



Foot-and-mouth disease status in India during the second decade of the twenty-first century (2011–2020)

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Received: 19 May 2022 / Accepted: 27 September 2022
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Abstract

Foot-and-mouth disease (FMD) is a major disease of livestock in India and causes huge economic losses. The formal FMD control program started in 2003–04 in selected districts and was gradually expanded. The present study provides a descriptive review of the FMD outbreaks, prevalent serotypes, and genetic and antigenic features of the FMD virus (FMDV) that circulated in the country between 2011 and 2020. FMD outbreaks were regularly reported in cloven-hoofed domestic livestock and wildlife, with three serotypes including O, A, and Asia1. During the study period, a total of 2226 FMD outbreaks were documented and serotypes confirmed. FMDV serotype O dominated the outbreak scenario, accounting for about 92% of all outbreaks, followed by Asia1 (5% of all outbreaks) and A (3% of all outbreaks). Two major epidemics of FMD on an unprecedented scale during the years 2013 and 2018 by serotype O were recorded. The spatial distribution of FMD was characterized by a larger number of outbreaks in the southern region of the country. In an annual-scale analysis, 2020 was the year with the lowest outbreaks, and 2013 was the year with the highest. The month-scale analysis showed that outbreaks were reported throughout the year, with the highest numbers between October and March. The emergence of three major lineages (O/ME-SA/Ind2001d, O/ME-SA/Ind2001e, and O/ME-SA/Ind2018) of serotype O was observed during the period. In the cases of serotype A and Asia1, the appearance of at least one novel lineage/genetic group, including A/G-18/non-deletion/2019 and Asia1/Group-IX, was documented. While serotype A showed the advent of antigenic variants, serotypes O and Asia1 did not show any antigenic diversity. It was noticed during the course of an outbreak that animal movement contributes significantly to disease transmission. Except for 2018, when numerous FMD outbreaks were recorded, the number of annual outbreaks reported after 2016 has been lower than in the first half of the decade, probably due to mass vaccination and COVID-19 pandemic-linked movement restrictions. Even during outbreaks, disease symptoms in ruminant populations, including cattle, were found to be less severe. Regular six-monthly immunization certainly has a positive impact on the reduction of disease burden and should be followed without fail and delay, along with intensive disease surveillance.

Keywords FMD outbreaks · India · Serotypes · Epidemics · Genetic lineage

Introduction

Foot and mouth disease (FMD) has long been recognized globally as a serious threat to the livestock population. The transboundary nature of the disease and the severe economic consequences that follow its introduction continue to be a

serious concern for FMD-free countries. Farming communities are affected by FMD occurrences, which eventually reduce herd viability, and nations are victimized by trade restrictions imposed on animals and animal derivatives. When large ruminants are afflicted with FMD, their milk production, performance, and ability to plough and traction are severely affected. The World Organization for Animal Health (WOAH) has officially recognized 69 nations and 21 zones around the world as FMD-free, with or without vaccination, and at the same time, more than 100 countries are still considered endemically or sporadically affected by the disease. The causative agent, FMD virus (FMDV), belongs

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to the *Aphthovirus* genus within the *Picornaviridae* family. Currently, FMDV serotypes O, A, Asia1, Southern African Territories (SAT)-1, SAT-2, and SAT-3 are the six antigenically distinct serotypes globally prevalent. FMDV serotype C has not been reported from any part of the globe since 2004 (Paton et al. 2021).

Early reports of FMD in India date back to 1864 (Selections from the Records of the Govt. of India, LXIX, Papers relating to Cattle Diseases, 1868). During 1943–1964, guinea pig cross-protection test (Waldmann and Trautwein 2003) was used to identify serotypes of field isolates, and the serotypes found in the country were recognized as serotypes O, A, and C. Subsequently, the presence of serotype Asia1 was confirmed on material obtained from an outbreak in May 1951 (Dhanda et al. 1957). The complement fixation test (CFT) was developed in 1964–1965 and was used to identify viral serotypes in field samples (Rai 1980). Later, the serotype-differentiating sandwich ELISA (S-ELISA) and concurrent cell culture isolation followed by serotype confirmation by S-ELISA (Bhattacharya et al. 1996) were standardized for the diagnosis of FMD. Additionally, multiplex RT-PCR (Giridharan et al. 2005) was developed and put to use to increase the proportion of virus serotype identification.

The FMDV serotypes O, A, and Asia1 are currently prevalent in India (Dahiya et al. 2021). The last report of serotype C was in 1995 and had been excluded from the vaccine formulation since 2003 (Pattnaik et al. 2012). The virus strains circulating in India were placed within pool 2, one of seven major virus pools identified based on their geographic distribution pattern. Serotype O is responsible for the majority of FMD outbreaks in the country, followed by serotypes Asia1 and A. Within the serotypes, the emergence of various genotypes and genetic lineages has been recorded from time to time. The official FMD Control Program (FMDCP) in India began in 2003–04 in 54 districts and has since been gradually expanded to include the entire nation by 2019. A uniform vaccine strain policy and standard vaccination strategy have now been implemented country-wide, with commercial vaccine manufacturers using strains identified and recommended by the ICAR-Directorate of Foot and Mouth Disease (ICAR-DFMD). FMD is recognized as a significant impediment to international trade. In a recent report by Govindaraj et al. 2021, the total farm-level economic loss due to FMD in India was estimated at USD 2768 million (INR 221,110 million), USD 237 million (INR 18,910 million), and USD 133 million (INR 10,610 million) respectively during severe, moderate, and mild outbreak settings. Disease control in the country presents various qualitative and quantitative hurdles in terms of livestock population, socio-economic conditions, and animal husbandry practices, which are very diverse. In India, control and eventual elimination of FMD is one of the national priorities as per

the National Animal Disease Control Program (NADCP) launched by the Govt. of India in 2019. In this review, we aim to reflect a comprehensive picture of the FMD situation in India during 2011–2020 by analyzing the available data and authenticated information retrieved from various reports of ICAR-DFMD.

Susceptible livestock population

The livestock sector plays an important role in the Indian economy. The sector currently contributes 25.6% to the Agricultural Gross Domestic Product (GDP) and 4.11% to the National GDP (Dash 2017). India has a large population of FMD-susceptible livestock, which includes 192.49 million cattle, 109.85 million buffalo, 74.26 million sheep, 148.88 million goats, 9.06 million pigs, 0.39 million mithun, and 0.06 million yak (20th Livestock Census 2019, Department of Animal Husbandry and Dairying (DAHD), Govt. of India, <https://www.dahd.nic.in>). For the purpose of the study, six geographical regions viz; southern [States of Tamilnadu, Kerala, Karnataka, Telangana, and Andhra Pradesh, and UTs of Pondicherry, Lakshadweep and A&N Islands], northern [States of Uttar Pradesh, Punjab, Haryana, Himachal Pradesh, and Uttarakhand, and UTs of Jammu & Kashmir, Ladakh, Delhi and Chandigarh], central [States of Madhya Pradesh and Chhattisgarh], western [States of Rajasthan, Gujarat, Maharashtra, and Goa and UT of Dadra & Nagar Haveli & Daman & Diu], eastern [States of Bihar, Odisha, West Bengal, and Jharkhand], and north-eastern [States of Assam, Manipur, Meghalaya, Mizoram, Nagaland, Arunachal Pradesh, Sikkim, and Tripura] were defined based on contiguous states. The population of FMD-susceptible livestock is distributed more or less evenly across the southern, western, eastern, and northern geographical regions, with each having 19–22% of the total population. In the central (10%) and north-eastern (5%) regions, the proportion of susceptible livestock is comparatively lower. By clinical disease, cattle are the most severely affected species, followed by buffalo, sheep, and goats. Furthermore, it has been observed that cross-bred cattle are more sensitive to disease than native cattle (Zebu) in terms of disease severity. Pigs, semi-domesticated animals like mithun and yak, and wild species like elephants, deer, nilgai, wild boar, and black buck have also been documented to have contracted FMD (Subramaniam et al. 2013b). During the FMD epidemic due to serotype O in 2013, frank and severe clinical symptoms were observed in elephants as well (Biswal et al. 2015; Rout et al. 2016). During 2011–2020, the majority of FMD outbreaks were reported in cattle and buffalo, which may possibly be due to the presence of overt clinical symptoms in these species. Since FMD in sheep and goats is generally mild and subclinical, it is entirely possible that it will be

missed during passive surveillance. Nevertheless, testing for 3AB3-NSP antibodies found that 13.6% of goats and 20.4% of sheep were positive, indicating significant virus circulation in both species (Rout et al. 2014). In a setting of mixed farming, these species are likely to play a role in virus amplification and silent spread of the disease (Muthukrishnan et al. 2020).

Laboratory diagnosis

Early virus detection and serotype identification are essential in disease surveillance and are crucial for disease control. The FMD surveillance network in India is made up of one national laboratory (ICAR-DFMD) and thirty state FMD regional and collaborating centres spread throughout the country. Besides, ICAR-DFMD is a member of the OIE/FAO FMD reference laboratory network and provides FMD status report to the World Reference Laboratory-FMD, The Pirbright Institute, UK for inclusion in the annual report. For FMD diagnosis, various serological tests like complement fixation test (CFT), virus neutralization test (VNT), enzyme-linked immunosorbent assay (ELISA), and molecular techniques such as polymerase chain reaction (PCR) were developed (Longjam et al. 2011). The liquid-phase blocking sandwich ELISA was developed for quantification of antibodies against FMDV (Hamblin et al. 1986). In India, several diagnostic assays were developed for the detection of FMDV

antigen, and the detection and quantification of antibodies against FMDV (Sharma et al. 2015). The ICAR-DFMD and FMD network laboratories routinely use sandwich ELISA (Bhattacharya et al. 1996) and multiplex PCR (Giridharan et al. 2005) for the screening of samples to detect FMDV serotypes. Between 2011 and 2020, a total of 9770 clinical samples received from suspected FMD outbreaks in various states were processed at state FMD centres and ICAR-DFMD for serotype identification (ICAR-DFMD. Annual Report 2011–12, 2012–13, 2013–14, 2014–15, 2015–16, 2016–17, 2017–18, 2018–19, 2019 and 2020, <https://www.pdfmd.ernet.in>). The samples were tested using sandwich ELISA and multiplex PCR and were also subjected to virus isolation in BHK-21 cells followed by virus typing. Clinical samples were subjected to preliminary screening at state FMD centres and then referred to ICAR-DFMD for confirmation and strain characterization. The FMDV serotype O was identified in most of the samples (46.8% of the total samples), followed by serotype Asia1 (2.5% of the total samples) and serotype A (1.5% of the total samples) (Table 1). FMDV serotypes O, A, and Asia1 were detected in 92.2%, 2.9%, and 4.9% of positive samples, respectively. Since there is no immunological cross-protection between FMDV serotypes, serotype identification is critical for the proper implementation of the vaccination-based control program. In some cases, the negative results obtained can be attributed to the poor quality of the clinical materials, improper transport, and even tardy arrival at the testing facility. Nevertheless,

Table 1 Number and proportion of FMDV serotypes identified in clinical samples during the last decade (2011–2020)

Year	Total No of samples tested	FMDV Serotype detected		
		Serotype O	Serotype A	Serotype Asia1
2011–12 (Apr-March)	962	246 (25.57), 95% CI:22.84–28.45	16 (1.66), 95% CI:0.95–2.69	85 (8.84), 95% CI:7.12–10.81
2012–13 (Apr-March)	859	263 (30.62), 95% CI:27.55–33.82	16 (1.86), 95% CI:1.07–3.01	52 (6.05), 95% CI:4.55–7.86
2013–14 (Apr-March)	3136	454 (14.48), 95% CI:13.26–15.76	8 (0.26), 95% CI:0.11–0.50	10 (0.32), 95% CI:0.15–0.49
2014–15 (Apr-March)	182	75 (41.21), 95% CI:33.98–48.73	0	1 (0.55), 95% CI:0.01–0.30
2015–16 (Apr-March)	671	244 (36.36), 95% CI:32.72–40.13	6 (0.89), 95% CI:0.33–1.94	2 (0.30), 95% CI:0.04–1.07
2016–17 (Apr-March)	523	150 (28.68), 95% CI:24.84–32.77	0	0
2017–18 (Apr-March)	520	146 (28.08), 95% CI:24.25–32.15	0	3 (0.58), 95% CI:0.12–1.68
2018 (Apr-Dec)	2396	347 (14.48), 95% CI:13.10–15.96	0	4 (0.17), 95% CI:0.05–0.43
2019 (Jan-Dec)	306	51 (16.67), 95% CI:12.67–21.32	1 (0.33), 95% CI:0.01–1.81	0
2020 (Jan-Dec)	215	38 (17.67), 95% CI:12.82–23.44	6 (2.79), 95% CI:1.03–5.97	1 (0.47), 95% CI:0.01–2.56
Total	9770	2014 (20.61), 95% CI:19.82–21.43	53 (0.54), 95% CI:0.41–0.70	158 (1.62), 95% CI:1.38–1.89

The dominance of FMDV serotype O over the other two serotypes is clearly evident

many clinical samples were usually taken from a single animal or outbreak, and most of the time, the serotype involved in an outbreak could be identified.

Prevalence of FMDV serotypes

Four FMDV serotypes (O, A, C, and Asia1) have so far been detected in India (Pattnaik et al. 2012). Serotype C has not been reported in the country since 1995. Historically, serotype O has been the most common and dominant type in India, followed by serotypes Asia1 and A. Between the years 2011 and 2020, a total of 2226 FMD outbreaks were recorded and the serotypes involved were confirmed (ICAR-DFMD. Annual Report 2011–12, 2012–13, 2013–14, 2014–15, 2015–16, 2016–17, 2017–18, 2018–19, 2019 and 2020, www.pdfmd.ernet.in). During the years 2013 and 2018, the country experienced the highest number of FMD outbreaks, while in 2020 it had the least (Fig. 1). The COVID-related lockdown, which imposed movement restrictions on humans and livestock for the majority of the period, may also be a reason for the low number of FMD outbreaks in 2020. The number of annual outbreaks recorded after 2016 has been lower than in the first half of the decade, with the exception of during 2018, when multiple FMD outbreaks were reported largely in the southern region of the country. More districts have been included in the FMD control program since 2011, expanding vaccination coverage and boosting herd immunity, which might have contributed to the decrease in FMD outbreaks. The percentage of serotype O outbreaks to annual total incidences ranged between 70.9 and 100%, with a mean of 92%. In the case of serotype A, it ranged between 0 and 13.0%, with a mean of 3%. Serotype Asia1 was responsible for 5% of FMD outbreaks, with a year-to-year variation between 0 and 24.5%. Incidences of serotype A have been steadily declining, and this serotype

was not reported in 2014–15, 2016–17, 2017–18, and 2018. There was a decline in serotype Asia1 occurrences as well, and this serotype could not be documented in any of the FMD outbreaks recorded in 2016–17 and 2019. FMD outbreaks caused by serotypes A and Asia1 have generally been less common in India compared to serotype O. On account of continuous vaccination since 2004 and increased vaccination coverage since 2011 (Gunasekera et al. 2022), the overall frequency of FMD has been extensively reduced. Because of this, the low proportion of serotype A and Asia1 incidences probably could not be noticed during the aforementioned period.

Spatial distribution of FMD outbreaks

The Union of India comprises 28 states and 8 union territories, which are further subdivided into 775 administrative districts. The southern region of the country experienced the highest proportion of FMD outbreaks (40%), followed by 20.5% in the eastern region, and 18.3% in the north-eastern region. The percentage of FMD outbreaks in the northern, western, and central regions varied between 6 and 8% (Fig. 2). An earlier study comparing five years of data from 2006–07 to 2010–11 (Subramaniam et al. 2013b) found a similar trend, with a substantial percentage of FMD outbreaks documented in the eastern and southern regions of the country. This discrepancy could be attributable to varying density of susceptible livestock population, the diverse types of cattle (crossbred/zebu cattle) raised throughout the nation, as well as a patchy FMD reporting system in certain regions and effective reporting in others. Training and capacity building for those working in the field of animal health and awareness campaigns for key stakeholders, mainly farming community are required to improve the effectiveness of reporting. The presence of a dense population of cross-bred and high-yielding animals

Fig. 1 Numbers of FMD outbreaks recorded in India between 2011 and 2020, along with the serotypes involved. The most prevalent serotype was O, followed by Asia1 and A

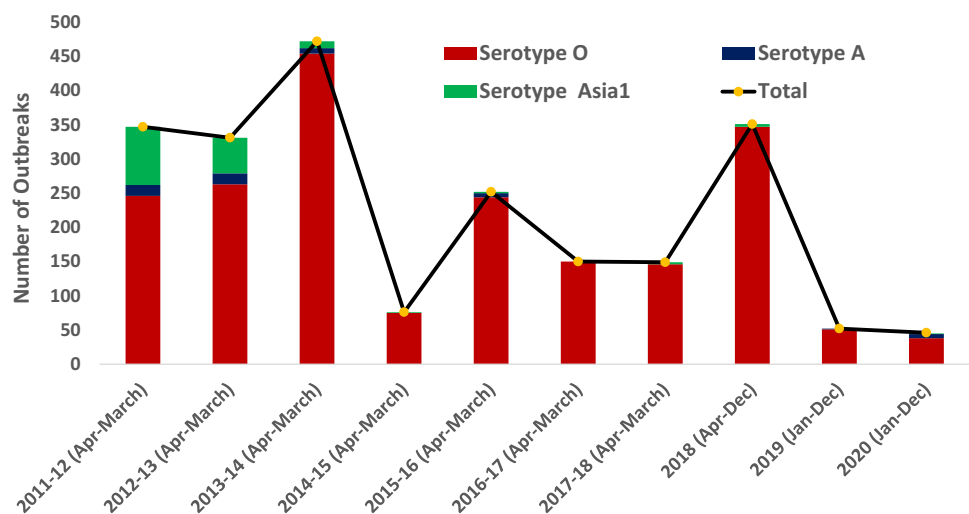
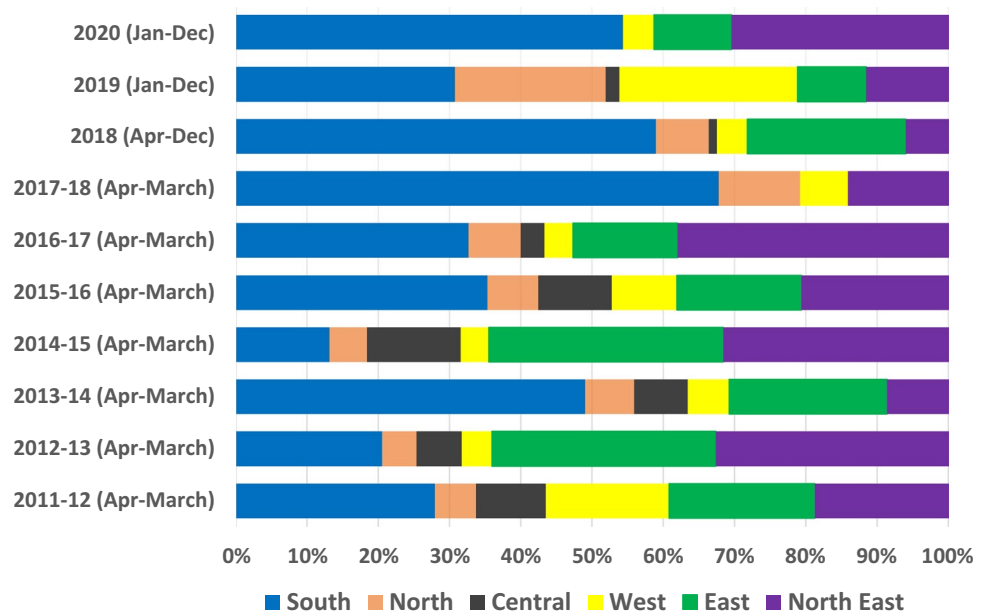


Fig. 2 FMD outbreak intensity by region from 2011 to 2020. The southern region recorded maximum incidences followed by the eastern and north-eastern region



has been linked to the higher frequency of FMD occurrence. Furthermore, in the southern and eastern regions, there was a significant year-to-year variation in the number of outbreaks reported, which might be linked to the persistence of infection-associated antibodies. It has been observed that high level of long-lasting protective antibodies were induced in FMD affected animals after widespread epidemics, preventing viral infection and transmission for the subsequent period (Dahiya et al. 2021). More outbreaks were seen once the antibody response began to decline.

During the study period, FMDV serotype O was widespread and was found in all the regions and states (Fig. 3). Serotypes A and Asia1, on the other hand, were sporadically

reported. For instance, serotype Asia1 was detected in the southern region in 2011–12, 2012–13, 2017–18, and 2020; in the central region during 2011–12, 2012–13, and 2011–14; in the western region during 2011–12, 2012–13, 2013–14, and 2017–18; in the eastern region during 2011–12, 2012–13, 2013–14, 2014–15, 2015–16, and 2018; and in the north-eastern region during 2011–12, 2012–13, 2015–16, and 2018. Surprisingly, during the period under study, this serotype was never found in the northern part of the country. In the eastern and western regions, serotype Asia1 incidences were found to be proportionately higher. Similarly, serotype A was found in the southern region in 2011–12, 2012–13, and 2015–16; in the northern region in

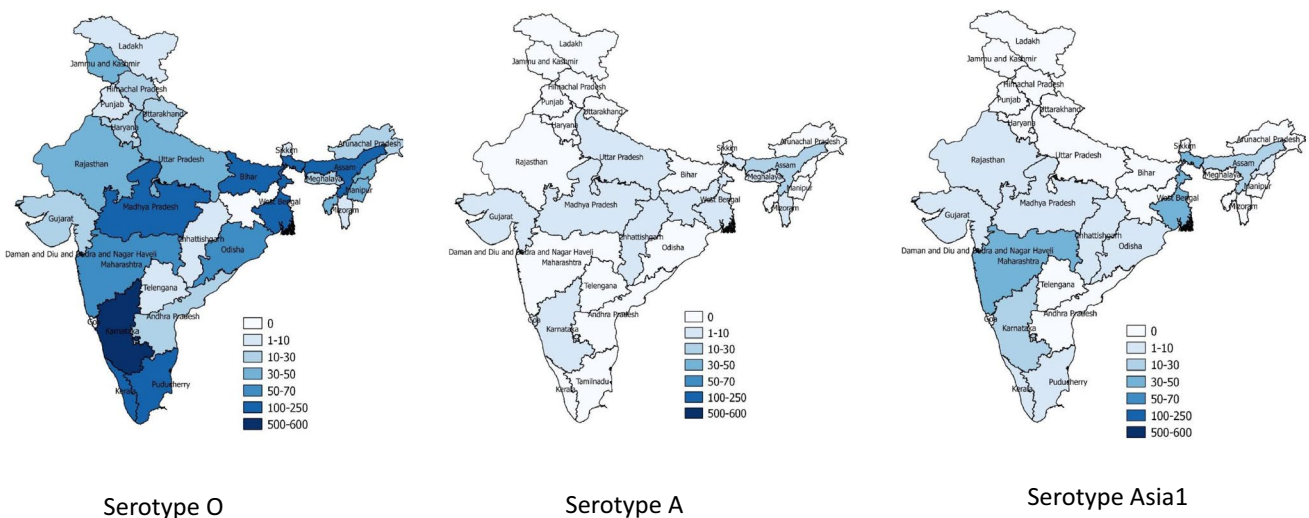


Fig. 3 Serotype-specific FMD outbreak intensity by state from 2011 to 2020. Serotype O is present in every state, while serotypes A and Asia1 are less common

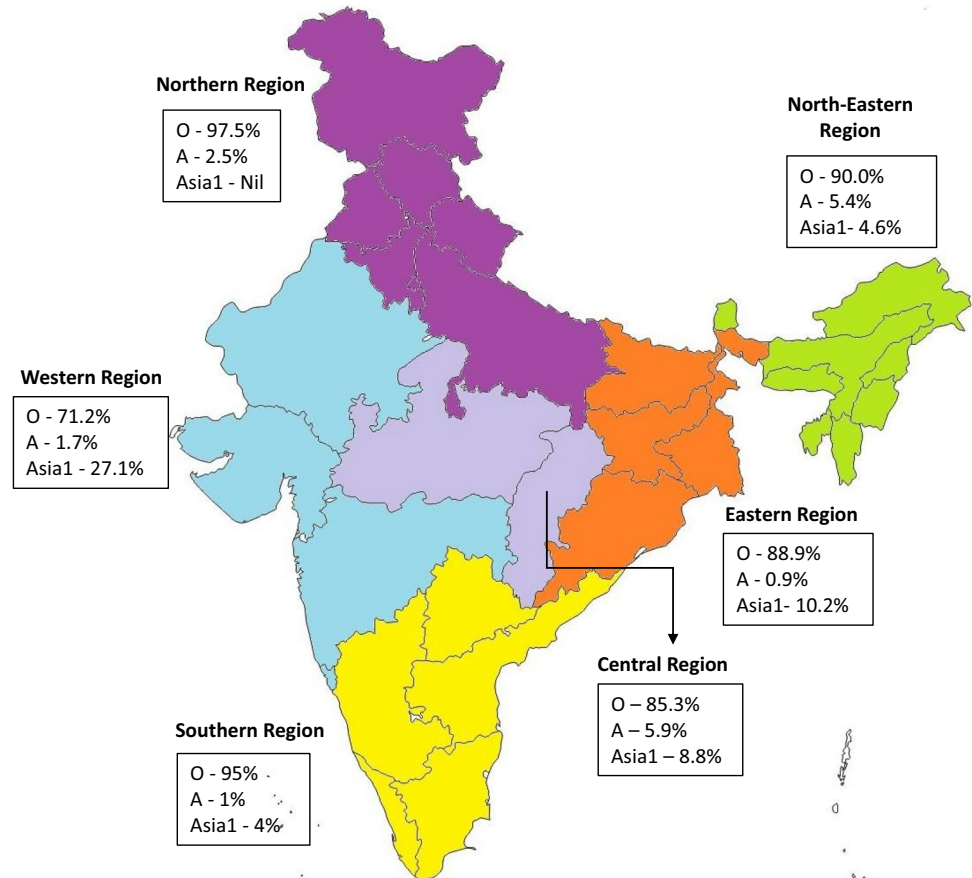
2012–13 and 2015–16; in the central region in 2011–12; in the western region in 2011–12, 2013–14, and 2019; in the eastern region in 2012–13 and 2013–14; and in the north-eastern region in 2011–12, 2012–13, 2013–14, and 2020. The region-wise distribution of FMDV serotypes during the last ten years is depicted in Fig. 4.

Temporal distribution of FMD outbreaks

Infectious disease prevalence often varies seasonally, with disease incidence rising and falling with the change in the season. Temperature, sunlight, humidity, water, and air pollution all have an impact on the host immune system, which contributes to the underlying mechanisms of infectious disease occurrence (Tang 2009). Weather conditions play a crucial role in the survival and transmission of aerosolized FMDV (Colenutt et al. 2016). For instance, the most favourable conditions for the airborne spread of FMDV occur during the winter months of December, January, and February (Hagerman et al. 2018). Other favourable factors which might help to maintain aerosolized FMD virus survival and onward transmission are

the absence of precipitation, stable wind flow direction, and low to moderate wind speeds (Gloster et al. 2005). In India, FMD is reported during the whole year with varying intensity. During 2011–2020, the period of October to March had witnessed the highest number of outbreaks (Fig. 5). During the FMD epidemics in 2013 and 2018, the outbreaks frequently started in August and reached their peak in November, and last into January. Weather conditions during these months appear to have played a significant role in the rapid spread of the virus across the country. Maximum FMD incidences in the post-monsoon and winter seasons may be ascribed to comparatively dry and cool weather, which may be favourable for virus survival and transmission. Dry and chilly air blowing from the north in a north-easterly direction prevails over India throughout the winter, which could be one of the reasons for the higher disease outbreaks in the winter. The low prevalence of FMD during the summer months may be due to the high ambient temperature which reduces the virus’ survival in the environment. Additionally, it is believed that high relative humidity (RH) and heavy rain during the monsoon impede virus aerosol transmission (Gloster et al. 2005).

Fig. 4 Regional distribution of FMDV serotypes from 2011 to 2020. Serotypes O and A are found in all the regions, however serotype Asia1 was not reported in the north



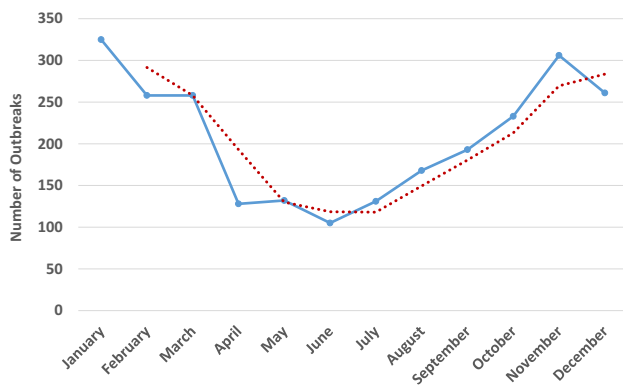


Fig. 5 Month-wise analysis of cumulative FMD outbreaks in India during 2011–2020. Cumulative outbreaks are shown as a solid blue line, while the moving average is shown as a dotted red line. The outbreaks were predominantly observed from October to March

FMD epidemics in 2013–14 and 2018–19

There was an upsurge in cases of FMD in India during the fiscal years 2013–14 and 2018–19. In both instances, almost 50% of the outbreaks occurred in the country's southern region. The genetic lineage responsible for the 2013–14 epidemic was identified as O/ME-SA/Ind2001d by phylogenetic analysis (Subramaniam et al. 2015). Surprisingly, the lineage that has been circulating in the country since 2008, causing isolated outbreaks, took quite a time before causing such widespread outbreaks in the year 2013. On the other hand, the outbreaks in 2018–19 were caused by the O/ME-SA/Ind2001e sub-lineage (Dahiya et al. 2021). This sub-lineage was identified in the country for the first time in 2015, and it gradually displaced O/ME-SA/Ind2001d from the field before causing the epidemic (Dahiya et al. 2021). The free movement of diseased animals, contaminated objects, and people has been speculated to be the primary mode of virus transmission. In addition, in some places, the animals were vaccinated in and around areas of outbreaks chaotically to limit the disease spread without following the biosecurity procedures properly, which accelerated the spread of the disease (Subramaniam et al. 2015; Dahiya et al. 2021). Field investigations revealed that appropriately vaccinated organized herds and animals in the villages did not manifest clinical FMD except for very few instances where mild illness was seen in vaccinated animals. In the case of FMD, vaccination is one of the control methods. However, other measures such as movement restrictions, zoo-sanitary measures, etc. are also required to achieve the desired level of vaccine effectiveness in the field (Knight-Jones et al. 2014), as FMD vaccine does not induce sterile immunity. Despite immunization, large-scale outbreaks are recorded every two to three years. This is plausible given that a natural infection results in a stronger immunity that lasts for more than a year. High

immunity to natural infection is relevant to all FMDV serotypes in general, notwithstanding possible minor changes in the duration of immunity across serotypes. In addition, the partially vaccinated animal population provides an opportunity for the virus to evolve genetically and antigenically, and evade immune response, resulting in cyclical outbreaks. This can be prevented by administering a high-quality, potent vaccine in the quickest timeframe possible, in accordance with pulse polio mode, as well as by administering timely high-density symmetrical vaccination twice a year.

Genetic profiles of FMDV serotypes

In India, various genotypes/lineages/genetic groups within serotypes O, A, and Asia1 have been identified (Table 2 and Fig. 6) through molecular epidemiological studies (Mohapatra et al. 2011; Subramaniam et al. 2013a; Dahiya et al. 2021). The emergence and disappearance of genotypes or lineages have been observed at different periods. The establishment and spread of FMDV genetic lineages in the country is aided by a high-density FMD-susceptible cattle population, vaccine and infection-induced partial antibody responses in some areas, and animal mobility. During the reporting period, all FMD outbreaks were caused by the FMD virus in pool 2, and no incursions from other pools were recorded.

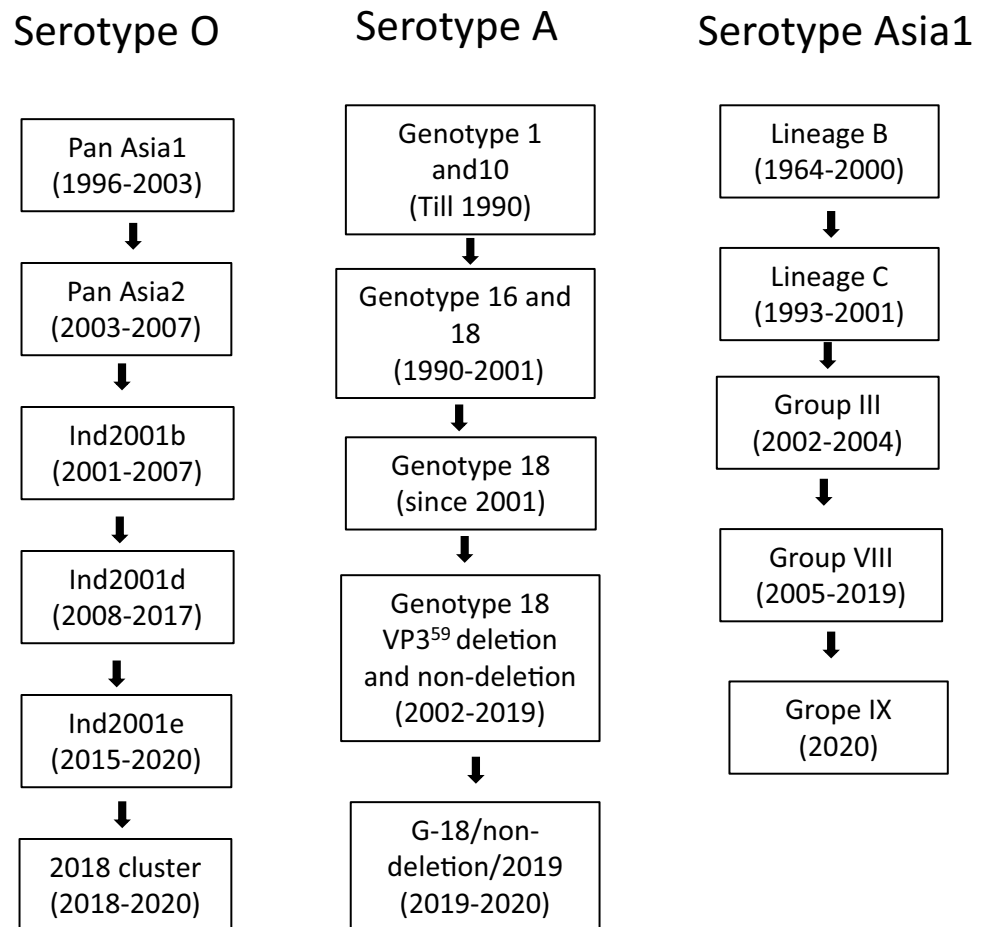
Serotype O

Globally, serotype O has 11 topotypes based on phylogenetic analysis of the VP1 coding region, namely Europe–South America (Euro-SA), Middle East–South Asia (ME-SA), Southeast Asia (SEA), Cathay (CHY), West Africa (WA), East Africa 4 (EA-1 to EA-4) and Indonesia-2 (ISA-1 and ISA-2) (Knowles et al. 2005). In India, only the ME-SA topotype has been identified so far. Several genetic groups within the ME-SA topotype were found to be in circulation, and lineages Ind2001 and PanAsia were identified to be the most prominent ones. The PanAsia lineage was found in India as early as 1982, although it wasn't recognized until the 1990s. This lineage was responsible for the majority of the outbreaks in the country between 1996 and 2003 (Subramaniam et al. 2013b). Later, within PanAsia, a divergent strain known as PanAsia-2 became predominant in 2002 and replaced the parent PanAsia strain in 2004. This type of evolution, where one strain dominates over the others after a period of co-circulation, occurs frequently in the field (Brito et al. 2017). The PanAsia-2 strain dominated the outbreak scenario in India during the years between 2005 and 2007. The O/ME-SA/Ind2001 lineage was first reported in the year 2001. After causing sporadic incidences of FMD

Table 2 Distribution of different lineages/genetic groups of FMDV serotypes during 2011–2020

Year	Serotype O	Serotype A	Serotype Asia1
2011	O/ME-SA/Ind2001d (69%) O/ME-SA/Ind2011 (25%) O/ME-SA/PanAsia (6%)	G-18/VP3 ⁵⁹ -deletion (67%) G-18/non-deletion (33%)	Group-VIII (100%)
2012	O/ME-SA/Ind2001d (99%) O/ME-SA/PanAsia (1%)	G-18/VP3 ⁵⁹ -deletion (100%)	Group-VIII (100%)
2013	O/ME-SA/Ind2001d (99%) O/ME-SA/PanAsia (1%)	G-18/VP3 ⁵⁹ -deletion (80%) G-18/non-deletion (20%)	Group-VIII (100%)
2014	O/ME-SA/Ind2001d (100%)	-	Group-VIII (100%)
2015	O/ME-SA/Ind2001d (38%) O/ME-SA/Ind2001e (62%)	G-18/VP3 ⁵⁹ -deletion (100%)	Group-VIII (100%)
2016	O/ME-SA/Ind2001d (13%) O/ME-SA/Ind2001e (87%)	G-18/VP3 ⁵⁹ -deletion (100%)	-
2017	O/ME-SA/Ind2001d (3%) O/ME-SA/Ind2001e (97%)	-	Group-VIII (100%)
2018	O/ME-SA/Ind2001e (73%) O/ME-SA/2018 (27%)	-	Group-VIII (100%)
2019	O/ME-SA/Ind2001e (86%) O/ME-SA/2018 (14%)	G-18/non-deletion/2019 (100%)	-
2020	O/ME-SA/Ind2001e (84%) O/ME-SA/2018 (16%)	-	Group-IX (100%)

Fig. 6 Genetic lineages/groups of FMDV serotypes reported in India. The parenthesis indicates the duration of active circulation



from 2003 to 2005, the Ind2001 lineage resurfaced in 2008 and continued its dominance in the field by overcoming the then-dominant PanAsia lineage in 2009. The lineage has diversified into at least five sub-lineages since its detection (Ind2001a, b, c, d, and e) (Bachanek-Bankowska et al. 2018). The sub-lineages Ind2001d (emerged in 2008), and Ind2001e (appeared in 2015) are the main strains involved in serotype O outbreaks in India during the second decade of the twenty-first century. The O/ME-SA/Ind2001d lineage has played a prominent role in causing FMD outbreaks in the country since 2008. The sub-lineage O/ME-SA/Ind2001e was responsible for sporadic outbreaks from 2015 to 2017, before causing outbreaks of epidemic proportions in 2018. With the emergence of O/ME-SA/Ind2001e, the circulation of the O/ME-SA/Ind2001d lineage decreased. Between 2015 and 2017, both lineages co-circulated for three years before O/ME-SA/Ind2001d was eventually phased out in the field in 2018 (Dahiya et al. 2021). In 2018, emergence of a novel genetic lineage designated as O/ME-SA/2018 cluster was reported (Dahiya et al. 2021). During the study period, serotype O was responsible for two major FMD epidemics in India, one in 2013 caused by the O/ME-SA/Ind2001d sub-lineage and the other in 2018 by the O/ME-SA/Ind2001e sub-lineage. In both instances, the field isolates shared a close antigenic relationship with the vaccine strain INDR2/1975 used in the country, implying that regular and rigorous vaccination might have prevented such large-scale spread.

Serotype A

Serotype A is genetically and antigenically more diverse than the other Euro-Asiatic serotypes and is classified into three continental topotypes, namely Africa, Asia, and Europe-South America (Euro-SA). A total of 26 global genotypes have been identified within three topotypes, each of which differs from the others at the VP1 nucleotide sequence level by > 15% (Mohapatra et al. 2011). In India, four genotypes (2, 10, 16, and 18) have so far been identified. Genotypes 2 and 10 were documented before 1990 and never had their genetic footprints found again thereafter. Between 1990 and 2001, endemic co-circulation of genotypes 16 and 18 was observed. Since 2001, genotype 18 has been exclusively prevailing in the field. Within genotype 18, a distinct lineage with an amino acid deletion at the 59th position of VP3 (VP3⁵⁹-deletion group) appeared in 2002 and dominated the field outbreak scenario in 2002 and 2003. The non-deletion and VP3⁵⁹-deletion lineages have been circulating in the field concurrently since then. The serotype A strains isolated in 2019 clustered within genotype 18, but distantly from both the deletion and non-deletion lineages. Within genotype 18, it appears to represent a novel genetic branch designated

as ‘G-18/non-deletion/2019’ lineage. In the case of serotype A, a systematic genotype replacement has been observed, and it was hypothesised that one genotype's higher replicative fitness may have contributed to its eventual dominance in nature (Mohapatra et al. 2012).

Serotype Asia1

Asia1 displays the least genetic diversity among all FMDV serotypes and contains a single topotype (Asia) and different genetic groups/lineages within the topotype. In India, three lineages (B, C, and D) have been recognized. Lineage B was prominently circulated from 1964 to 2000, and lineage C (designated as sub-lineage CI) has been in circulation since 1979. Lineage D was first identified in 2001 and circulated exclusively between 2002 and 2004. Lineage C resurfaced in 2005 (designated as sub-lineage CII), and it has been the source of all Asia1 outbreaks since 2006. Outbreaks owing to serotype Asia1 have been regularly observed in the western, eastern, and north-eastern regions of the country. Globally, isolates of serotype Asia1 collected after 2004 have been divided into nine genetic groups (G I-IX) (Valarcher et al. 2009). Isolates collected in India between 2001 and 2004 (designated as lineage D) clustered in Group III and those circulated from 2005–2019 (designated as sub-lineage CII) clustered in Group VIII. Recently, serotype Asia1 isolates collected in 2020 were clustered within G-IX (BD-18), a new genetic group that emerged in Bangladesh in January 2018 (Ali et al. 2019; Subramaniam et al. 2020). In the past, in the case of serotype Asia1, a dramatic form of clade replacement occurred in India on two occasions, in 2002 (Group III replaced sub-lineage CI) and 2006 (Group VIII replaced Group III) (Subramaniam et al. 2013a). As previously stated, there is an even greater likelihood that G-IX will eventually replace G-VIII.

Vaccine matching assessment

Until 2003, FMD vaccine manufacturers in India used different vaccine strains. Since the launch of the Foot-and-Mouth Disease Control Programme (FMDCP) in the year 2003–04, a uniform vaccine strain policy was adopted and all vaccine manufacturers within the country incorporate the same strains in their vaccine formulation. ICAR-DFMD undertakes the responsibility of supplying the appropriate vaccine strain to FMD vaccine manufacturers. The vaccine strains incorporated in the trivalent vaccine formulation used currently in India are O/IND R2/1975 (O/ME-SA/Branch B), A/IND40/2000 (A/Asia/Genotype 18), and Asia1/IND63/1972 (Asia1/Lineage B). It is essential to choose the right vaccine strain since the antigenic heterogeneity between and within

serotypes limits cross-reactivity and, consequently, in vivo cross-protection. For the FMD vaccination to be successful, the strains utilized in the vaccine formulation must antigenically match the field isolates. The antigenic relatedness of the field strains to the vaccine strains has been assessed using a two-dimensional micro-neutralization assay employing bovine vaccinal serum (BVS) against the current vaccine strains. During 2011–2020, vaccine matching of 416 FMDV isolates (serotype O-317, serotype A-41, and serotype Asia1-58) was carried out. The vaccine strains O/IND/R2/1975 and Asia1/IND63/1972 showed a good antigenic match to 88% and 80%, respectively, of the field isolates collected between 2011 and 2020. This suggests that these vaccine strains are suitable for use in the current FMD vaccine formulations used in India. The vaccine strain O/IND R2/1975 was reportedly shown to have broad cross-reactivity with the serotype O isolates from other countries (mainly from Asia and Africa) as well (Mahapatra et al. 2014). In the case of serotype A, however, a large percentage of field viruses (75.6%) showed antigenic drift from the current serotype A vaccine strain A/IND 40/2000, necessitating a search for a new strain. The emergence of genetically and antigenically diverse lineages/genotypes, as well as inadequate inter-genotypic antigenic coverage, is a major problem in serotype A (Rudreshappa et al. 2012). To cover such antigenic divergence observed in recent strains, an alternate vaccine candidate strain (A/IND27/2011) complying with all the vaccine attributes has been selected (Mahapatra et al. 2018; Sreenivasa et al. 2021). In general, FMDV serotype O vaccine strains, including the very old strain O1 Manisa, provide broad-spectrum protection and are being used in many countries. Serotype A outbreaks, on the other hand, provide a unique set of challenges since they periodically give rise to antigenically distinct variants, necessitating the development of new vaccine strains, often every 5 to 10 years (Mahapatra et al. 2016).

Conclusions

In India, FMD was widely prevalent during 2011–2020. Serotype O dominated over the other two serotypes in causing FMD outbreaks. FMDV serotypes A and Asia1 have caused only sporadic incidences. The appearance of a new genetic group and the elimination of an older one (lineage turnover) is a well-known phenomenon (Brito et al. 2018; Di Nardo et al. 2021) and was quite evident during the decade. Emerging lineages of FMDV serotype O were responsible for two nationwide FMD epidemics in 2013 and 2018. India banks heavily on systematic preventive vaccination for controlling FMD. The Govt. of India launched a vaccination-based FMD control program in August 2003–04, covering 54 districts across the country. The program expanded in

a phased manner until the entire country was covered by the NADCP scheme in 2019. All cattle and buffaloes are targeted to be vaccinated twice a year with an FMD trivalent (O, A, and Asia1) vaccine. Many areas of the country have shown a decline in disease incidences since the implementation of the control program. Furthermore, the FMD-affected animals showed only mild clinical signs in the vaccinated areas, with a quicker recovery from the disease. Under Indian socio-economic conditions, maintaining a strict six-monthly immunization regimen has proven to be a challenge due to various factors, including but not limited to vaccine availability, stakeholder participation, resource coordination, etc. The temporary drop in milk yield in dairy cows is a major deterrent to owners vaccinating their animals, resulting in low vaccination coverage. The situation is expected to improve with the nationwide deployment of the NADCP program. It is critical to have consistent vaccination timing and coverage, as well as a regionally focused strategy for regular and rapid surveillance. It is expected that the livestock industry's sanitary conditions will be improved through public–private partnerships to contain the spread of the disease. A scrupulously followed regular six-monthly immunization program certainly has a positive impact on the reduction of disease burden (Gunasekera et al. 2022). In order to reduce the risk of virus transmission, the free movement of animals across the nation should also be regulated. Given that the disease is endemic in the sub-region and has a transboundary nature, it is crucial to establish Epidemiology Network Units at porous international borders and improve communication between member nations in the SAARC area (Pattnaik et al. 2012). Control and eventual elimination of FMD could create endless possibilities for the country in the international export market for livestock and livestock products. However, it needs more focused and concerted efforts from all the stakeholders in the livestock value chain.

Acknowledgements Indian Council of Agricultural Research provided the necessary facilities to carry out this work. We sincerely thank all the scientific and technical staff associated with state FMD regional and collaborating centres for providing required data.

Author contribution All authors contributed to the conception and design. Conceptualization was performed by S.Subramaniam, J.K.Mohapatra and R.P.Singh. The first draft of the manuscript was written by S.Subramaniam, and all authors commented on previous versions of the manuscript. N.R.Sahoo, A.P. Sahoo, S. S. Dahiya, M Rout, J.K. Biswal, K.S.Ashok, S. Mallick, R. Ranjan and C. Jana checked the data and edited the draft. All authors read and approved the final manuscript.

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Consent to participate Not applicable.

Consent for publication Not applicable.

Statement of animal ethics Ethical statement is not applicable.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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