Indian J Anim Health (2022), 61(2)- Special Issue: 83-94
DOI: https://doi.org/10.36062/ijah.2022.spl.03022

Invited Review Article

Impact of climate change on the free-living larval stages and epidemiological pattern of gastrointestinal nematodes in livestock

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Abstract

Climate change has a negative impact on living organisms including livestock, and it can affect the pattern of distribution and transmission of different pathogens including helminth parasites to animals and humans. Gastrointestinal nematodes (GIN) are ubiquitous in nature in ruminants throughout the world. The free-living larval stages of GIN of ruminants are strongly influenced by climatic factors in the environment. Temperature, moisture and rainfall are the most important meteorological factors that control the hatching, development and survivability of infective larvae on the pasture and subsequent transmission to the susceptible host. These climatic variables altogether influence the seasonal pattern of GIN infections in ruminants, as well as geographical variation in the epidemiology and relative importance of different GIN species in a particular region. Epidemiological knowledge of any pathogen is a prerequisite for adopting any control measures against that particular agent. The traditional knowledge on GIN epidemiology and control should be supplemented with the modern predictive epidemiological models, which are built on the understanding of the impact of climate on larval availability. However, husbandry practices have to be taken into consideration as it also has an important role in determining the occurrence of GIN infection, and climate change also influence the management practices for livestock production. Therefore, the current approaches should take into account of climatic and environmental factors that influence the parasites' biology and ecology, and the farming system of ruminants and management decisions.

Key words: Climate change, Epidemiology, Gastrointestinal nematodes, Livestock, Predictive model

Highlights

- Climate influences the development and survival of gastrointestinal nematode (GIN) larva.
- There is a complex interaction between the free-living stages of GIN and climate.
- Distribution of GIN infections extend due to the adaptation of GIN larvae to climate change.
- Control strategy should consider climate and managemental practices based on predictive models.

INTRODUCTION

The major components of climate change, warming, altered pattern of rainfall/precipitation and an increased incidence of extreme climatic conditions (Solomon *et al.*, 2007) are evident around the world. Climate change has a great impact on the structure and function of the ecosystem, and it differs significantly with place and time. Climate change is the alteration in the components of the climate system that persists for a longer period. Climate change is a natural process in terms of changes in global temperature or changes in the composition of the atmosphere, but human activities in modern-day civilization have also significantly contributed to the current precarious state of climate change (Semenza and Menne, 2009). Population dynamics, individual physiology, and seasonal phenology of animals are strongly connected to natural climatic regimes in their geographic distribution (Kochmer and Handel, 1986). Changing climate can affect the pattern of transmission of different pathogens infecting animals and human in terms of the rate of development, mortality and reproduction of free-living stages of parasites, vectors and hosts.

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Besides the behavioural changes of hosts, vectors and parasites and alterations in host susceptibility have also been implicated due to changes in climatic conditions.

The direct consequence of climate change is easily noticed in terms of extreme weather events. The indirect consequence may not be easily seen but may result in an increase or change in the endemicity of parasitic diseases by changing the spatial distribution of parasites, vectors and host population (Short *et al*., 2017). Host and parasite interactions are complex (Dallas *et al*., 2017; Cuesta-Astroz *et al*., 2019), which play a key role in the survivability of parasites, and these interactions could be altered by climate change and cause parasitic diseases. Global climatic change can extend the natural range of pathogens and can make the previously uninhabitable region into an inhabitable zone for parasites (Lafferty, 2009). Climate change is the driving force for the intensification of host-parasitic interaction, creating opportunities for the invasion of a new pathogen or facilitating the transmission of already prevalent organisms. This process ultimately leads to a higher prevalence of pathogens/diseases in the native host population (Dobson *et al*., 2006; Johnson and Thieltges, 2010; Keesing *et al*., 2010; Rohr *et al*., 2011). The interaction between climate and parasite shows a non-linear relationship (Hernandez *et al*., 2013) and transmission of parasitic diseases is strongly related to behavioural and physiological properties of the host, parasites, intermediate host and vectors (McMichael *et al*., 2006; Halstead, 2008). Therefore, there is a need for more sophisticated and empirical research for obtaining long-term data from host-parasite ecosystems to have a better understanding of the interaction between parasites and climate and to design large-scale and long-term predictive models for parasitic diseases in a particular area.

The objective of this article was to assemble the information obtainable from the literatures relating to the epidemiology of GIN of livestock, highlighting the climatic as well as environmental variables that influence development, survival and movement of free-living stages of GINs in the pasture microhabitat and subsequent transmissible to the susceptible host. These facts are the important basis for developing control strategies which are directed to environmental management to reduce pasture contamination and consequently, to control the parasites in the animal. These concepts may encourage the correct, intelligent and sustainable use of anthelmintic treatments to extend the useful life of anthelmintic drugs that are commonly used to control GIN infections in livestock under the field conditions.

Environmental factors influencing transmission of gastrointestinal helminth

Environmental conditions, including climates, play a major role in the development and survivability of GIN population, particularly the free-living stages of nematodes on the pasture. The pasture is the place of helminth egg deposition and hatching, development and ingestion of infective larvae by the definitive host. Meteorological factors such as temperature, rain, humidity, barometric pressure, sunlight, cloud cover and wind, quality of vegetation as well as the effect of birds, insects, fungi and wild animals are the environmental conditions influencing the population of the free-living stages of GINs on the pasture (Bautista-Garfias *et al*., 2022). The environmental factors are highly variable and may vary annually and even in different seasons (Stromberg, 1997). The hatching of eggs as well as development of infective larvae (L_3) is particularly dependent on the optimum level of moisture and temperature. These environmental conditions influence the larvae activity on the pasture. Variable atmospheric humidity/ moisture arising from regular rains has a direct effect on the survivability of infective larvae in the pasture. However, it is important to note that humidity contained in the faecal mass is enough for development of larvae in absence of rain. The confinement of larvae within the faecal mass protects against solar rays and decreases larval desiccation. Therefore, the disruption of faecal put by birds, earthworms, arthropods and by cattle themselves may lead to a reduction of the infective larval population on the herbage. The eggs deposited onto the pasture must have to be survived and develop into infective stage before transmission to the definitive host.

The infective larvae must move away from the faecal pat and wander onto the surrounding pasture in order to be ingested by the definitive host and this movement is dependent on moisture (Bryan and Kerr, 1988; Stromberg, 1997). Adequate moisture provides a film of water for migration of larvae, and temperature also plays an important role (Krecek *et al.*, 1990) and also the type of vegetation influences the movement of larvae (Tarshis, 1958). The microclimate at the base of the herbage is favourable for larvae survival and infective larvae of GIN can survive for weeks to months depending on parasite species, stage of development of free-living larvae and environmental conditions (Stromberg *et al.*, 1991). Break up and distribution of faecal part over the pasture by beetles and earthworms cause drying up faecal materials which adversely influence the survival and development of GIN larvae.

Environmental factors particularly related to the pasture microclimate directly influence the numbers of GINs in the pasture and can cause an increased rate of infection. In tropical regions like India, the environmental conditions including the climatic factors are favourable for livestock production, but unfortunately, the same environmental conditions also favour the survival, development and multiplication of infective larvae on the pasture all-round the year. In India, highest rate of intensity of GIN infection is observed during monsoon in livestock (Jas *et al.*, 2017, 2020; Brahma *et al.*, 2018; Das *et al.*, 2018; Thakre *et al.*, 2019). In India, the environmental factors during the monsoon are favourable for larval development and also, monsoon causes some climatic stress to the animals leading to suppressed immunity, and this may ultimately lead to highest rate of infection. Lowest prevalence of GI helminths during summer (Singh *et al.*, 2012; Brahma *et al.*, 2015; Thakre *et al.*, 2019) have been recorded in India due to high temperature and low relative humidity and drying up off small water-bodies which are not favourable for survival of free-living stages of nematodes. Temperature and precipitation are found to be positively correlated with the intensity of GIN infections. However, high air temperature was negatively correlated with GIN infection (Pilarczyk *et al.*, 2022).

Temperature is one of the important environmental variables for development and survivability of larvae of GIN of livestock. Temperature can accelerate larval development as well as reduce larval survivability (Heckler and Borges, 2016). Silangwa and Todd (1964) reported that the optimum temperature for larval development of *Haemonchus*, *Cooperia* and *Trichostrongylus* was around 26.6°C and Amaradasa *et al.* (2010) observed that temperature around 23 to 31°C did not interfere in movement of *H. contortus* larvae. When temperature is favourable then solar radiation (luminosity of approximately 620 Lux) may be a determining factor in the stimulation of larval migration on the pasture.

The larval microhabitat is composed of vegetation cover which may provide its own microclimate to the survival of infective larvae. The relationship between environment and transmission of GIN larva is complex, and different environmental factors may have additive, multiplicative or antagonistic and non-linear effect on transmission of GIN to the host (Cable *et al.*, 2017). There is considerable uncertainty about future climatic change which will influence parasitic disease dynamics.

Effect of climate change on GIN of livestock

The livestock industry has been severely affected by climatic change globally. The rise in atmospheric temperature and carbon dioxide concentration and altered pattern of precipitation showed negative impact on animal performance, forage quality, water availability, reproduction and disease transmission (Nardone *et al.*, 2010). The indirect effect of changing temperature and altered pattern of rainfall becomes observable through more grazing periods in the temperature regions leading to an increased accumulation of infective larvae on the pasture and subsequently increased rate of infection to the susceptible host (Lafferty, 2009). Recent trends of intensive livestock rearing may lead to decrease in the transmitted disease but increases the diseases associated with poor hygiene (Bautista-Garfias *et al.*, 2022). Gastrointestinal namatodosis is widely prevalent in ruminant livestock throughout the world. Most of the studies gave emphasis on poor sanitary conditions and lack of awareness of anthelmintic use; however, climatic and ecological conditions are considered to be predisposing factors to the prevalence of helminth infections (Kates, 1965).

The knowledge of population dynamics and epidemiology of GIN and the predominant species present in the most diverse types of ruminant breeding systems are the basis for designing strategic control measures against GIN in ruminant livestock. In tropical countries like India, *Haemonchus*, *Oesophagostomum*, *Trichostrongylus*, *Teladorsagia* (*Ostertagia*), *Bunostomum*, *Cooperia* and *Strongyloides* are the main GIN parasites infecting ruminant livestock (Pathak and Pal, 2008; Singh *et al.*, 2013; Jas *et al.*, 2017; Thakre *et al.*, 2019) and causing several problems to the animal health. The climate and vegetation of a particular geographic region have a significant impact on the development and survivability of infective larvae and the availability of larvae in the pasture varies seasonally throughout the year (Amarante *et al.*, 2014). The survivability of infective larvae is dependent of a series of factors including climatic variations. The infective larvae of GIN are very active, and they apparently migrate in any direction (Sciacca *et al.*, 2002) and remain attached to grass blades. In any season, the higher concentration of infective larvae is found in the pasture during the coolest part of the day, always near the sunrise and sunset (Heckler and Borges, 2016). These larvae need moisture/humidity to survive in the vegetation; however, very low humidity or scarcity of rainfall tends to decrease the larvae population in the pasture. On the other hand, low rainfall with relatively mild temperature extends the survivability of larvae inside the faecal pat and remain as a source of pasture contamination (De-Almeida *et al.*, 2005). Precipitation helps the larvae to leave the faeces by moistening and softening it, and then larvae migrate to the pasture. Infective larvae have been found in environmental conditions that were not at all suitable for their survival (Bishop and Stear, 1997). Therefore, this complex relationship between free-living larvae and environment must be taken into consideration before planning a suitable control program for gastrointestinal nematodosis in livestock.

Various studies have reported the impact of climate change on the temporal and spatial distribution of GIN (Rodríguez-Diego *et al.*, 2013). Temperature is one of the critical factors controlling free-living part of life cycle of GIN. Rise in temperature shortens the duration from hatching of eggs to the development of infective larvae and thus increasing the larval population in the pasture. The infective larvae of *H. contortus* can be obtained within 4 to 5 days from the faecal culture in the tropical area, whereas, it can take about 7-10 days in the temperate laboratory condition (Bahuaud *et al.*, 2006; Castañeda-Ramírez *et al.*, 2017). Accelerate development of *H. contortus* in warm climate and delayed development in cold climate have been reported (Bautista-Garfias *et al.*, 2022), and nematodes from different geographical regions showed variability in different *in vitro* tests (Chan-Pérez *et al.*, 2016). Many authors suggested that highest number of GI parasites occurred in the past monsoon period (Liebano *et al.*, 1998).

Hot and humid conditions in most part of India including West Bengal favour the development and survivability of GIN both within the host and in the environment. During the monsoon, the climatic conditions like moisture and temperature remain very much favourable for GIN. Highest intensity of infection in terms of eggs per gram of faeces have been recorded in monsoon in different parts of India (Wadhwa *et al*., 2011; Singh *et al*., 2013; Thakre *et al*., 2019) including West Bengal (Brahma *et al*., 2018; Jas *et al*., 2020). Eggs are deposited on the pasture during the later part of monsoon hatch and develop into larvae and easily migrate to the newly grown green grasses in the past monsoon period and become easily available to the susceptible host and thereby resulting in higher infection in the post-monsoon period.

Distribution and adaptation of GIN to the changing climate

Parasites including GIN are perhaps subjected to rapid evolution under the changing climate conditions. Effective population size increases, generation times become short, but transmission inflicts a strong filter to exclude ill adaptation in GIN population in the epoch of changing environmental conditions. The complex link between environmental variation and transmission rate of GIN infective larvae suggested that the identification of anthropogenic activities influencing the evolutionary response of GIN to the natural variation could be difficult. The prediction models in this regard suggest that increased seasonal climatic variation would steer the increased resilience of GINs to environmental oscillations.

There is no published data on the distribution and biogeography of GIN of livestock in many parts of the world (Morgan and van Djik, 2012) including the Indian sub-continent. Several studies have been carried out to record the prevalence of GIN at diverse localities in the world (Ibrahim *et al*., 2014; Owusu *et al*., 2016; León *et al*., 2019) including sporadic studies in India (Singh *et al*., 2012; Brahma *et al*., 2015, 2018; Jas *et al*., 2017, 2020). These studies provide a qualitative picture of the distribution and relative importance of different GIN species in different regions. Under field conditions, mixed infections with different types of GINs are evident in all the regions. In India, *H. contortus* is the predominant species both in the hotter parts as well as cooler parts of the country indicating its better adaptation with the changing climatic condition. *Haemonchus contortus* is better suited in the hot and humid condition, but it is also prevalent in arid and semi-arid regions of Rajasthan, India (Suresh *et al*., 2022). Similarly, in Europe, Kao *et al*. (2000) reported that *H. contortus* was more common in wormer Southern Europe, while, *Oestertagia* (*Teladorsagia*) *circumcincta*, *Nematodirus battus* were more prevalent in the temperate region and colder Northern Europe. However, the prevalence of *H. contortus* has started to increase in temperate and cold Northern Europe (Kenyon *et al*., 2009), and it is becoming an important disease condition in that region (van Dijk *et al*., 2008, 2009). These observations have raised the question of whether *H. contortus* is adapting to cooler condition/lower temperature. Troell *et al*. (2005) suggest that rather than adaptation, it was the tolerances of the free living stages of *H. contortus* to the hostile environment, and that could be due to increased hypobiosis as a strategy for over wintering (Troell *et al*., 2006). Complementary to hypobiosis, the phenotypic adaptation, the tendency of *H. contortus* larvae to undergo developmental arrest in adverse climatic conditions could account for natural selection.

In contrast to *H. contortus*, *Nematodirus battus* has been better adapted in the cooler and temperate region of northern Europe because eggs of *N. battus* require chilling at a temperature below 11°C before hatching (van Dijk and Morgan, 2008). In southern Europe, where winter temperature is higher than 11°C, *N. battus* has been found to infect ruminant livestock (Torina *et al*., 2004). The survivability of the parasite to a warmer climate in Southern Europe might be through rapid adaptation to the changing environmental condition to modify its requirement for hatching and development (van Dijk and Morgan, 2009). The mechanism of adaptation of GINs to local climate change are not properly understood and not been detected by experimental comparison of specific traits (Morgan and van Dijk, 2012). A better understanding of these mechanisms is a prerequisite to predict parasite distribution and behaviour in changing climatic conditions as well as in the environment.

Control programmes and predictive models for epidemiology

Very less information is available currently on climate change and GIN infection in animals. Effective climate-based forecasting had been developed for ruminants Fasciolosis about the five decades ago (Fox *et al.*, 2012). Exploration of the effects of climate change on GIN ecology offers many opportunities for useful comparisons across GIN and hosts and across the ecosystem (Polley *et al.*, 2010). Alterations in parasite ecology, epidemiology and evolution have a great impact on the monitoring and control of parasitic diseases including GIN in livestock. The evidence-based risk assessments and targeted surveillance are the most important tasks to prevent economic losses due to subclinical GIN infections in small ruminants (Wilson and Mellor, 2008). Despite the severe economic impacts of GI helminths on the livestock production system and their interaction with climatic conditions, prediction of long-term threats due to climate change has so far been concentrated on heat stress in animals (Nardone *et al.*, 2006; Beatty *et al.*, 2008; Gregory, 2010). Although a number of studies aim to link the recent variation in helminth prevalence and distribution with altered environmental conditions (O'Connor *et al.*, 2006; Mas-Coma *et al.*, 2008; van Dijk *et al.*, 2008), there is a lack of an appropriate model for GIN infection prediction.

Mathematical and simulation models can improve the predictive ability in the face of climate change and variable GIN challenges and focus on the judicious use of anthelmintic to delay the process of anthelmintic resistance. Mainly two types of predictive models, correlative model and mechanistic model, have been described to predict the occurrence of GI helminths infection based on meteorological parameters.

The correlative models are framed on Hutchinson's ecological niche theory, where current geographic distribution is utilized to deduce the environmental conditions required by a species (Lawler *et al.*, 2006; Leathwick *et al.*, 2006; Engler and Guisan, 2009; Pagel and Schurr, 2012). The present, past or future distribution of GI helminths has been predicted based on these requirements (Hijmans and Graham, 2006). A number of programmes are available to represent GI helminths and climate interaction by matching current distribution with climatic parameters, such as CLIMEX (Sutherst and Maywald, 1985), HABITAT (Walker and Cocks, 1991), DOMAIN (Carpenter *et al.*, 1993) and SPECIES (Pearson *et al.*, 2002). In India, the software FROGIN for forecasting of GI nematodoses in sheep has been developed. FROGIN is a mathematical model (regression analysis) based on development and mortality rate, climatic data and these data are used to predict the level of pasture contamination and subsequent possible intensity of infection (Shinde *et al.*, 2016.).

The second model is process based mechanistic approach which are based on detailed knowledge of parasite physiology, and it has attempted to copy the basic mechanisms that drive the parasite's response to environmental components (Robertson *et al.*, 2003). In practice, it is very hard to find distinction between correlative and mechanistic modelling techniques and therefore, an integration of both techniques may be needed for future improvements in prediction. Regular collection of active surveillance data and actual data on physiological responses of GINs to climate change would ultimately steer the development as well as validation of meaningful prediction of GIN epidemiology

(Fox *et al.*, 2012). Future model should take an account of management factors as they have an important effect on infection patterns (Morgan and Wall, 2009; Wall *et al.*, 2011). Good models would be able to focus on anthelmintic treatment to have a maximum sustainable economic benefit and also identify suitable management interventions to decrease the negative impact of climate change on the infected host.

Although the climate is an important driving factor of helminth distribution, transmission to livestock is also influenced by husbandry practices. The adoption of mitigation and adaptation strategies for livestock management is essential under continuing environmental change. Management of heat stress in cattle has been explored including shade provision (Kendall *et al.*, 2006) and different feeding and sprinkling regimes (Mader and Davis, 2004). Additionally, certain breeds of animals are more susceptible to extreme weather conditions, and therefore, the breed structure of livestock is to be considered to ensure optimum production levels. Also, different breeds of animals have varying levels of susceptibility to diseases (Harle *et al.*, 2007; Wilson and Mellor, 2008; Eguale *et al.*, 2009), and the differing degree of resistance for future breed structures need to be incorporated in transmission models. There is a tendency for the predictive models to include ever refined climate prediction; however, these will not provide meaningful indications of future risk. The impact of these adaptation and alleviation strategies must be incorporated in parasite transmission models. The aim of all these strategies and interpretations is to control the naturally occurring GIN in ruminant livestock.

Use of anthelmintics is the corner-stone for controlling helminths in ruminant livestock, however, emergence of anthelmintic resistance is the main constraint (DeVaney *et al.*, 1992; Yadav *et al.*, 1995; Ketzis *et al.*, 2006; van Dijk *et al.*, 2008) and resistance development could be enhanced due to global warming (Wolstenholme *et al.*, 2004). Therefore, it is the need of the hour to adopt strategies to decrease the dependence on chemicals and prevent the spread of resistance (Ketzis *et al.*, 2006; Waller, 2006; Torres-Acosta and Hoste, 2008). With the increasing prevalence of anthelminthic resistance, there is a need for strategic treatment to target animals to keep the resistant nematode population at a level below the economically damaging level and to maintain susceptible genotypes of GIN in the refugia (Coles, 2002). There is number of alternative strategies that are being evaluated for green animal production. Grazing management is one of the alternative strategies to lower the number of infective larvae on the pasture. Selective breeding of GIN-resistant animals would be a promising, sustainable and affordable alternative approach to control GIN infection (Baker *et al.*, 2001; Lôbo *et al*, 2009; Karrow *et al.*, 2014; McRae *et al.*, 2014; Aguerrea *et al.*, 2018) as it can be transmitted to future generation, improves animal performance, reduce pasture contamination and enhance socio-economic viability of livestock owners. Knowledge of the impact of climate on the epidemiology of GIN is essential, and it can be supplemented by better understanding of the interaction effects between the climatic factors and managemental practices on larval availability and infection to the host.

Conclusion

Climate change has harmful effects on livestock throughout the world. Changes in the epidemiological pattern of GIN require new studies on the biology and physiology of those GIN to design effective measures in the changing trend of climate in an area. There should be an integrative, multidisciplinary and ecological approach that would make possible to identify parasitic infections likely to be susceptible to climate change and with adjustments for regional variations. The segregation of each environmental components to define its level of interaction with the larval behaviour on the pasture is not yet practicable. The contribution of the forage species as well as the species of GIN is also notable in the free-living larval population on the pasture. Knowledge of these facts should be correctly implemented to plan for strategic anthelmintic treatment in the infected population of livestock. Further, laboratory and field data on the understanding of the effects of some climatic factors are crucial elements for an improved predictive model of GIN infection occurrence in ruminant livestock. Models should be developed with the framework to incorporate the interacting effects of changes in climate, management and control strategies.

Conflict of interest: Authors have no conflict of interest in this study.

Author's contribution: RJ: Conceptualization; supervision and final editing; AH: Preparing original draft; SD: Resources; SP: Data presentation; SB: Resources; MK: Editing.

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Received- 25.10.2022, Accepted- 23.11.2022, Published- 01.12.2022 (Print)

Section Editor: Dr. I. Samanta, Associate Editor