Anti-3AB antibodies in the Chinese yellow cattle infected by the O/Taian/99 foot-and-mouth disease virus

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Abstract

The O/Taiwan/99 foot-and-mouth disease virus (FMDV), a South Asian topotype of serotype O, was introduced into Taiwan in 1999. The Chinese yellow cattle infected by the virus did not develop clinical lesions under experimental and field conditions. A blocking enzyme-linked immunosorbent assay (ELISA) kit with the 3AB antigen, a polypeptide of FMDV non-structural (NS) proteins, was used to evaluate the development and duration of anti-3AB antibodies, proving active viral replication, in the Chinese yellow cattle. The specificity of the assay was 99%, as was established with negative sera from regularly vaccinated and from naïve cattle. The sensitivity tested with sera from naturally infected animals was approximately 64% and it was lower than that obtained by serum neutralization (SN) test. Under experimental infection, the Chinese yellow cattle developed lower anti-3AB antibodies than that developed in other species. Duration of anti-3AB antibodies was traced in two herds of naturally infected animals, indicating that anti-3AB antibodies persisted for approximately 6 months after outbreaks. On the basis of this study, we propose that the Chinese yellow cattle may have natural resistance, which limits viral replication and reduces the development of anti-3AB antibodies.

Keywords: Foot-and-mouth disease virus; Cattle viruses; 3AB non-structural protein; Anibodies; Chinese yellow cattle

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1. Introduction

Foot-and-mouth- disease (FMD) is widespread in many regions of the world including parts of Africa, Asia, Middle East and South America. Recently, FMD in ruminants caused by a strain of South Asian topotype of serotype O (Kitching, 2000) has spread to most regions of Asia, including China, Cambodia, Vietnam, Thailand, Lao, South Korea, Japan, Russia, Mongolia, and Taiwan. It has caused an economically devastating impact on affected countries mostly because of trade barriers, which are imposed where the disease occurs.

For those parts of the world where FMD is prevalent, commercial vaccines are widely used to control the disease. Intensive vaccination programs have the benefit of reducing the probability of spread to neighboring regions where vaccination is not practiced. Considering the ability of foot-and-mouth disease virus (FMDV) to establish persistent infection in ruminants (Kitching, 1992; Salt, 1994; Woodbury, 1995), a reliable tool to estimate the asymptomatic viral activity in animal populations should be an important contribution for monitoring the FMD situations. Recently, the possibility to differentiate infected from vaccinated animals based on the development of antibodies against non- structural (NS) proteins of FMDV has been intensely studied (Villinger et al., 1989; Rodriguez et al., 1994; Lubroth and Brown, 1995; Silberstein et al., 1997; Mackay et al., 1998a; Sorensen et al., 1998). Now there is agreement that the detection of antibodies to the NS polyproteins 3ABC and 3AB is the most reliable indicator of previous infection with FMDV (De Diego et al., 1997; Mackay et al., 1998a; Sorensen et al., 1998; Lubroth et al., 1998; Malirat et al., 1998; Brocchi et al., 1998). Enzyme-linked immunosorbent assays (ELISAs) based on recombinant FMD NS viral antigens produced by various expression systems (Sorensen et al., 1998; Mezencio et al., 1998; Mackay et al., 1998b; Bergmann et al., 2000) have been used to evaluate the development and duration of anti-NS proteins antibodies. One of these studies (Mackay et al., 1998b) indicates that the levels of anti-3ABC antibodies in infected animals may be related to the development of clinical signs. For example, all animals, which showed clinical lesions seroconverted to 3ABC by 1 month after experimental infection and remained seropositive for longer than 12 months. However, response to 3ABC in vaccinated and sub-clinically infected animals developed slowly and only 80% of the animals were seropositive at 2 months after infection (Mackay et al., 1998b). These studies have suggested that the detection of antibodies to 3ABC is optimal on a herd basis to test viral activity in an asymptomatically infected population.

The O/Taiwan/99 FMDV caused a series of outbreaks during 1999-2000 in Taiwan. It was introduced into Taiwan through the sub-clinical infection of the Chinese yellow cattle. In a previous study (Huang et al., 2001), we have reported that the Chinese yellow cattle, a native species of beef cattle, infected by the O/Taiwan/99virus do not develop clinical lesions under experimental and field conditions. As the Chinese yellow cattle may act as carriers to transmit virus to new hosts, a reliable approach to differentiate the infected from the vaccinated animals and to detect the dub-clinical infection in the Chinese yellow cattle is critical for practicing the FMD eradication programs. To establish the detection approach, we have used a 3AB-ELISA kit to evaluate the development and duration of anti-3AB antibodies in the infected Chinese yellow cattle.

The most surprising feature in this study was that the Chinese yellow cattle developed variable patterns of anti-3AB antibodies either in field or in experimental infections. Our study

provided further data for understanding the immune response to 3AB in the sub-clinically infected animals.

2. Materials and methods

2.1 Cell cultures and viruses

BHK-21 cells, a continuous cell line of baby hamster kidney, were used to replicate FMDV and to perform the serum neutralization (SN) test. Two virus isolates of serotype O, the O/Taiwan/97 and O/Taiwan/KM1/99, were used in this study. The O/Taiwan/97 virus used to perform the SN test is a pig-adapted virus strain, which does not infect ruminants in natural route (Dunn and Donaldson, 1997; Huang et al., 2000). The O/Taiwan/KM1/99 virus, isolated from the Chinese yellow cattle in Kinmen Island during the 1999 outbreaks (Huang et al., 2001), was used to study the susceptibility of species in experimental infections.

2.2 Animal inoculation and in-contact transmission

The O/Taiwan/KM1/99 virus used in animal experiments was grown in BHK-21 cells and titrated for infectivity containing a titer of $10^{7.3}$ $TCID_{50}$/ml. Three cattle (one Chinese yellow cattle and two dairy cattle, Holstein, from 5 to 6 months of age) and one goat (4 mouths old) were separately housed in the good laboratory practice (GLP) animal rooms at National Institute for Animal Health, Taipei, for studying the development of anti-3AB antibodies following infection by the O/Taiwan/KM1/99 virus. The Chinese yellow cattle and one of the dairy cattle were inoculated intradermally on the tongues with a dose of $10^{7.3}$ $TCID_{50}$/ml of the O/Taiwan/KM1/99 virus. One of the dairy cattle used to study the in-contact transmission was housed in the same room with the infected dairy cattle. The goat was inoculated with $10^{4.6}$ $TCID_{50}$/ml of the virus. All animals were observed daily for clinical signs of FMD (body temperature and formation of vesicular lesions). Sera of each animal were collected every 1-3 days up to 54 days post-exposure, and then the sera were tested for the titers of serum neutralizing antibodies and the levels of anti-3AB antibodies.

2.3 Serum samples

For preliminary specificity study, stocks of known negative samples collected in 1997 from vaccinated and non-vaccinated dairy cattle were examined. A total of 114 negative sera, derived from non-vaccinated animals negative in SN test, were tested for the anti-3AB antibodies. In addition, 93 sera of animals vaccinated with a monovalent vaccine contain- ing Campos strain of serotype O were tested for the SN and anti-3AB antibodies. For the sensitivity study, a total of 220 sera, collected from 10 herds of Chinese yellow cattle during the 1999 outbreaks caused by the O/Taiwan/99 virus, were examined.

2.4 Immunoassays

The titers of SN antibodies were determined in a microdilution test using the BHK-21 cells. Serial sera dilutions were incubated with a virus dose of 100 $TCID_{50}$ (Bolwell et al., 1989) of

the O/Taiwan/97 virus. The cut-off level of positive results chosen for SN test (≧45X) was according to the OIE Manual (Donaldson et al., 1996).

Detection of serum antibodies to FMDV 3AB protein were determined by an ELISA kit, the Danish Veterinary Institute for Virus Research (DVIVR) NSP ELISA kit, based on a competitive assay using a recombinant baculovirus producing 3AB NS protein (Sorensen et al., 1998). The procedure and the interpretation of results were carried out as described by the producer (Sorensen et al., 1998).

3. Results

3.1. Detection of NS protein antibodies based on a 3AB polypeptide

The specificity of the 3AB-ELISA in the Chinese yellow cattle was evaluated with negative sera collected from non-vaccinated and vaccinated animals. A total of 114 negative sera from non-vaccinated cattle were tested for antibodies to 3AB, observing that only 1 out of 114 sera gave a positive reaction (Table 1). In addition, 97 sera, collected from vaccinated cattle with SN titers ranging from low to high (data not shown), were also tested, indicating that 1 out of 97 gave a positive reaction (Table 1). Thus, the specificity of the 3AB-ELISA was approximately 99% when used to examine field sera independently on previous vaccination (Table 1). The sensitivity of the assay was evaluated by examining 220 serum samples from 10 herds of the Chinese yellow cattle involved in the field outbreaks of O/Taiwan/99 silent infection, as proven by virus isolation or by identification of virus nucleotide sequences from the OP fluids directly (Huang et al., 2000). Results (Fig. 1) were compared with those obtained by SN test, indicating that approximately 64% (97/152) of the infected animals with a positive SN titer (≧45X) were positive for anti-3AB antibodies. Interestingly, only 53% (9/17) of the animals with SN titers ≧724X were positive for anti-3AB antibodies, 68% (56/82) of the animals with SN titers between 512 and 256X and 60% (32/53) with SN titers between 128 and 64X seroconverted to positive in anti-3AB antibodies.

3.2. Duration of anti-3AB antibodies in the infected Chinese yellow cattle

We have traced the duration of the antibodies against 3AB in two herds of the Chinese yellow cattle on Kinmen Island, in which anti-3AB antibodies were detected during the

Table 1
Specificity of the 3AB-blocking ELISA

Origin of cattle	3AB-blocking ELISA	
	No. positive/no. tested	Specificity (%)
Negative sera without vaccination	1/114	99.1
Negative sera with vaccination	1/97	99.0

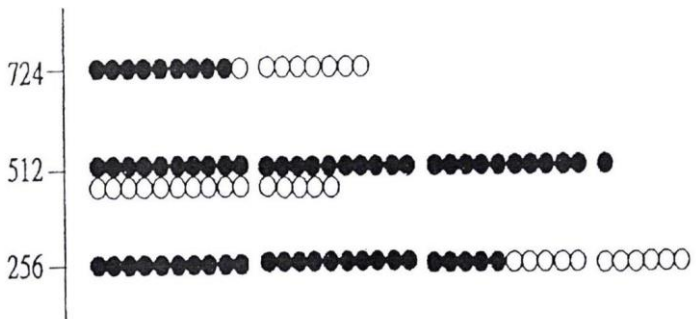

Fig 1. Relationship between SN antibodies and anti-3AB antibodies. A total of 220 serum samples, collected from 10 herd of Chinese yellow cattle during the 1999 outbreaks, are measured for SN and anti-3AB antibodies. For the SN test, sera are diluted to 724X. The solid symbols indicate that the 3AB-ELISA is positive and the empty symbols indicate that the 3AB-ELISA is negative. The cut-off level is 45X for the SN titer.

period of the 1999 outbreaks, but infectious virus particles were not isolated from the OP fluids, and virus-specific nucleotide sequences were not amplified by RT-PCR. We suppose that the two herds had been infected by FMDV previously, so they were kept under observation and monitored for FMDV neutralizing and anti-3AB antibodies at 2-3 month intervals. The results showed that anti-3AB antibodies persisted in the Chinese yellow cattle for approximately 6 months after outbreaks, then simultaneously converted to negative in the ninth month post-outbreaks. Interestingly, some of the animals failed to develop anti-3AB antibodies or presented detectable levels of antibodies for shorter time during the period of experiment (Fig. 2). The titers of SN antibodies in animals, which had a rapid promotion in the fourth and ninth month, were the results of boosters caused by two vaccinations in the first and eighth month.

3.3. Development of the anti-3AB antibodies in experimental animals

In a previous study, we have showed that dairy cattle, pigs, and goats were susceptible to the O/Taiwan/KM1/99 virus under experimental conditions (Huang et al., 2001). To

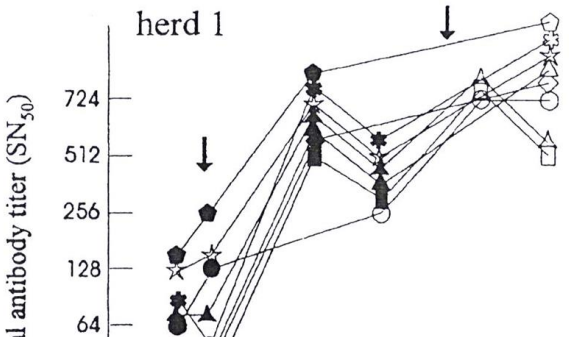

Fig. 2. Duration of the anti-3AB antibodies in the Chinese yellow cattle. Two herds of Chinese yellow cattle were traced for duration of the anti-3AB antibodies after outbreaks. The serum samples were collected from each animal every 1-3 months and tested for SN and anti-3AB antibodies (0 month indicates the first sampling available). The solid symbols indicate that the 3AB-ELISA is positive, the empty symbols that the 3AB-ELISA is negative and the arrow symbols indicate the times of vaccinations.

compare the development of anti-3AB antibodies in different susceptible species, we have experimentally inoculated the O/Taiwan/KM1/99 virus into one Chinese yellow cattle, one dairy cattle, and one goat. As described in Section 2, another dairy cattle was housed in contact with the infected one. The kinetics of antibody responses examined in SN test and 3AB-blocking ElISA were studied on sera collected sequentially every 1-3 days up to 54 days post-infection. The results (Fig. 3) showed that all animals developed similar titers of SN antibodies. The SN antibodies were first detected between 6 and 11 days post-infection, and remained at plateau level up to the 54th day. Seroconversion against 3AB was first detected between 7 and 8 days post-infection in goat and dairy cattle and on the 13th day in the in-contact dairy cattle. These animals remained seropositive for anti-3AB antibodies throughout the period of the experiment. However, in the infected Chinese yellow cattle antibodies to 3AB were detectable only between the 13th and the 15th day post-infection,

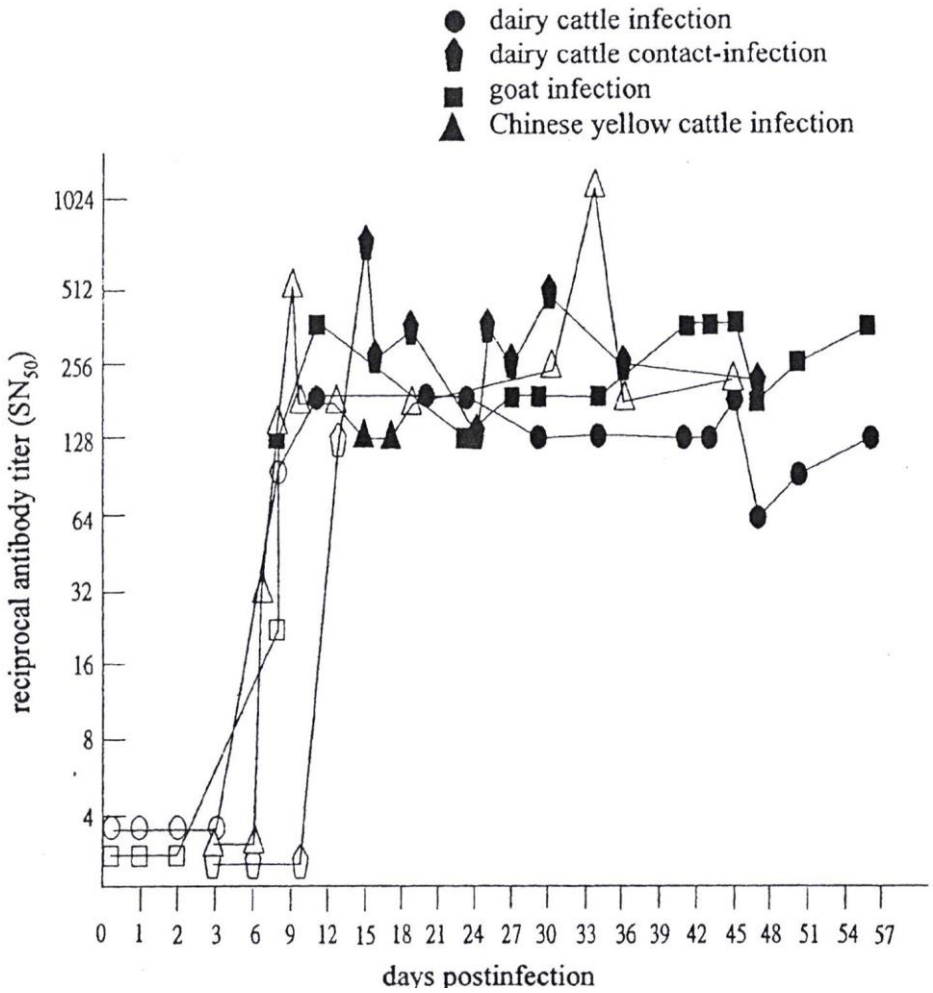

Fig. 3. Development of the SN and the anti-3AB antibodies in various species. One Chinese yellow cattle and one dairy cattle received $10^{7.3}$ $TCID_{50}$/ml of the O/Taiwan/KM1/99 virus. One goat received $10^{4.6}$ $TCID_{50}$ of the virus. One dairy cattle without receiving virus was housed in the same room with the infected dairy cattle to study the in-contact transmission. Sera were collected every 1-3 days up to the 54th day and tested for SN and anti-3AB antibodies. The solid symbols indicated that the 3AB-ELISA is positive and the empty symbols indicate that the 3AB-ELISA is negative.

Then declined to negative (Fig. 3). Because the experimental animals are very expensive, only one animal for each was species used for the experimental infection. Therefore, the final conclusions cannot be considered as statistically significant.

4. Discussion

Previous studies had shown that antibody to FMDV polyprotein 3ABC and 3AB are the most reliable marker of previous infection (Bergmann et al., 1993; Rodriguez et al., 1994; De Diego et al., 1997; Mackay et al., 1998a; Sorensen et al., 1998). The work reported here describes the development and duration of anti-3AB antibodies in silent infections by the O/Taiwan/99 FMDV in the Chinese yellow cattle.

The Danish 3AB-blocking ELISA kit was used and its preliminary evaluation using both uninfected and vaccinated animals, was approximately 99% (Table 1), consistently with previous studies using either the 3ABC and 3AB antigen (De Diego et al., 1997; Brocchi

et al., 1998; Sorensen et al., 1998). However, the sensitivity of the 3AB-ELISA used to examine the asymptomatic infections of the Chinese yellow cattle was approximately 64% with respect to the SN test (Fig. 1). High titers of specific antibodies against FMDV may be caused by vaccination programs or by natural infection. Here we were sure that the 10 herds investigated in this study (Fig. 1) did not receive vaccinations prior to the 1999 outbreaks, and that both the SN and the anti-3AB antibodies were caused by natural infection during the outbreaks. According to our findings the low detection rate in the Chinese yellow cattle was species-specific and depending on the situations of individual animal.

Several lines of evidence would suggest the diversity of the immune response to 3AB in the Chinese yellow cattle. In experimental infections, only the Chinese yellow cattle developed lower and transient anti-3AB antibodies. In contrast, the goat and dairy cattle developed anti-3AB antibodies earlier and longer persisting (Fig. 3). Although only one animal for each species had been used for the experimental infection, and the conclusions cannot be considered as statistically significant, the results support the hypothesis dis- cussed. Similarly, individual animals naturally infected in the same herd developed fluctuating levels of anti-3AB antibodies (Fig. 2) and one cattle failed to develop anti- 3AB antibodies during the period of observation. Finally, there was no correlation between SN and anti-3AB antibodies in Chinese yellow cattle infected under field conditions (Fig. 1). For example 47% (8/17) of the infected animals with the SN titers $\geqq$724X were undetectable in 3AB-ELISA (Fig. 1), with respect to 27% (4/15) of the animals with lower SN titer (64X). These studies proved evidence that the development of anti-3AB antibodies is highly variable in the Chinese yellow cattle.

The mechanisms generating less antibody response to 3AB remain obscure. As suggesting by previous studies the individual immunotolerance to NS proteins or a poor sensitivity of the test could be possible causes. Here we found that most of animals which failed to raise anti-3AB antibodies developed SN antibodies regularly, with levels similar to those observed in dairy cattle and goat experimentally infected with the same isolate of virus (Figs. 2 and 3). Moreover, in experimental infection dairy cattle and goat developed detectable 3AB antibodies during the period of experiment (Fig. 3). These findings indicate that a poor sensitivity of the 3AB-ELISA was found in the infected Chinese yellow cattle. The failure to develop anti-3AB antibodies was dependent on the feature of the 3AB antigen or on the amounts of 3AB presented to the immune system. In a previous study (Huang et al., 2001), we found that the Chinese yellow cattle infected by the O/Taiwan/99 virus secreted infectious levels of virus particles into the OP fluids but did not present detectable virus particles in blood stream, as tested by virus isolation, in the viraemic phase after experimental infection. This study supported our allegation that the Chinese yellow cattle may have natural resistance, which limits viral replication and reduces the devel- opment of anti-3AB antibodies, as well as clinical lesions, although it plays a role as virus carrier.

Species with natural resistance to the FMDV infection have been observed in previous studies (Hedger et al., 1969; Samara and Pinto, 1983; Hedger and Condy, 1985). Of these species, the African buffalo (*Syncerus caffer*) was recorded to have absence of clinical lesions by natural infection, however, it did transmit infectious levels of virus particles to new hosts (Dawe et al., 1994). Epidemiological evidence and the analysis of virus nucleotide sequence (Huang et al., 2000, 2001) have indicated that the O/Taiwan/2000

virus, which caused the outbreaks occurred in the year 2000 in Taiwan is almost identical to the O/Taiwan/99 virus. This result revealed that some Chinese yellow cattle remained as the virus

carriers escaping from the eradication programs and transmitted virus to other species such as dairy cattle and goats.

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黃牛感染O/Taiwan/99口蹄疫病毒後抗3AB抗體之發展

黃金城*、李璠、杜文珍、李淑慧、黃天祥、林有良、鍾明華、林士鈺

摘要

O/Taiwan/99口蹄疫病毒於1999年入侵台灣。黃牛在實驗室或野外感染此病毒都不會發展成水疱性臨床症狀。我們使用ELISA的方法法，以口蹄疫病毒結構蛋白3AB為抗原，評估3AB抗體的發展及持續時間之長短，此評估可以了解病毒在黃牛體內增殖之情形。首先使用疫苗免疫產生之抗血清及未感染的陰性血清測得ELISA試劑的專一性約99%，而敏感性測試則使用黃牛自然感染之陽性血清測得為60%。在實驗動物的學習則顯示黃牛比其他動物發展較低的抗3AB抗體。另外我們追蹤天然感染的黃牛3AB抗體持續時

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間，發覺爆發感染
後約維持6個月即建
消失。這些結果強之
議黃牛似有較強毒之
抵抗性限制病毒之
增殖及減少3AB
抗體的發展。