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Research paper

Molecular epidemiology of swine influenza A viruses in the Southeastern United States, highlights regional differences in circulating strains

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ABSTRACT

Swine influenza A virus (IAV) can cause widespread respiratory disease with high morbidity, low mortality, and have a substantial economic impact to the swine industry. Swine infection may contribute to pandemic IAV given their susceptibility to both avian and human IAVs. Currently, three IAV subtypes (H1N1, H3N2 and H1N2) circulate in swine in North America frequently combining gene segments from avian or human viruses. This study investigated the prevalence of IAV in commercial swine herds. A total of 1878 oral fluid samples were collected from pigs of all ages from 201 commercial farms located in North Carolina and South Carolina. Sixty-eight oral fluid samples from 35 farms were positive by MP gene PCR with an overall IAV-positivity of 3.6%. On the herd level, the percentage of IAV positivity was 17.4%. Fifty-six viruses were subtyped, while 12 were partly subtyped or not subtyped at all. Using *de novo* assembly, complete sequences were obtained for 59 HA genes. The majority of IAVs subtyped had an H1 HA demonstrating a considerable prevalence over H3 viruses. Furthermore, only six out of eleven HA types were detected which has implications for the selection of vaccines used by swine producers in the region.

1. Introduction

Influenza A viruses (IAVs) are Orthomyxoviruses and are single-stranded RNA viruses with a segmented genome (Nicholson et al., 2003). The two surface proteins, haemagglutinin (HA) and neuraminidase (NA), facilitate the entry and release of the virus and they are the primary targets recognized by the immune system after infection and vaccination (Mori et al., 2002; Wiley and Skehel, 1987). Together, HA and NA determine IAV subtypes. The genetic and antigenic changes at these two genes result in virus alteration.

IAVs are among the leading respiratory pathogens in humans, typically causing the death of more than 500,000 people annually and substantial hospitalization (CDC). Waterfowl are the natural reservoir of IAVs; however, a wide range of species can be infected by IAVs such as domesticated poultry, humans, and swine (Ozawa and Kawaoka, 2013; Wahlgren, 2011). The zoonotic capability of IAVs and their potential to reassort have raised health concerns about IAVs emerging in animals and humans. For example, the 2009 H1N1 pandemic virus (pdmH1N1) highlighted the importance of swine in the ecology of IAVs and the protection of public health (Vincent et al., 2014).

IAV in swine cause one of the most important viral diseases and place a heavy economic burden on the pork industry. In the US, the annual losses due to swine IAV are estimated between $360 million and $1 billion (Dykhuis Haden et al., 2012; Holtkamp and Garcia, 2007). The clinical manifestation of the disease in swine range from asymptomatic to widespread respiratory disease characterized by abdominal breathing, coughing, sneezing, fever, anorexia and lethargy (Van Reeth et al., 2008). Three subtypes of IAVs have been identified in swine worldwide: H1N1, H3N2 and H1N2 (Kyriakis et al., 2011; Lewis et al., 2016; Nelson et al., 2015b; Simon et al., 2014). Until the late 1990s, only H1N1 virus was found in swine in North America. This IAV strain is known as the "classical swine" H1N1, and has directly descended from the 1918-19 pandemic virus. Since 1998, a variety of additional IAVs have been detected resulting from multiple reassortant events (Anderson et al., 2013; Gramer et al., 2007; Vincent et al., 2009; Webby et al., 2000). H1N1, H3N2 and H1N2 viruses with HA and NA of human origin and different combinations of internal genes have been circulating in the swine population. The so-called "triple reassortant

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Table 1
Reference sequences used for hemagglutinin classification.

HA Type	Lineage		Reference Virus	HA accession no.
H1	Classical	Alpha	A/swine/Minnesota/02053/2008	CY099119
		Beta	A/swine/Texas/01522/2007	CY157999
		Gamma	A/swine/North Carolina/02403/2008	CY158217
	Human-like	Delta 1	A/swine/Ohio/A01279503/2012	KC355809
		Delta 2	A/swine/Indiana/A01049964/2011	JN652518
	Pandemic		A/California/07/2009	NC026433
H3	Cluster	I	A/swine/Minnesota/593/1999	AF251427
		II	A/swine/Colorado/23619/1999	AF268128
		III	A/swine/Illinois/21587/1999	AF268124
		IV	A/swine/Iowa/01700/2007	CY099027
	Novel human-origin		A/swine/Missouri/A01476459/2012	KP137795

Table 2
Swine influenza A viruses identified by multiplex RRT-PCR.

		Number of samples (percent)
Single infection:		
	H1N1	24 (35.3)
	H3N2	11 (16.2)
	H1N2	16 (23.5)
Mixed infection:		
	H1N1 and H3N2	3 (4.4)
	H1N1 and H1N2	2 (2.9)
Partial subtype:		
	H1Nx	2 (2.9)
	H3Nx	2 (2.9)
	HxN1	1 (1.5)
	HxN2	1 (1.5)
No subtype identified:		6 (8.8)

cassette" that includes internal protein genes of human, avian and classical swine has become established as the dominant backbone of IAVs in swine with different combinations of HA and NA proteins. With the introduction of the pdmH1N1 virus to swine, additional reassortment has been observed in swine both in North America and Europe (Bowman et al., 2012; Watson et al., 2015). While the pdmH1N1 has not been able to become established in the swine, reassortant viruses that include one or more genes of pandemic origin are frequently isolated. In 2012-13 the introduction of human seasonal H3 gene in viruses with swine-origin NA and internal protein gene backbone was identified (Rajao et al., 2015). Overall, 11 genetically distinct HAs, including six H1 and five H3 IAVs, have been identified in swine in North America (Anderson et al., 2015; Lewis et al., 2014).

Given the need to better understand IAV epidemiology, a surveillance study in swine focusing on producers in North Carolina was undertaken. Swine production in the United States is characterized by a disproportionately high number of sow farms in North Carolina approaching 1 million sows, which annually wean about 22 million piglets (USDA, 2012). Weaned piglets (age of 21 to 28 days) are subsequently shipped to the Midwest where they are raised until they are consumed at approximately six months of age. When pigs from different sources are mixed, IAVs have the opportunity to reassort, thus this region of the United States has an important role in the epidemiology of IAVs. In this study, we report the results of our active surveillance of IAVs in the swine population, including viral subtypes and HA gene types identified in the summer of 2014. In summary, a high prevalence of H1N1 and H1N2 viruses was observed compared to H3N2 IAVs, while H1 HA antigenic types were absent, thus these findings have important implications for vaccine selection.

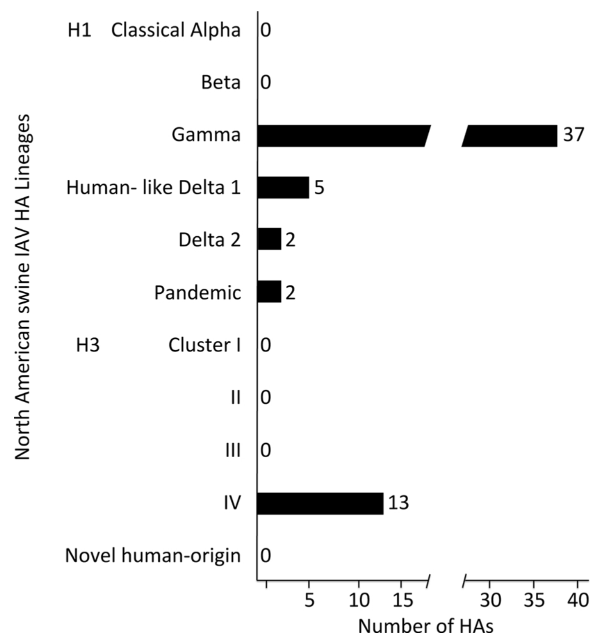

Fig. 1. Classification of hemagglutinin genes by North American lineages.

2. Materials and methods

2.1. Sampling

Between June and August 2014, we performed an active surveillance on swine farms in North Carolina and South Carolina. For active surveillance, clinical specimens are taken on a regular basis regardless of their health status. A total of 1878 oral fluid samples were collected from 201 farms. Oral fluids are sampled by hanging a cotton rope in a swine pen, allowing the animals to chew on it, and then by collecting fluid that accumulate on the rope. Thus, each sample is not from an individual animal, but from multiple swine, which is an advantage of this sampling method (Decorte et al., 2015). While oral samples contain contaminants, such as faeces and feed, they are not the ideal medium for virus isolation, thus this approach has been proven to be efficient for pathogen screening in swine (Goodell et al., 2016).

2.2. Influenza A Virus (IAV) screening

RNA was extracted by the RNAzol RT method (Chomczynski et al., 2013). Briefly, 200 µl of each clinical specimen was mixed with 500 µl of an acid guanidinium thiocyanate-based commercial product (RNAzol® RT, Molecular Research Center, Inc. USA) and 200 µl of molecular grade water. Following centrifugation at 12,000g for 15 min, 700 µl of supernatant were transferred in a new tube and RNA was

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