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Genetic, host and environmental factors associated with a high prevalence of *Anaplasma marginale*

Jeiczon Jaimes-Dueñez, Omar Triana-Chávez, Ana M. Mejía-Jaramillo*

Grupo BCEI, Universidad de Antioquia UdeA, Calle 70 No. 52-21, Medellín, Colombia

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ABSTRACT

Anaplasma marginale is the most prevalent vector-borne pathogen in the livestock industry in Colombia, causing economic losses of approximately USD 4.2 million per year. The present study reports the seasonal transmission patterns, genetic diversity and phylogeographic traits of *A. marginale* strains in cattle and buffaloes from Colombian livestock areas. A three-point longitudinal survey was designed to evaluate the above characteristics of farms in the Caribbean and Orinoquía regions. The *A. marginale* prevalence was evaluated in 1432 cattle blood samples, 152 buffalo blood samples and the hemolymph of 439 ticks using semi-nested PCR (sn-PCR) targeting the *msp5* gene. The molecular prevalence in cattle and buffaloes was 54.8% and 13.1%, respectively, with higher values during the wet and late wet seasons. Factors such as age and production system were significantly associated with the infection. *Rhipicephalus microplus* was the only carrier of *A. marginale* DNA, with an infection rate of 17.2%. On the other hand, the tandem repeat and microsatellite analyses of the *msp1α* gene showed high genetic diversity and new tandem repeats that suggested strain adaptation to different transmission modes. Phylogeographic analysis using the *msp4* gene showed a relationship between Colombian isolates and Mexican, Brazilian, Venezuelan, European and Asian isolates, as well as two worldwide haplogroups that were associated with the geographical origin of each isolate. In conclusion, this study shows that *A. marginale* occurs under enzootic stability in both hosts, with a high prevalence of infection during wet months and in animals dedicated to beef production. The genetic variability analyses suggest that a high strain diversity is associated with multiple selective pressures in the study area, while phylogeographic traits suggest a high genetic similarity between Mexican and South American strains.

1. Introduction

Anaplasmosis, caused by the intraerythrocytic rickettsia *Anaplasma marginale* (Rickettsiales: Anaplasmataceae), is an economically important disease of livestock that is endemic in tropical and subtropical regions of the world (Aubry and Geale, 2011; Kocan et al., 2004). Clinical signs such as anemia, icterus, fever, and lethargy are most notable in cattle, but other ruminants, including water buffalo, bison and African antelopes, can also become infected (Kuttler, 1984). Although cattle are susceptible to infection, those that survive the acute infection develop persistent infections characterized by cyclic rickettsemia (French et al., 1999) and lifelong immunity with resistance to symptomatic disease (Kocan et al., 2003), and they act as reservoirs for pathogen transmission (Palmer et al., 2001).

A. marginale is transmitted biologically by approximately twenty tick species (mainly in the genera *Rhipicephalus*, *Dermacentor* and *Ixodes*), mechanically by biting flies (mainly Diptera of the genera *Tabanus* and *Stomoxys*), or by blood-contaminated fomites (Ewing, 1981; Hawkins et al., 1982; Kocan, 1986). The latter is considered to be the major route of dissemination in areas of Central and South America and Africa, where tick vectors do not occur and where *Rhipicephalus microplus*, the tropical cattle tick, does not appear to be a biological vector of *A. marginale* (Coronado, 2001; Figueroa et al., 1998). Additionally, transplacental transmission has been reported in cattle (Grau et al., 2013; Zaugg, 1985), showing an evolutionary ability that allows the bacterium to adapt to different modes of transmission, depending on the ecological conditions (Estrada-Peña et al., 2009).

Many geographic strains of *A. marginale* have been identified worldwide, which differ in morphology, antigenic characteristics and their ability to be transmitted by ticks (Cabezas-Cruz et al., 2013; de la Fuente et al., 2001a; Kocan et al., 2004; Smith et al., 1986). Therefore, its genetic characterization has been crucial to the development and implementation of epidemiological studies and control strategies (Cabezas-Cruz and de la Fuente, 2015). In this sense, major surface proteins (MSPs) of *A. marginale* involved in the interaction with the host cells and its tick vector have been used as genetic markers for the

* Corresponding author at: Grupo Biología y Control de Enfermedades Infecciosas, Universidad de Antioquia, Calle 70 No. 52-21, Medellín, Antioquia, Colombia.
E-mail address: anamejia25@gmail.com (A.M. Mejía-Jaramillo).

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characterization of worldwide strains (Cabezas-Cruz et al., 2013; Palmer et al., 1999). MSP1a is encoded by the *msp1α* gene, and it is involved in adhesion of bacteria to bovine erythrocytes and tick cells (de la Fuente et al., 2001b; McGarey et al., 1994). The genetic features of this marker include a tandem repeat coding for amino acids at the N-terminal domain, which show higher mutability than the rest of the protein (Bowie et al., 2002), and a microsatellite ((G/A TTT)m(GT)nT) region, located in the 5′UTR between the putative Shine-Dalgarno sequence (GTAGG) and the translation initiation codon (ATG) (Estrada-Peña et al., 2009). Strains with different tandem repeat patterns differ in the biology and transmissibility by ticks (de la Fuente et al., 2007), while changes in the length of the microsatellite are correlated with the expression level of MSP1a, possibly affecting the pathogenicity and transmission of *A. marginale* (Estrada-Peña et al., 2009). On the other hand, the *msp4* gene, although it codes for an immunogenic protein, MSP4 (Molad et al., 2004), has shown phylogeographic relationships between isolates from Mexico, Brazil, Argentina, Australian and India, suggesting similar evolutionary processes between these isolates (de la Fuente et al., 2004; George et al., 2017).

Colombia is the third largest livestock producer in South America, with approximately 22.7 million cattle and 250,000 buffaloes, which represent around 5% of the national gross domestic product (ICA, 2016). In this country, *A. marginale* is endemic at altitudes lower than 1000 m, causing economic losses of approximately USD 4.2 million per year (Corrier and Guzman, 1977; Otte, 1992; Viscaíno and Benavides, 2004). In these areas, previous parasitological and molecular surveys of *A. marginale* conducted in commercial cattle showed prevalences between 14.5 and 59.3% (Blanco et al., 2016; Herrera et al., 2008; Jaimes-Dueñez et al., 2017), while for buffaloes, 56% prevalence was observed (Ríos-Osorio et al., 2010). These studies showed that although in most herds, *A. marginale* occurs under enzootic stability without clinical signs associated with the infection, significant differences in its prevalence were observed (Herrera et al., 2008; Jaimes-Dueñez et al., 2017; Timaran and Leon, 2013), modifying the immunological state of the population and causing clinical outbreaks in the susceptible ones. Given that the transmission rate of *A. marginale* can be modulated by several factors, including environmental conditions, management systems, and host and parasite traits (Estrada-Peña et al., 2009; Guglielmone, 1995; Zaugg, 1990), the aim of this survey was to investigate the dynamic of transmission of *A. marginale* in cattle and buffaloes from Colombian livestock regions. Moreover, the genetic diversity and phylogeographic relationship of *A. marginale* isolates were analyzed to understand the genetic traits of Colombian strains and their similarity with strains of neighboring countries.

2. Materials and methods

2.1. Study area

This study was performed from October 2014 to March 2016 on ten farms of the Antioquia department (A–J) (Fig. 1A) and ten farms of Arauca (K–T) (Fig. 1B), which represented 11.7% and 4.6% of the national livestock population, respectively (ICA, 2016). The farms of Antioquia were located in the municipalities of Necoclí and Turbo in the Caribbean region in the northwest section of the country (Fig. 1A), at altitudes under 8 m, with an annual biotemperature average of 26 °C and rainfall of 2400 mm, distributed over a dry season from January to March, a wet season from April to September, and a late wet season from October to December (IDEAM, 2014). The farms of Arauca were located in the municipalities of Arauquita, Saravena and Tame in the Orinoquía region in the east of the country (Fig. 1B), at altitudes under 231 m, with an annual biotemperature average of 27 °C and rainfall of 2500 mm, distributed over a dry season from November to March, a wet season from April to July, and a late wet season from August to October (IDEAM, 2014).

Ninety-five percent of the farms employ extensive farming systems, where animals are fed with *Brachiaria* spp., and native grasses are at densities of 1.314 (SD = 0.359) livestock units (LUs) per hectare (ha), and the rest use the intensive farming system. The main species of cattle is *Bos indicus*, with breeds such as the Brahman, Gyr and Guzerat, and its crosses with *B. taurus*, including breeds such as Limousin, Brown Swiss and Holstein Friesians. For buffaloes, the main species is *Bubalus bubalis*, with breeds such as Carabao, Mediterranean, Murrah and their crosses. *A. marginale* control is based on vector control carried out with insecticides and acaricides such as avermectins, organophosphates and pyrethroids, as well as the use of antibiotics such as oxytetracycline. Additional information about the geographic location and characteristics of each farm is shown in Table S1.

2.2. Study design

According to previous epidemiological studies (Reye et al., 2010; Saetiew et al., 2014; Velusamy et al., 2014), a three-point longitudinal survey was designed to examine seasonal variations of *A. marginale* infection in the study area in cattle, buffaloes and ticks during the dry season (February), wet season (June) and the late wet season (October) (Fig. 1C and D).

2.3. Blood sample collection

Cattle samples (Table S1) were collected on nine farms of Antioquia (A-I) (Fig. 1A) and ten farms of Arauca (K–T) (Fig. 1B), whereas buffalo samples were collected on three farms of Antioquia (H–J) (Fig. 1A). The sample size was calculated using Epi Info™ 7.0, taking into account the number of cattle or buffalo in the farms of each department, a 22.5% probability of being infected according to Herrera et al. (2008), a 95% confidence interval and a statistical error of 5%. Within each farm, the samples were collected randomly, considering the percentage of animals ≤ 1 year old and > 1 year old according to Amorim et al. (2014) and Jaimes-Dueñez et al. (2017). For each animal, 5 ml of blood was collected from the coccygeal or jugular vein using EDTA.K3 Vacutainer tubes (Improve Medical, Guangzhou, China) and stored at 4 °C until processing. Additional information about the number of samples collected on each farm during each sampling is detailed in Table S1.

2.4. Tick sample collection

Between five and twenty ticks were collected from the highly infested animals selected for blood sampling, along with others located on the same farms, using entomological forceps through examination of the perineum surface according to Baker and Ducasse (1967). All collected specimens were directly preserved in 70% ethanol and stored at 4 °C until processing.

2.5. Sample processing

Blood samples were transferred within six hours after collection into a glass micro-hematocrit capillary tube containing Na-heparin (80 IU/ml) (Vitrex Medical, Copenhagen, Denmark), sealed at one end with Cristaseal (Hawksley, Lancing, United Kingdom) and centrifuged for 5 min at 9000 rpm at room temperature to measure the packed cell volume (PCV) in a micro-hematocrit capillary tube reader (Bacto, Sydney, Australia). Genomic DNA was extracted from 200 µl of blood using the Genomic DNA Purification Kit (Invisorb, Birkenfeld, Germany) according to the manufacturer's instructions. Total DNA was diluted with 100 µl of elution buffer and stored at −20 °C until molecular diagnosis.

Tick samples were initially examined under a stereomicroscope (Leica Microsystems, Mannheim, Germany) and classified up to the species, sex and life stage according to morphological keys reported for ticks of veterinary importance in South America (Barros-Battesti et al., 2006). After that, the specimens were grouped in pools of one to five

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