile climatic conditions reduce the number of L3s on pasture and therefore the refugium, which is expected to result in a higher selection pressure, accelerating development of resistance against anthelmintic drugs. The aim of the current experiments was to investigate the effects of drought stress and different temperature/humidity ranges over time on the survival and fitness of *Cooperia oncophora* L3s and their distribution in grass and soil under controlled conditions using a climate chamber. Grass containers inoculated with L3s were analysed after 1–6 weeks using descriptive statistics as well as linear models. A large proportion of L3s was recovered from soil where fitness was also better preserved than on grass. Numbers and fitness of recovered L3s declined with duration in the climate chamber under both temperature profiles. However, the results of the linear models confirmed that higher temperatures (20–33 °C versus 17–22.6 °C) significantly impaired survival, distribution and fitness of L3s. Application of drought stress, known as another important factor, had a surprisingly smaller impact than its duration or higher temperatures. The climate chamber enabled exclusion of confounding factors and therefore accurate interpretation of the investigated climatic aspects. The obtained results highlight the relative importance of those factors, and will help to design better models for the population dynamics of L3s on pasture in the future. Additionally, the outcomes of these investigations may offer explanations regarding interdependencies of development of anthelmintic resistance and the presence of hot/dry weather conditions.

1. Introduction

Trichostrongylid gastrointestinal (GI) nematodes have been shown to impair cattle productivity worldwide, mainly by decreasing weight gain and milk production (Stromberg et al., 2012). More severe infections can lead to inflammation of the abomasum or small intestines, which causes pain and therefore impairs animal welfare. *Cooperia oncophora* is one of the most common GI nematodes in Europe (Demeler et al., 2009) and is usually accompanied by other trichostrongylids (e.g. *Ostertagia ostertagi*) which can lead to severe parasitic gastroenteritis. In Europe, mixed infections of *Cooperia* and *Ostertagia* spp. are predominant in grazing cattle, but due to the assumed higher pathogenicity of *Ostertagia* most studies concentrate on the prevalence and effects of this genus (Forbes et al., 2008; Delafosse, 2013). Herein, the species *C. oncophora* was also chosen since this is usually the predominant species in Europe (El-Abdellati et al., 2010; Areskog et al., 2013), but particularly in countries with higher temperatures (Rivera et al., 1983; Pfukenyi and Mukaratirwa, 2013). It has been shown that e.g. *Cooperia pectinata* survives/develops better at high temperatures and under drought stress (DS) compared with other trichostrongylids (Pfukenyi and Mukaratirwa, 2013). Accordingly, *Cooperia* spp. may benefit more from the predicted climatic changes in Europe rather than temperature-sensitive species such as *Trichostrongylus* spp. and *Ostertagia* spp., where more intensified effects of DS and high temperatures can be expected. A number of studies have been published reporting different temperature thresholds for parasite development and survival (Pandey, 1972; Young et al., 1980; van Dijk and Morgan, 2008) or the impact of temperature and humidity on migration (Callinan and Westcott, 1986), but only a few studies were performed using a controlled

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climate chamber approach to investigate possible influences of climate change in the temperate region. Since L3s are able to survive over long periods in soil and on pasture (Knapp-Lawitzke et al., 2014b), they play an important role in population dynamics and were therefore the focus of the current experiments. *Cooperia oncophora* was also chosen in order to fill the knowledge gap regarding survival parameters for this species. While simulation models of the effect of climate and climate changes on free-living stages have been recently described for *Haemonchus contortus*, *Teladorsagia circumcincta* and *O. ostertagi* (Rose et al., 2015), no such information is available for *C. oncophora*.

To control nematode infections as well as to minimise their effects in regard to productivity, anthelmintic treatments are applied in almost all livestock production systems. Facing increasing anthelmintic resistance (AR) problems, combined with the rising consumer demand to reduce the overall number of chemical treatments given to livestock and the predicted changes in the climate, detailed information is required regarding the possible impact of changing climate on nematode abundance.

Research has shown that changes in climate will probably occur over the next decades and that therefore the weather in Europe will also change over the next 100 years (Jacob et al., 2012). Based on models for future weather development, studies predict that higher temperatures and longer lasting droughts in the future will on one hand directly harm dairy production by heat-induced stress and on the other hand also indirectly influence the dairy industry by impairing fodder production (Gauly et al., 2013). GI nematodes have a direct life cycle, where the adult parasites produce eggs in the host, while development from the egg to the infectious L3 occurs outside the host on pasture. Parasite development and survival on pasture are therefore dependent on the weather conditions. Parasite-hostile conditions reduce the refugium and thereby, in the context of anthelmintic treatments, the selection pressure increases (van Wyk, 2001), possibly leading to an increased development of AR. It is noticeable that publications reporting AR in GI nematodes (Anziani et al., 2001, 2004; Fiel et al., 2001; Mejia et al., 2003; Soutello et al., 2007; Suarez and Cristel, 2007) are more frequently from drought affected and/or warm continents, e.g. Africa, South America and Australia than from Europe with more temperate climatic regions (Kaplan, 2004; Sutherland and Leathwick, 2011). This is of concern to most cattle producers since it may negatively impact the currently available options for worm control and prevention of worm-associated diseases. The refugium contains the infra-population (nematode populations in untreated animals and hypobiotic stages) and the supra-population (nematode populations on pasture). The number of L3s in the supra-population is influenced by the number of eggs that are excreted by infected hosts as well as by their development and survival rates, and finally the transition of larvae from faeces to grass (Rossanigo and Gruner, 1994). Additionally, the parasite-host dynamic is affected through climate change. For example, with higher winter temperatures L3s will be active too early and may not find suitable hosts, leading to reduced pasture infectivity during spring/early summer. This could be compensated by shifting turn-out times towards the beginning of the year, but might not be suitable in all areas due to insufficient growth of pasture or other management factors. Hudson et al. (2006) points out that global warming with longer summers allows the host to excrete parasite offspring over longer time spans. Since naïve calves are susceptible to gastrointestinal nematodes, this corresponds to more reproductive cycles for the parasite during the grazing period.

In general, temperature and humidity have been identified as crucial survival parameters for free-living stages of parasites (O'Connor et al., 2006). In Germany, where the average annual air temperature rose during the last 40 years (Chmielewski et al., 2004), changes in the climate are meanwhile evident. The research consortium "KLIFF" financed by the Ministry of Science and Culture in Lower Saxony, Germany, used the A1B scenario of the Intergovernmental Panel on Climate Change (IPCC) (Solomon, 2007) to develop two models, REMO and CLM, for prospective weather conditions in Lower Saxony, Germany. The REMO model (climate model from the Max-Planck-Institute for Meteorology) predicts that the average summer temperature in Germany will increase by 2.5 °C and the precipitation will decrease by 18–22% until 2099. The climate model CLM predicts a slightly higher temperature increase of 3 °C and a decline of precipitation by 22–28% for the summer months (Haberlandt et al., 2010; Jacob et al., 2012). Kutz et al. (2005) reported that an increase of only 1 °C of the average daily temperature led to a significant increase of the development rate of nematodes in the arctic, while Hoar et al. (2012) additionally highlighted the effects of increasing temperature on hosts as being important for nematode transmission. Warmer temperatures also boost the parasite development from egg to the infective L3 stage in temperate climate zones, for which REMO and CLM also predict milder winters. Van Dijk et al. (2010) reviewed that *H. contortus* is susceptible to frost events while other trichostrongyles may benefit from cold winters by going into an immotile state which allows restriction and conservation of energy. However, no defined minimum threshold temperatures are available yet for a particular species. Furthermore, high temperatures during summer have been reported to shorten the lifespan of trichostrongyles (Todd et al., 1976; Boag and Thomas, 1985; Grenfell et al., 1986). In field studies (Shorb, 1943; Agneessens et al., 1997; Waruiru et al., 1998; Nogareda et al., 2006) humidity has been identified as another important parameter for development and survival of GI nematodes in sheep and cattle. Other studies investigating the effect of temperature and rain for successful L3 development and survival were often exclusively field experiments, which are mostly dependent on the number of GI nematode eggs excreted per gram faeces (EpG) and/or on the use of/or tracer animals. The interpretation of data obtained from those field experiments is therefore often complicated since other factors such as age, immunity and grazing behaviour of the animal, and fecundity of the parasite species, alter the outcome of the EpG. The variety of conditions which cannot be controlled in field experiments led to the trend of more closely simulated field conditions in laboratory studies (Callinan and Westcott, 1986; O'Connor et al., 2008; Van Dijk and Morgan, 2011). The significant negative effect of over 4 weeks of DS on the occurrence of *C. oncophora* L3s on herbage was recently shown in a greenhouse experiment (Knapp-Lawitzke et al., 2014a). Even though this greenhouse experiment was performed under semi-controlled conditions, numbers of L3s in the soil could not be determined precisely, since only sub-samples of the upper part of the soil (up to 10 cm depth) could be examined (total volume 30 L) and the experimental containers were not closed units.

The aim of the current experiments was to design a climate chamber model that enables the complete analysis of grass and soil under controlled temperature, humidity and light conditions in order to identify key climatic parameters for the survival of *C. oncophora* L3s. The parameters addressed here were temperature, humidity, DS and the duration of the application of those factors. Additionally it was investigated whether larvae are likely to migrate into the soil and if this has an impact on their chance of survival. The design of the study allowed the multifactorial analysis of possible influencing parameters. The obtained data can subsequently be used to feed parasite models in order to enable better predictions for sustainable control of *C. oncophora* in temperate regions in the future.