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Review

Acaricide resistance in cattle ticks and approaches to its management: The state of play

Rao Z. Abbas[a,*], Muhammad Arfan Zaman[b,c,**], Douglas D. Colwell[d], John Gilleard[e], Zafar Iqbal[a]

[a] Department of Parasitology, University of Agriculture, Faisalabad, Pakistan
[b] Section of Parasitology, Department of Pathobiology, College of Veterinary and Animal Sciences, Jhang, Pakistan
[c] Sub-Campus University of Veterinary and Animal Sciences, Lahore, Pakistan
[d] Livestock Parasitology, Agriculture and Agri-Food Canada, Lethbridge Research Centre, 5403 1st Avenue South, Lethbridge, AB T1J 4B1, Canada
[e] Department of Comparative Biology and Experimental Medicine, Faculty of Veterinary Medicine, Room HSC 2557, 3330, Hospital Drive, University of Calgary, Calgary, Alberta T2N 4N1, Canada

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ABSTRACT

Cattle ticks are an important constraint on livestock production, particularly in tropical and subtropical areas. Use of synthetic acaricides is the primary method of tick control; therefore, it would be imperative to develop strategies to preserve the efficacy of existing acaricides. This paper summarizes the status of acaricide resistance in cattle ticks from different parts of the world and reviews modes of action of currently used acaricides, mechanism of resistance development, contributory factors for the development and spread of resistance, management of resistant strains and strategies to prolong the effect of the available acaricides. Use of vaccines, synthetic and botanical acaricides and educating farmers about recommended tick control practices are discussed, along with the integration of currently available options for the management of drug resistance and, ultimately, the control of cattle ticks.

Contents

* Corresponding author. Mobile: +92 3006682811.
** Corresponding author at: Section of Parasitology, College of Veterinary and Animal Sciences, Jhang, Pakistan. Tel.: +92 463 513554; fax: +92 47 9200393; mobile: +92 3332008334.
E-mail addresses: raouaf@hotmail.com (R.Z. Abbas), arfan.zaman@uvas.edu.pk (M.A. Zaman).

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1. Introduction

Rhipicephalus microplus (formerly *Boophilus microplus*), the tropical or southern cattle tick, is considered to be the most important tick parasite of livestock in the world. Heavy tick burdens cause huge economic losses through blood loss, general stress and irritation, decrease in productivity, depression of immune function, damage to hides and transmission of pathogens (de Castro, 1997; Alim et al., 2012; Valente et al., 2014) like *Babesia bigemina*, *B. bovis* and *Anaplasma marginale*.

R. microplus control chiefly depends upon prophylactic chemotherapy with acaricides (Angus, 1996; Mendes et al., 2013). Acaricides form the center of control and eradication efforts because they offer relatively quick and cost-effective suppression of tick populations. Long-term use, however, has generated acaricide resistance (Table 1) in many tick species (Harris et al., 1988; Raynal et al., 2013); thereby, reducing the ability to control them. Periodic monitoring of the ticks for development of resistance against commonly used acaricides is, therefore, very important for economic livestock production. Increased awareness and improved socio-economic conditions of the farmers in addition to state sponsored animal health facilities in industrialized/developed countries have led to frequent reports on the acaricides resistance (Hagen, 1997; Baxter and Barker, 1999; Chen et al., 2007; Rodriguez-Valle et al., 2012a; Molento et al., 2013). This paper discusses different aspects of acaricide resistance in the following sections for better understanding and control of resistant tick species with particular emphasis on *R. microplus*.

2. What is resistance?

Resistance is generally first recognized as failure of a drug to control parasitism but the formal definition of resistance is a shift in the target species susceptibility to a drug (Sangster, 2001; Corley et al., 2013). World Health Organization Scientific Group (1965) has developed the definition of resistance in broad terms as "the ability of a parasite strain to survive and/or to multiply despite the administration and absorption of a drug given in doses equal to or higher than those usually recommended but within the limits of tolerance of the subject". Such a general definition could be accepted as a basis for discussions on acaricide resistance.

3. Types of resistance

3.1. Acquired resistance

Acquired resistance is defined as "resistance that results from heritable decreases in sensitivity to drugs with the passage of time" (Chapman, 1997; Meyer et al., 2012). For example, acquired resistance was induced in *Tetranychus cinnabarinus* against two acaricides. After 42 generations of selection with abamectin and 20 generations of selection with fenpropethrin in the laboratory, *T. cinnabarinus* developed 8.7 and 28.7-fold resistance, respectively (Lin et al., 2009; Feng et al., 2011).

There is a direct relationship between concentration of the drug and degree of resistance. A strain controlled by one dose of a drug may show resistance when a lower concentration of the same drug is administered (Mitchell, 1996; Lees et al., 2013). This may allow for the selection of initially resistant mutants to low levels of drug (Lin et al., 2009; Faza et al., 2013). Continued exposure to an acaricide results in removal of the susceptible members of the population with a concomitant increase in the proportion of the resistant strains, i.e., a process of selection for resistance.

Table 1
Reports of resistance in cattle ticks against acaricides.

Drug (approximate date introduced)	Country	Reference	Year	Species studied
Organochlorines (1946)				
DDT	Australia	Stone and Webber	1960	B.m
BHC	Australia	Stone and Webber	1960	B.m
Dieldrin	Australia	Stone and Meyers	1957	B.m
	Australia	Stone and Webber	1960	B.m
	Tanzania	Kagaruki	1991	B.m; B.d; A.spp.; R.spp.
	Ethiopia	Regassa and de Castro	1993	B.d; R.spp.
	Mexico	Ortiz et al.	1995	B.m
	Brazil	Arantes et al.	1996	B.m
	Colombia	Romero et al.	1997	B.m
Lindane	equatorial and southern Africa	Baker and Shaw	1965	R. spp.
	Tanzania	Kagaruki	1991	B.m; B.d; A.spp.; R.spp.
	Mexico	Ortiz et al.	1995	B.m
Toxaphene	Australia	Norris and Stone	1956	B.m
	Ethiopia	Regassa and de Castro	1993	B.d
	Colombia	Benavides	1995	B.m
	equatorial and southern Africa	Baker and Shaw	1965	R. spp.
Organophosphates (1955)				
Coumaphos	Colombia	Benavides	1995	B.m
	Venezuela	Coronado	1995	B.m
	Mexico	Ortiz et al.	1995	B.m
	Colombia	Romero et al.	1997	B.m
	Mexico	Rosario et al.	1997	B.m
Cyclophos	Colombia	Benavides	1995	B.m
Chlorpyriphos	Mexico	Ortiz et al.	1995	B.m
Chlorfenvinphos	Venezuela	Coronado	1995	B.m
	Colombia	Romero et al.	1997	B.m
Diazinon	Colombia	Benavides	1995	B.m
	Mexico	Ortiz et al.	1995	B.m
	Colombia	Romero et al.	1997	B.m
Dioxathion	Zambia	Luguru et al.	1987	B.d; A.spp.
	Zimbabwe	Bruce and Mazhowu	1992	B.d
	Mexico	Ortiz et al.	1995	B.m
Dimethoate	Zambia	Luguru et al.	1987	B.d; R.spp.
	Mexico	Ortiz et al.	1995	B.m
Ethion	Colombia	Benavides	1995	B.m
	Mexico	Ortiz et al.	1995	B.m
Carbamates (1955)				
Carbaryl	Jamaica	Rawlins and Mansingh	1978	B.m
	India	Basu and Haldar	1997	B.m
	Mexico	Li et al.	2005	B.m
Formamidines (1975)				
Amitraz	Colombia	Benavides	1995	B.m
	Brazil	Martins et al.	1995	B.m
	Australia	Baxter and Barker	1999	B.m
	Mexico	Soberanes et al.	2002	B.m
	New Caledonia	Chevillon et al.	2007	B.m
	US	Chen et al.	2007	B.m
Pyrethroids (1977)				
Alpha cypermethrin	India	Bagherwal et al.	1995	H. spp.
	Brazil	Arantes et al.	1996	B.m
	Colombia	Romero et al.	1997	B.m
	Mexico	Rosario et al.	1997	B.m
Cypermethrin	Australia	Schnitzerling et al.	1989	B.m
	Zimbabwe	Bruce and Mazhowu	1992	B.d
	Colombia	Benavides	1995	B.m
	Mexico	Ortiz et al.	1995	B.m
	Brazil	Martins et al.	1995	B.m
	Brazil	Arantes et al.	1996	B.m
	Colombia	Romero et al.	1997	B.m
	Brazil	Mendes et al.	2007	B.m
	Iran	Khaladj et al.	2007	H. spp.
	Iran	Enayati et al.	2010	R. spp.
λ-Cyhalothrin	Brazil	Mendes et al.	2007	B.m
	Iran	Enayati et al.	2010	R.spp.

Table 1 (*Continued*)

Drug (approximate date introduced)	Country	Reference	Year	Species studied
Permethrin	New Caledonia	Beugnet	1996	B.m
	USA	Davey and George	1998	B.m
	Panama	Miller et al.	2001	R.spp.
	Brazil	Baffi et al.	2007	B.m
	Iran	Enayati et al.	2009	R.spp.
Deltamethrin	New Caledonia	Brun	1992	B.m
	New Caledonia	Beugnet et al.	1994	B.m
	Colombia	Benavides	1995	B.m
	Mexico	Ortiz et al.	1995	B.m
	Brazil	Martins et al.	1995	B.m
	Brazil	Arantes et al.	1996	B.m
	Colombia	Romero et al.	1997	B.m
Cyfluthrin	Brazil	Arantes et al.	1996	B.m
	USA	Hagen	1997	B.m
Flumethrin	Zimbabwe	Bruce and Mazhowu	1992	B.d
	New Caledonia	Beugnet et al.	1994	B.m
	Mexico	Ortiz et al.	1995	B.m
	New Caledonia	Beugnet and Chardonnet	1995	B.m
	Brazil	Martins et al.	1995	B.m
	Colombia	Benavides	1995	B.m
	New Caledonia	Beugnet	1996	B.m
	USA	Hagen	1997	B.m
Fenvalerate	New Caledonia	Beugnet et al.	1994	B.m
	New Caledonia	Beugnet and Chardonnet	1995	B.m
Macrocyclic lactones (1981)				
Avermectin	Brazil	Martins and Furlong	2001	B.m
Ivermectin	Mexico	Perez-Cogollo et al.	2010	B.m

B.m. *Boophilus microplus*; B.d. *Boophilus decoloratus*; B.a. *Boophilus annulatus*; A.ssp. *Amblyomma species*; H.spp. *Hyalomma species*; R.spp. *Rhipicephalus species*.

3.2. Cross-resistance

Cross-resistance is the sharing of resistance among different acaricides with a similar mode of action. A significant pattern of cross resistance has been shown among two organophosphates (coumaphos and diazinon) and one carbamate (carbaryl) acaricides in several strains of *R. microplus* (Li et al., 2005; Madder et al., 2011; Perez-Gonzalez et al., 2014). Both carbamates and organophosphates acaricides exert their toxic effects on insects or ticks by inhibiting acetylcholinesterase (AChE), a key enzyme critical to the function of the nervous system of invertebrates (Siegfried and Scharf, 2001; Jensen et al., 2011). Insensitivity of AChE is considered as an important mechanism of resistance against carbamates and organophosphates (Fournier and Mutero, 1994; Dawkar et al., 2013). Rotation or alternation of different groups of acaricides that have no cross resistance reduces the selection pressure for resistance to any one acaricide group.

3.3. Multiple resistance

Multiple resistance is a resistance to more than one drugs, even though they have different modes of action. In Mexico, Foil et al. (2004) have shown a significant occurrence of multiple resistance in populations of southern cattle ticks, *R. microplus*, to many classes of acaricide including chlorinated hydrocarbons (DDT), pyrethroids, organophosphates and formamidines (amitraz). Target site mutations were the most common resistance mechanism observed in the Mexican ticks for these chemicals, but multiple resistance against acaricides with different modes of action also leads one to suspect that resistance may be metabolic (Sammataro et al., 2005; Bielza et al., 2007).

4. Factors involved in resistance development

4.1. Genetic factors

Parasite genetic factors include dominance of resistance alleles, number of genes involved, initial frequency of resistance genes, genetic diversity of population, relative fitness of resistant organisms, chance of linkage disequilibrium and opportunity for genetic recombination (Georghiou and Taylor, 1977; Mulchandani et al., 1998).

Sutherst and Comins (1979) describe the genesis of resistance in three steps. The first is establishment of resistance, second step is development of resistance and the third is emergence of resistance. In many cases, it is possible that genes responsible for the onset of resistance are already present at very low levels in the tick population before the introduction of a new acaricide (Nolan, 1987; Alonso-Diaz et al., 2013). The frequency of resistant alleles increases with the continued selection pressure of acaricide (Aguilar-Tipacamu et al., 2011; Rodriguez-Vivas et al., 2011). The length of time required for resistant alleles to become established and for the control of ticks to break down and the rate at which it becomes established in the population depend on many factors. These factors include the frequency of original mutation in the population before treatment, the mode of inheritance of the resistant allele (dominant, co-dominant or recessive), the frequency of acaricide treatment, the concentration gradient of the acaricide and the proportion of the population in refugia (i.e.

the population of ticks not exposed to acaricide) (Sangster, 2001; Bardosh et al., 2013).

Although frequency of resistant genes initially increases slowly, however, by the time declining efficiency of treatment is noticed, the frequency of resistant genes is usually high (Stutzer et al., 2013). In the initial phase, the frequency of heterozygous resistant individuals (single allele mutation) within the population and the rate of increase in the frequency of the resistant allele are low. In the emerging phase, given continued exposure to a drug, the frequency of heterozygous resistant individuals within the population increases. Finally, sustained selection pressure results in increasing numbers of homozygous resistant individuals, which ultimately predominate in the population. Selection for some organisms may involve a single gene for resistance or several genes may be selected, often sequentially. However, genetic factors are hard to manage as they are not under human control (Chevillon et al., 2013).

4.2. Operational factors

Operational aspects include chemical nature of drug, possibility of cross resistance, drug persistence in the host and drug clearance kinetics. Drug application factors include application and selection threshold, life stage(s) selected, mode of application, frequency of treatment, timing of treatments, spatial use of treatments and using other forms of control. Another contributing factor in the development of acaricide resistance may be under dosing which may be the result of poor drug quality. This may allow for the selection of mutants initially resistant to low levels of acaricides (Bianchi et al., 2003; Shyma et al., 2012; Rezende et al., 2013). Drug-resistant parasites are more likely to be selected if parasite populations are exposed to sub-therapeutic drug concentrations through (1) unregulated drug use, (2) use of inadequate treatment regimens and (3) the use of long half-life drugs.

Among operational factors, the most important one is the frequent use of the same acaricide for a long period of time. A study in Queensland, Australia, showed that greater than five treatments per season is a positive risk factor for acaricide resistance (Jonsson et al., 2000) suggesting that high treatment frequency predisposes cattle ticks to selection for resistance. It is also important to know that the degree of resistance against different classes of acaricides may show great variations in different countries because of variations in their use of frequency. In several Mexican tick strains, the resistance ratios for organophosphates were lower than those for pyrethroids (Céspedes et al., 2005; Mendes et al., 2007), although in some cases, *R. microplus* was resistant to pyrethroids but susceptible to coumaphos (Jonsson et al., 2000; Alonso-Diaz et al., 2013). But, in contrast to Mexican ticks, Iranian ticks showed lower resistance ratios for pyrethroids than those for organophosphates (Enayati et al., 2009, 2010). The authors suggested that this might be because pyrethroids have not been heavily used for tick control and general agricultural activities in Iran.

Unlike genetic factors, operational factors can be controlled by proper management by the operators, particularly, by educating the livestock farmers about the rationale use of the acaricides.

4.3. Biological factors

Biological factors are classified as biotic or behavioral. Biotic factors include generation time, offspring per generation and breeding patterns. Behavioral aspects are those that affect gene flow and the chance of selection (Abdullah et al., 2012). These include isolation, mobility, migration, monophagy or polyphagy (host range), fortuitous survival and refugia.

The biological aspects, mainly associated with the host–parasite relationship, also influence the mechanism of selection for resistance. For example, parasites which induce effective immunity in their hosts will be under weaker selection pressure for resistance because immunity selects parasites irrespective of drug-resistance status and this reduces the chance of resistant parasites surviving and reproducing. The pathogenicity of the parasite will influence how many parasites are required to affect production and, therefore, how often treatments are given. It is well known that higher the proportion of population in refugia, slower will be the selection for resistance (Sangster, 2001; Abdullah et al., 2012).

5. Mechanisms of acaricide resistance

It is impossible to understand the mechanisms involved in the development of resistance in cattle ticks without understanding basic knowledge of mode of action of acaricides (summarized in Table 2).

5.1. Resistance against organochlorines

Organochlorines have been in use as acaricides since 1946. They were the first synthetic insecticides to be marketed and many of them were formulated for the control of ticks on cattle. The mode of action of these compounds is thought to involve binding at the picrotoxinin site in the γ-aminobutyric acid (GABA) chloride ionophore complex (Lawrence and Casida, 1983; Hope et al., 2010) which inhibits Cl^- flux into the nerve (Bloomquist and Soderlund, 1985; Corley et al., 2012). With the function of the GABA-ergic inhibitory neurons impaired, hyperexcitation results which ultimately causes death. Furthermore, some researchers (Tanaka et al., 1984; Zheng et al., 2003) have also shown the binding of several organochlorines at the picrotoxinin site at which t-butylbicyclophosphorothionate (TBPS) also binds. The mechanisms of resistance have been suggested to be primarily enhanced metabolism and reduced absorption of the chemical (Brown, 1969).

5.2. Resistance against organophosphates and carbamates

Organophosphates (OPs) were among the first chemical groups used to control arachnids. Both OPs and carbamate acaricides exert their toxic effects on ticks by inhibiting

Table 2
The common acaricides with their mode of action.

Class of acaricides	Commonly used acaricides	Site of action	Mode of action	Reference
Organochlorides	Lindane & dieldrin	Nervous system	GABA-gated chloride channel antagonists	Lawrence and Casida (1983)
Organophosphates	Coumaphos & diazinon	Nervous system	Acetylcholine esterase inhibitors (irreversible)	Li et al. (2003)
Carbamates	Carbaryl	Nervous system	Cholinesterase inhibitors	Li et al. (2005)
Pyrethrins/pyrethroids	Cypermethrin & permethrin	Nervous system	Sodium channel modulators	Narahashi (1971)
Macrocyclic lactones	Avermectins & milbemycins	Nervous system	Chloride channel activator	Clark et al. (1995)
Formamidines	Amitraz	Nervous system	Octopamine agonists	Chen et al. (2007)

AChE, a key enzyme vital to the function of the nervous system (Faza et al., 2013; Temeyer et al., 2013a,b). When ticks are poisoned with a cholinesterase inhibitor, the cholinesterase is not available to help break down the acetylcholine, and the neurotransmitter continues to cause the neuron to "fire," or send its electrical charge. This results in over stimulation of the nervous system and ultimately arachnid dies. The first decline in the sensitivities of arachnids against OPs occurred in the early fifties. Since then, arachnids have developed resistance to more than 30 OPs and carbamates in 40 countries (Van Leeuwen et al., 2009, 2010; Arivalagan et al., 2013). Target-site insensitivity in arachnids seems to be the most common OP resistance mechanism. In 1964, Smissaert was the first to identify the association of AChE insensitivity with organophosphate resistance. Since then, insensitivity of AChE has been considered the principle mechanism for the emergence of OP resistance worldwide (Van Leeuwen et al., 2009; Lwande et al., 2012). *R. microplus* resistance to OPs such as coumaphos, chlorpyrifos and chlorphenvinphos has been recorded and insensitivity of AChE is considered as an important mechanism of resistance in Mexican tick strains (Rosario et al., 2009a; Perez-Gonzalez et al., 2014).

The molecular mechanisms of OP resistance are well understood in insects and have been extensively reviewed (Oakeshott et al., 2005; Carvalho et al., 2013). To date, several point mutations have been identified as the cause of OP resistance. Three putative sequences of AChE from *R. microplus* have been reported (Herenandez et al., 1999; Temeyer et al., 2004, 2007; Aïzoun et al., 2013). Six mutations were identified in BmAChE3 from an OP-resistant strain of *R. microplus* (Temeyer et al., 2007). A substitution of glutamine (Q) for arginine (R) at position 86 in BmAChE3 was the most common mutation. Enzyme kinetics of recombinant BmAChE3 has confirmed that the R86Q substitution increased substrate affinity and conferred insensitivity to paraoxon inhibition (Feng et al., 2011; Corley et al., 2013). Temeyer et al. (2013a) further observed that the frequency of R86Q mutation was higher in OP-resistant tick strains compared to that of OP-susceptible strains. However, none of the mutations alone was sufficient to produce the OP-resistant phenotype at the organismal level because a number of susceptible individuals were found to be homozygous for all the six mutations. The authors concluded that additional mutations in BmAChE3, mutations in additional acetylcholinesterase genes, or additional resistance mechanisms (e.g. oxidative metabolism) that contribute to expression of the OP resistance are likely to occur.

5.3. Resistance against amidines (Amitraz)

Amitraz, triazapentadiene compound, is a member of the amidine class. Amitraz has been an effective treatment against the ticks of cattle. Amitraz has been in use for more than 30 years (Jonsson and Hope, 2007) but resistant populations have been reported (Soberanes et al., 2002; Chevillon et al., 2007; Mendes et al., 2013). The mode of action of amitraz is thought to be its toxic effects on a receptor for the neuromodulator, octopamine. Bioassays with synergists suggest the involvement of P450 cytochrome monooxygenases together with modification of the target site (Ducornez et al., 2005; Gong et al., 2013). The molecular basis of target-site resistance was addressed by Chen et al. (2007) and Corley et al. (2013) who found that there were two nucleotide substitutions in octopamine receptor in the resistant strains of ticks that result in amino acids different from all the susceptible strains. Discovery of these mutations only in amitraz-resistant ticks provided the first evidence for the possibility of an altered target site as a mechanism of amitraz resistance in ticks. But the exact mechanism of resistance to amitraz is still unknown (Guerrero et al., 2012; Pohl et al., 2012).

5.4. Resistance against pyrethrins/pyrethroids

Pyrethrins are naturally-occurring compounds derived from members of the chrysanthemum family. While they have a quick knock-down effect against arachnids, they are unstable in the environment and may not remain active long enough to kill arachnids. Pyrethroids are synthetic adaptations of pyrethrins, specifically designed to be more stable than the pyrethrums and thus have a longer lasting effect. Both pyrethrins and pyrethroids are potent neurotoxins. They act on sodium ion channels and thus cause nerve excitation as a result of changes in nerve membrane permeabilities to sodium and potassium ions (Narahashi, 1971; Weston et al., 2013).

The involvement of esterases (Miller et al., 1999; Guerrero et al., 2000; Jamroz et al., 2000; Guerrero et al., 2002; Hernandez et al., 2002; Baffi et al., 2007; Li et al., 2013), p450s (Chevillon et al., 2007) and Glutathione S-transferases (He et al., 1999; da Silva Vaz et al., 2004; Konus et al., 2013) in pyrethroid resistance has been

demonstrated for many species of ticks. Miller et al. (1999) found that two populations were resistant to the pyrethoid acaricides. In addition, these populations were shown to be resistant to DDT. Synergists did not increase the susceptibility of these populations which suggests that mechanisms other than biotransformation are involved in the resistance of these populations. Target site mediated resistance was confirmed by Frank et al. (2013) who discovered a mutation on the Na^+ ion channel. Functional characterization revealed that this mutation substantially decreases the channel sensitivity to pyrethroids (Tan et al., 2005; Oliveira et al., 2013). This mutation has also been reported from the ticks of Mexican, Australian and Brazilian cattle (Rosario et al., 2009b; Miller et al., 2013).

In a second example of pyrethroid resistance, there was no cross-resistance to DDT. Triphenylphosphate (TTP) synergized pyrethroid toxicity in this population suggesting the involvement of metabolic resistance. A specific metabolic esterase with permethrin-hydrolyzing activity, CzEst9, has been associated with high resistance to permethrin in Mexican tick population. Jamroz et al. (2000) supported this hypothesis with the discovery that CzEst9 esterase activity was much higher in this population and this was further supported by an increased permethrin hydrolysis in resistant tick homogenates (Miller et al., 2013).

5.5. Resistance against macrocyclic lactones

Macrocyclic lactone acaricides include the avermectins and milbemycins. The naturally occurring avermectins and milbemycins are fermentation products of actinomycetes in the genus *Streptomyces*. Avermectins are produced by the soil microorganism, *Streptomyces avermitilis*, which was first isolated in 1976 from a soil sample in Japan (Campbell et al., 1984). Milbemycins were first described from a culture of *Streptomyces hygroscopicus* and are structurally similar to the avermectins but lack the disaccharide at C13 (Takiguchi et al., 1980). Mishima et al. (1975) first reported the acaricidal activity of milbemycins.

Macrocyclic lactones block the transmittance of electrical activity in nerves and muscle cells by stimulating the release and binding of gamma-aminobutyric acid (GABA) at nerve endings (Bloomquist, 1996, 2003; Martin et al., 2012). This causes an influx of chloride ions into the cells leading to hyperpolarisation and subsequent paralysis of the neuromuscular systems (Bloomquist, 1993).

Macrocyclic lactones have been effectively used in controlling the Southern cattle tick (Shoop et al., 1995; Aguilar-Tipacamu and Rodriguez-Vivas, 2003; Lopes et al., 2013). Because of intensive use, partial resistance have been reported in *R. microplus*, but the exact mechanism of resistance is still unknown in ticks and parasitic mites (Martins and Furlong, 2001; Perez-Cogollo et al., 2010; Lovis et al., 2013). However, on the basis of the hypothesized mechanism of resistance in nematodes against macrocyclic lactones (Blackhall et al., 1998), Lovis et al. (2013) concluded that resistance in ticks and mites might be due to target site insensitivity of the GABA or glutamate-gated chloride ion channels.

6. Resistance management

6.1. Rationale use of acaricides

Knowledge about monitoring, rotation and use of combination of acaricides may help in preserving the efficacies of existing compounds.

6.1.1. Regular monitoring

Monitoring can become an essential part in delaying the development of resistance. Application of acaricides every 3 weeks during the tick season is suggested in areas where tick resistance is common (Sugimoto and Osakabe, 2013) but, high frequency of acaricide application is a positive risk factor for the emergence of resistant strains. It is therefore strongly recommended that acaricide treatments should not exceed more than five per season (Jonsson et al., 2000; Thullner et al., 2007). It is suggested (Sun et al., 2011) that cases of field resistance should be confirmed in the laboratory and correlated against known management practice. Ideally, to reduce the development of resistance, the knowledge of the tick species present and the resistance status should be kept in mind before the selection of acaricides.

6.1.2. Rotation of acaricides

Rotation or alternation of acaricides having different modes of action reduces the selection pressure for resistance to any one acaricide group. But, so far, only few laboratory reports are available regarding the beneficial effects of acaricides rotation in terms of delaying the development of strong resistance in a population that had initially a low level of resistance for an acaricide. Thullner et al. (2007) showed that in a *R. microplus* strain selected with deltamethrin, resistance to deltamethrin was very high (resistance factor [RF] = 756) after 11 generations, and in *R. microplus* strain selected with deltamethrin then coumaphos in rotation, resistance to deltamethrin was very low (RF = 1.6) after 10 generations. Further field trials are required to evaluate the beneficial effects of rotation/alternation of acaricides of veterinary importance (Adakal et al., 2013). But rotation of acaricides is costly and not easy to practice; there is no evidence as to what length of time between changes should be adopted, although most veterinarians suggest this should not be less than every two years (Maggi et al., 2011). In other parasite systems it has been said that if a drug, for which the parasite has developed resistance, is withdrawn from use for some time, the sensitivity to that drug may return (Gharbi et al., 2013).

6.1.3. Using combinations of acaricides

The use of mixtures of acaricides is another attractive approach to delay the emergence of resistance (Lovis et al., 2013). This approach is based on the likelihood that one individual will not have resistant alleles to two chemicals with different modes of action. This strategy has been tried in South Africa and simulation modeling indicates its promise. Likewise, Fernández-Salas et al. (2012) evaluated the synergestic effect of amitraz and permethrin against a permethrin-resistant *R. microplus* strain from Mexico. Permethrin showed almost no mortality in the resistant strain

even at the highest concentration but addition of amitraz to permethrin led to a dramatic increase in larval mortality. In this strategy, the chemicals in a combination product must be compatible and of equal persistence on the animal and they must be used at recommended concentrations.

6.2. Vaccination

Enhancing immunity in cattle is an important tool for tick control. Commercially available vaccines against cattle fever ticks that are approved for use outside of the United States, including Gavac® (Heber Biotec; Havana, Cuba), TickGARD (Hoechst Animal Health; Australia), and TickGARD^{PLUS} (Intervet Australia; Australia), are based on the recombinant form of the concealed antigen, Bm86, obtained from the mid gut of *R. microplus* (Freeman et al., 2010). Recent research is providing new indication that the target might be conserved in a number of tick species, resulting in some successes against *Boophilus annulatus* (Pipano et al., 2003; Popara et al., 2013), *Hyalomma anatolicum anatolicum* and *H. dromedarii* (de Vos et al., 2001; Rodriguez-Valle et al., 2012a; Nabian et al., 2013). In the field, promising results have been obtained by using vaccines alone (De La Fuente et al., 1998; Redondo et al., 1999; Shahein et al., 2013; Stutzer et al., 2013) or in combination with acaricides (Beugnet et al., 1998; McKenna et al., 1998; Cunha et al., 2012; Olds et al., 2012). However, field trials of the Tick-GARD vaccine (produced in Australia) in some areas of Brazil revealed that it alone was not able to control the target tick (Pereira et al., 2008). Vaccine efficacy varies from area to area because of strain variation; therefore, a tick vaccine produced from the Australian strains might not be effective against Brazilian strains. A possible reason for such type of variation in vaccine efficacy is amino acid sequence divergence between the recombinant Bm86 vaccine component and native Bm86 expressed in ticks from different geographical regions of the world (Freeman et al., 2010; Ben Said et al., 2012a,b). Therefore, the preliminary screening of vaccine efficacy is prerequisite before launching it in a new geographical area. The rationale use of vaccines in combination with chemotherapy is required to reduce the need of the acaricides and thus may delay the onset of resistance to the commonly used acaricides.

6.3. Nutritional management

Protein–energy deficiency is an important cause of defective T-cell function (Chandra, 1984; Lichtman, 2013) and T-cells have been shown to play pivotal role in mediating acquired resistance to ticks (Maharana et al., 2011; Wikel, 2013). In an experimental study (Rechav and Hay, 1992), rabbits and sheep were exposed to low and highprotein diets and subsequently infested with adults of *Rhipicephalus appendiculatus* and *R. evertsi evertsi*. Hosts maintained on a lowprotein diet failed to acquire resistance to ticks, lost weight and developed anemia while those on a highprotein diet developed resistance, maintained weight and did not develop anemia. Furthermore, there was a significant decrease in the weight gains of the engorged females of both tick species from hosts fed high protein diets compared to those fed on low protein diets.

In cattle breeds naturally resistant to ticks (i.e. *Bos indicus* and their cross-breeds), the host's immune system would appear to be the single most important factor that regulates this resistance (Mattioli et al., 2000; Maryam et al., 2012). In a field trial in eastern Queensland (Australia), feeding on poor quality pastures resulted in a significant loss of resistance in the *Bos taurus* (British) and *B. indicus* × *B. taurus* (Zebu x British) steers and heifers to *R. microplus* (Sutherst et al., 1983; Tolleson et al., 2010). Poor quality feed not only resulted in the loss of resistance but also delayed its recovery. Likewise, O'Kelly and Seifert (1969), showed that nutritional stress was one of the major causes for greater tick burdens in European (*Bos taurus*) cattle. Improving host resistance to tick infestation through nutritional management should also be given consideration in integrated tick management program.

6.4. Using botanicals

Because of the high cost of developing new drugs and vaccines, development of drug resistance and concerns over drug residues associated with the continuous use of these chemicals (Ahmad et al., 2012; Muhammad et al., 2012; Abbas et al., 2014a), there is a renewed interest in the use of botanicals for safe, effective and cheap control of cattle ticks (Babar et al., 2012). The application of botanicals to livestock in order to control the ectoparasites of veterinary importance is widespread particularly in the developing countries (Zaman et al., 2012). Chabra and Saxena (1998) provide an excellent brief review of plants that have been in use effectively for controlling the acarids in Indian subcontinent. Twenty-one plants were suggested with the acaricidal activity. Likewise thirteen plants having acaricidal properties have also been documented in Uganda which are being used in the field by the experienced old farmers with promising results (Robert et al., 2010). It is clear from the following examination of reports that there are many botanical products that can kill ticks or inhibit oviposition.

The candidate plants with acaricidal properties include *Commiphora erythraea* (Carroll et al., 1989), *Artocarpus altilis* (Williams, 1993), *Stemona collinsae* (Jansawan et al., 1993), *Gutierrezia* spp. (Miller et al., 1995), *Margaritaria discoidea* (Kaaya et al., 1995), *Ocimum suave* (Mwangi et al., 1995), peel oil of *Citrus* spp. (Chungsamarnyart and Jansawan, 1996), *Pimenta dioica* (Brown et al., 1998), *Gynandropsis gynandra* (Lwande et al., 1999), *Cleome hirta* (Ndungu et al., 1999), custard seed oil (Kalakumar et al., 2000), *Stylosanthes scabra* (Khudrathulla and Jagannath, 2000), *Tamarindus indicus* (Chungsamarnyart and Jansawan, 2001), *Eucalyptus* spp. (Chagas et al., 2002), *Copaifera reticulate* (Fernandes and Freitas, 2007), *Senna italica* subsp. *Arachoides* (Magano et al., 2008) and *Lippia javanica* (Madzimure et al., 2011).

A number of the above-mentioned reports relating to acaricidal effects of plant extracts support the suggestion that many botanicals have the potential to be used for the control of ticks. Therefore, in some countries plant based commercially available formulations such as MyggA®

Natural and Citriodiol® are being used for controlling ticks (Gardulf et al., 2004; Jaenson et al., 2006; Freitag and Kells, 2013). MyggA® Natural (Bioglan, Lund, Sweden), contains 30% of *Corymbia citriodora* oil with a minimum of 50% p-menthane-3,8-diol (PMD), an active ingredient of many mosquito-repellent products. Citriodiol®, manufactured by Citrefine International Limited, contains 64% PMD (a mixture of the cis and trans isomers of p-menthane-3,8-diol). Citriodiol® has been notified under the European Biocidal Products Directive 98/8/EC and is currently proceeding through the registration process with the Heath and Safety Executive in the UK. Many of ethnoveterinary bioactive products and plant essential oils are extensively being tested to establish the efficacy of their parasiticide activity, their mechanism of action and their target parasite species (Athanasiadou et al., 2007; Masood et al., 2013; Abbas et al., 2014b). A thoughtful integration of ethnoveterinary products with synthetic acaricides may be expected to produce better effects in terms of controlling ticks and delaying the resistance than the use of acaricides alone.

Another attractive measure is the growing of grasses that repel or do not favor the development of ticks. Among species recognized as inhibiting the development of ticks are *Stylosanthes* spp., *Melinis minutiflora* and *Andropogon gayanus* (Jonsson and Piper, 2008; Soares et al., 2010) but the main drawback with such type of grass species is that they do not have the proper nutritional characteristics for cattle.

6.5. Improving genetic resistance in cattle

It has long been documented that some cattle breeds carry fewer ticks than others under the same environmental management (Roberts, 1968a; Wagland, 1975; Solomon and Kaaya, 1996; Uilenberg, 1999). Such natural resistance is because of animals' abilities to respond immunologically to tick infestation (Roberts, 1968b). Improved tick control following the use of tick-resistant cattle has been demonstrated in various breeds of cattle but this is manifested more strongly in zebu cattle and their crosses (Riek, 1962; Wilkinson, 1962; Seifert, 1971; Ayres et al., 2013; Rodriguez-Valle et al., 2013). Therefore, in some countries having serious tick problem, *B. indicus* cattle are being replaced with the more tick-resistant zebu breeds and tick-resistant *B. indicus* lines have also been developed (Frisch et al., 2000; Rodriguez-Valle et al., 2012b).

In general, resistant cattle require one or two treatments per season compared with three or four in susceptible breeds. A combination of resistant cattle and pasture spelling can remove the need for chemical treatment entirely (Sutherst et al., 1979). It is, therefore, suggested that the natural tick resistance character of zebu cattle and their crosses should be given more emphasis in the tick control.

6.6. Environmental management

6.6.1. Pasture burning

In many countries like Australia (Jonsson and Matschoss, 1998), South Africa (Spickett et al., 1992), Zambia (Baars, 1999) and USA (Davidson et al., 1994; Cully, 1999) burning pasture to induce a "green flush" in the dry part of the year (winter) is widely used practice for controlling ticks. Burning pasture is a named component of the Cuban government directed integrated tick management program (Cordoves et al., 1986). Regular monitoring of burning pasture is pertinent for controlling all stages of ticks because ticks recolonize burnt areas (Davidson et al., 1994). However, the burning of pastures on a routine basis may be difficult for the resource poor livestock raisers in the developing countries.

6.6.2. Pasture alternation and/or rotation

Another pasture management approach consists of keeping grazing areas free of cattle until the larvae die. Pasture alternation and/or rotation combined with applications of chemical acaricides has been proved as an effective way for the control of cattle ticks (Stachurski and Adakal, 2010). Barnard et al. (1994) studied a number of integrated pest management (IPM) strategies for *Amblyoma americanum* in forage areas utilized by *Bos taurus*, *B. indicus* and crossbred cattle (*B. taurus* × *B. indicus*) over a five years period. Pasture rotation combined with acaricide applications or habitat conversion was the most economically feasible IPM strategy in reducing tick burden ranging from 77% to 89%. In contrast to pasture burning method, rotation and/or alternation of pastures can also be adopted by the resource poor farmers.

6.6.3. House management

It is assumed that feedlots, particularly in tropical and semitropical countries, have more possibilities to increase tick infestation rates by maximizing host finding ability of the larvae (Céspedes et al., 2005), but, the risk of tick infestations in feedlot cattle might be reduced by making the environment unsuitable for the free-living stages of the tick. The main factors of consideration in the feedlot cattle management are good ventilation, thorough clean out on routine basis, removal of hidden sources, optimum animal density, low stress and good feed and water management. Furthermore, elimination or exclusion of wildlife hosts of particular tick species has also been recommended to control ticks. It is, therefore, suggested to avoid rearing the buffalo along with cattle (Young et al., 1988).

6.7. Improving resistance diagnostic tests

The most widely used in vitro bioassays are larval packet test (LPT) (FAO, 1984), larval immersion test (LIT) (Shaw, 1966) and the adult immersion test (AIT) (Drummond et al., 1973). In LPT, tick larvae are exposed to chemically impregnated filter papers and their subsequent mortality is quantified after 24 h. In LIT, seven to ten days old tick larvae are immersed in different dilutions of acaricide. Results are evaluated 24 h after each treatment by counting the number of live and dead larvae. In AIT, dose mortality responses of ticks to acaricides are determined by treating engorged female ticks with a range of dilutions of an acaricide and comparing treated and untreated ticks to assess the effect of a treatment on fecundity and fertility.

These bioassays are valuable for their portability and low cost. However, these tests do not provide direct information about the genetic mechanism of resistance development, are not sensitive enough to detect the emergence of resistance in early stages and take long time to obtain results.

It would be useful to determine the resistance status of tick samples with a rapid sensitive test that could be performed on single tick and that could also guide the selection of an acaricide which would be both effective and prudent in an acaricide resistance management program. PCR-based assays are being designed to be completed within a day, determine the specific resistance mechanism and be performed on individual ticks, using whole tick larvae or adult hemolymph or cuticular material. Progress in this area includes the development of PCR assay to detect target site resistance to pyrethroids and organophosphates (Guerrero and Pruett, 2003; Carvalho et al., 2013). In addition to providing the molecular basis for acaricide resistance, these assays are designed to provide useful information for resistance management programs. When the full array of molecular tests is available, the initial detection of resistance can be done by PCR assays, followed by larval packet test if desired, to allow for the quick selection of the best choice of acaricide for eradication of out break (Aïzoun et al., 2013).

7. Conclusions

A number of methods ranging from dipping to injecting systemic acaricides are available for treating cattle, but regardless of any treatment procedure used, farmers need to be trained in the application procedures to achieve maximum treatment benefits. Regular monitoring of cattle ticks for development of resistance against different classes of chemical acaricides has a crucial role in the management of resistance and making a correct choice of an effective drug. Use of vaccines, synthetic and botanical acaricides in combination and educating the farmers by launching extension programs about recommended tick control practices as strategic and/or tactic measures for the control of cattle ticks would be rewarding. Integration of currently available options for the management of drug resistance is an important operational and research priority.

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