Journal of Integrative Agriculture 2026, 25(8): 3503–3507

Available online at ScienceDirect

Journal of Integrative Agriculture



LETTER

Genetic diversity and recombination analysis of NADC34-like porcine reproductive and respiratory syndrome viruses

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Highlights

- Recombinant variants represent a substantial proportion (56.82%) of the analyzed NADC34-like PRRSV strains.
- Twelve consistent recombinant patterns (R1–R12) were defined across 176 NADC34-like whole-genome sequences.
- Recombination hotspots in Chinese strains shifted from structural genes to ORF1a after 2020.
- Lineage 1.8 is the primary minor parent driving NADC34-like genetic diversification.

Porcine reproductive and respiratory syndrome virus (PRRSV), a member of the family *Arteriviridae* within the order *Nidovirales*, causes porcine reproductive and respiratory syndrome (PRRS), resulting in substantial economic losses to the global swine industry (Cai *et al.* 2023). The PRRSV genome is about 15 kb in length with a 5′ cap and 3′ poly(A) tail, containing at least 10 open reading frames (ORFs): ORF1a, ORF1b, ORF2–7 (Ma *et al.* 2021; Dey *et al.* 2024). The complex architecture of the viral genome, particularly the 3′-region with overlapping genes, highlights significant genetic intricacy and the challenges associated with genetic manipulation (Dey *et al.* 2024). High mutation and recombination rates of PRRSV facilitate rapid adaptation and immune evasion, leading to diverse strains with varying degrees of pathogenicity, complicating control strategies (Sun *et al.* 2024). A comprehensive understanding of both viral genomes and their evolutionary mechanisms is therefore crucial for developing effective countermeasures (Kim *et al.* 2022; Sun *et al.* 2024).

The classification of PRRSV strains has evolved substantially, transitioning from initial methods based on restriction fragment length polymorphism (RFLP) patterns derived from ORF5 sequencing to more comprehensive approaches incorporating additional genomic regions, such as the region coding the nonstructural protein 2 (Nsp2), and ultimately, whole-genome sequencing (WGS) (Liu *et al.* 2023; Tian *et al.* 2025). PRRSV is primarily classified into two major genotypes: PRRSV-1 (European) and PRRSV-2 (North American) (Crisci *et al.* 2020). Phylogenetic analysis of ORF5 sequences within PRRSV-2 has uncovered multiple lineages and sublineages, providing a valuable framework for tracking the virus's spread and evolution (Tian *et al.* 2025). WGS provides the most detailed method for classifying PRRSV, enabling the detection of recombination events and providing a more precise understanding of the genetic map (Kim *et al.* 2022). Previous studies have characterized recombination events in specific PRRSV strains, such as highly pathogenic PRRSV (HP-PRRSV) and NADC30-like viruses within China (Cui *et al.* 2022; Zhang *et al.* 2023, 2025; Sun *et al.* 2024), highlighting the importance of WGS studies in providing a comprehensive understanding of the virus. NADC34-like PRRS viruses have gained attention due to their widespread prevalence and variable pathogenicity (Li *et al.* 2021; Yuan *et al.* 2022; Zhao *et al.* 2022; Kim *et al.* 2023). First identified in the USA in 2014, these strains have disseminated to other countries, including China, South Korea, Japan, and Peru (van Geelen *et al.* 2018; Xu *et al.* 2022; Jeong *et al.* 2025; Yonezawa *et al.* 2025). They are characterized by a 1-7-4 RFLP pattern in ORF5 (van Geelen *et al.* 2018; Xia *et al.* 2023). The pathogenicity of NADC34-like PRRSV strains varies, ranging from high to low, causing substantial economic losses to the swine industry (Yuan *et al.* 2022).

Here, we classified 176 NADC34-like PRRSV strains by updating the phylogenetic classification of PRRSV based on

Received 23 August 2025; Received in revised form 4 December 2025; Accepted 23 December 2025; Available online 7 January 2026
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doi: 10.1016/j.jia.2026.01.006

1,598 whole-genome sequences retrieved from the GenBank database in June 2025 (Appendix A). Phylogenetic trees were constructed using the maximum-likelihood method (IQ-TREE) with 1,000 bootstrap replicates to ensure reliability. Intra-lineage nucleotide distances among NADC34-like PRRSV strains in this study were generally low (5.68%, SD±3.74). In contrast, inter-lineage distances typically exceeded 14.89%, consistent with established PRRSV genotyping thresholds (>11%) (Tian *et al.* 2025) (Appendix B). Among the 176 strains, 142 were from the USA, 30 from China, and 4 from South Korea. Additionally, we determined 100 recombinant strains using RDP4 with seven algorithms (RDP, GENECONV, BootScan, MaxChi, Chimaera, SiSscan, and 3Seq) verified by SimPlot software. A recombination event was considered significant only if supported by at least three methods with a *P*-value<0.05 (Bonferroni corrected). Recombination rates differed by country: China (8/30), the USA (88/142), and South Korea (4/4). As illustrated in Appendix C, a significant upward trend was observed from 2014 to 2021 in the USA. Recombinant strains exhibited a rapid increase during this period, coinciding with a decline in the detection of non-recombinant strains. A significant increase in NADC34-like PRRSV strains was observed in China between 2017 and 2020. Unlike the USA, recombinant strains did not show a comparable increase. Notably, four whole-genome sequences of recombinant NADC34-like strains were first submitted from South Korea in 2023 (Appendices A and C). The results demonstrated that NADC34-like PRRSV strains exhibit distinct temporal and recombination trends across different countries.

We further examined the recombination patterns of NADC34-like PRRSV recombinant strains. Statistical analysis revealed the contribution of minor parental lineages to recombinant segments, which were subsequently visualized (Appendices D-a and E). Six minor parental lineages were identified (L1.8, L3, L5, L6, L8, and L8.7). Notably, L1.8 served as a minor parent most frequently (54.84%), with most events occurring on the nsps (Appendix D-a). Among the 100 recombinant strains, NADC34-like strains have served as the primary parental lineage for 11 distinct recombination modes. The most prevalent mode, L1.8+L5+L8 (51%), is found exclusively in the USA (Appendix D-b). This high proportion likely reflects both the prevalence of these strains and the repeated use of modified live vaccines (Kikuti *et al.* 2021; Yim-Im *et al.* 2023). The USA swine industry's multi-site structure causes varied disease risks due to different farm management and biosecurity (Makau *et al.* 2021). L1.8 modes were more common in China, while South Korea had only one observed mode: L1.8+L3+L5+L8 (Appendix D-b). The results also reflect the high prevalence of lineages in China and South Korea (Jeong *et al.* 2025; Zhang *et al.* 2025). The temporal dynamics of recombination events revealed that L1.8 works as the largest population for recombination with the major parental NADC34 in three countries from 2014 to 2024 (Appendix D-c).

As shown in Appendix D-d, the most frequent recombination hotspots in the viral genome were in ORF1ab in the USA and South Korea (Appendix D-d). In contrast, ORFs encoding structural proteins exhibited the most frequent recombination targets between 2017 and 2019 in China. Since 2020, ORF1a has become the region with the most recombination events for Chinese strains (Appendix D-d). Appendix D-e revealed frequent recombination in nsp3 in ORF1a in the USA (31.4%) during 2017, 2018, and 2021. In China, however, most events were found on nsp2 (35.7%) in 2018 and 2020 (Appendix D-f). Similarly, in South Korea, nsp2 (23.9%) and nsp3 (23.9%) showed the highest number of recombination events (Appendix D-g). Above all, most events are primarily associated with L1.8. Within ORF1b, nsp9 and nsp10 are more commonly detected in both the USA (particularly in 2018 and 2021) and South Korea (Appendix D-e and g). Most nsp9 events in the USA are associated with L8 (44.1%), while in South Korea they are associated with L3 (42.9%). Nsp10 events in the USA and South Korea are both associated with L1.8, with proportions of 94.9% and 56.0%, respectively (Appendix D-e and g). In China, very few recombinant events on ORF1b were identified. Overall, the frequency of recombination events in ORF1ab was approximately 57.0% higher than in ORF2-7 in all samples from the three countries.

Using the previously established methods, NADC34-like strains were categorized into three groups: consistent recombinant NADC34-R (R1–R12), nonrecombinant NADC34-NR, and irregular recombinant IR (Fig. 1-A and B) (Zhao *et al.* 2017; Kikuti *et al.* 2021; Zhang *et al.* 2025). Notably, among the consistent recombinant patterns, NADC34-R1 strains account for the largest proportion (36/84). The average pairwise genetic distances within and between groups support this classification (Appendix F). Intra-group distances for NADC34-R1 to R12 were about 2.78% (SD ±2.21). In contrast, distances between groups generally exceeded 10%. The mean genetic distance between NADC34-IR and the 12 NADC34-R strains was 10.67% (SD ±1.43) (Table 1). These values align with prior criteria (Zhang *et al.* 2025).

We then analyzed and summarized the pathogenic traits of NADC34-like PRRSV strains as previously described (Zhang *et al.* 2025) to investigate potential patterns in their pathogenicity (Appendix G). Ten NADC34-like PRRSV strains have been assessed for their pathogenicity, showing a range from low to high, with high pathogenicity being the most prevalent (5/10) (Appendix G) (van Geelen *et al.* 2018; Liu *et al.* 2022; Yuan *et al.* 2022; Rawal *et al*. 2023; Cui *et al*. 2025). However, no consistent virulence patterns emerged among different recombinant groups.

Geographically, the NADC34-R7 strain was exclusively found in South Korea. Comprehensive analysis of 29 out of 30 NADC34-like PRRSV strains in China revealed a wide distribution of their PRRSV genomes across 12 Chinese provinces (Appendices H-a and I). Heilongjiang (11/30), Liaoning (4/30), and Sichuan (5/30) accounted for the largest proportions (Appendices H-a and I). In the USA, complete genomes of NADC34-like PRRSV were sequenced from nine states, predominantly located in New York (44/142), Iowa (43/142), Minnesota (22/142), and North Carolina (13/142) (Appendices H-b and I). NADC34-R1 strains were sequenced mainly from New York (13/36) and Minnesota (20/36) in the USA (Appendices H-c

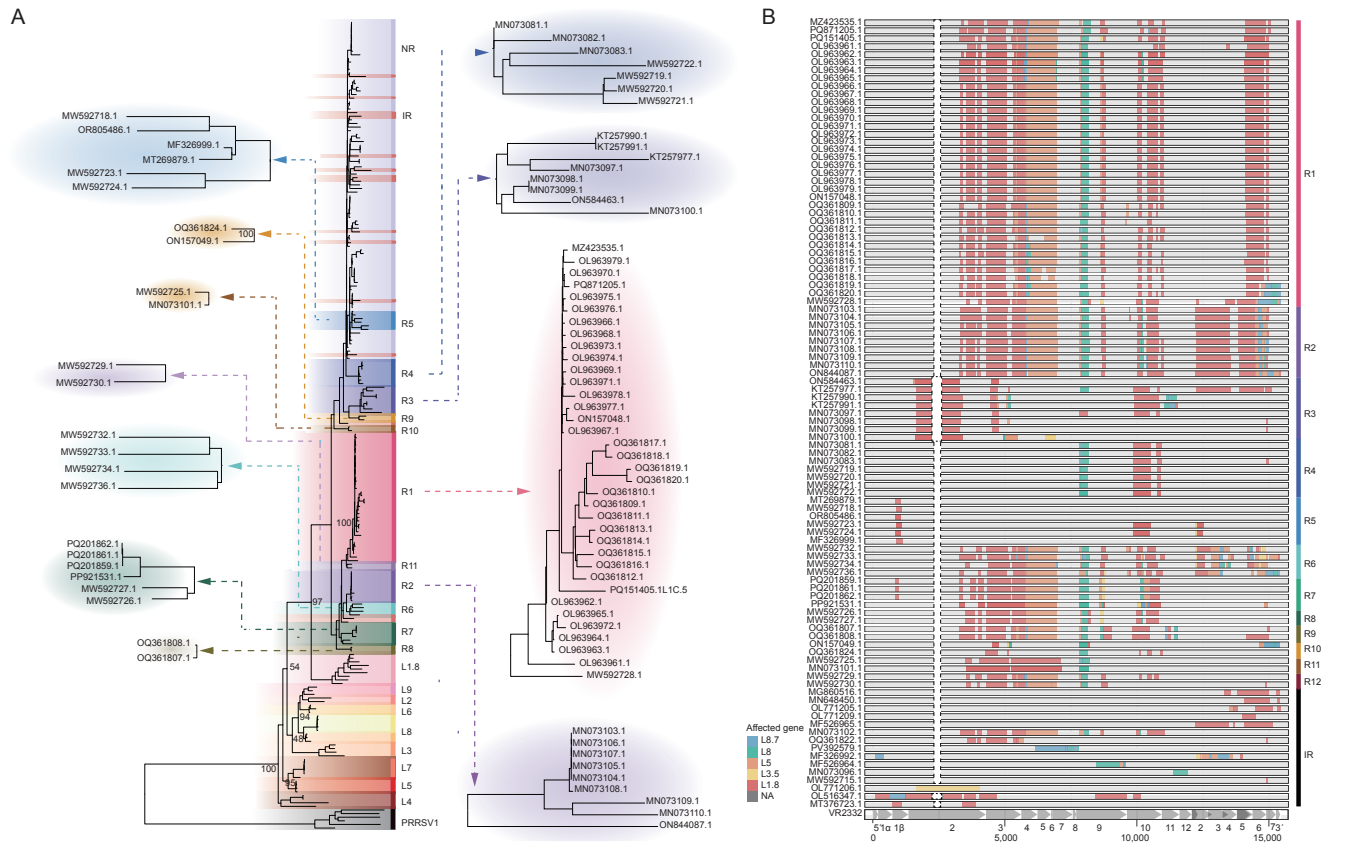


Fig. 1 Classification of NADC34-like PRRSVs based on phylogenetic analysis and recombination patterns. A, phylogenetic tree of 176 NADC34-like PRRSVs. The tree was created using complete genome sequences of NADC34-like PRRSVs and reference strains. B, genomic maps illustrate parental lineages and recombination patterns of 100 NADC34-like PRRSVs. The full-length genome structure is shown with VR-2332 as the reference, highlighting the locations of major ORFs and NSPs. The dotted line marks the characteristic deletion in the nsp2 hypervariable region of NADC34-like PRRSVs and NADC30-like PRRSVs.

Table 1 Average genetic distance (% nucleotide difference) within and between NADC34-like PRRSV strains

Subgroup	NR	IR	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12
	n=76	*n*=16	*n*=36	*n*=9	*n*=8	*n*=7	*n*=6	*n*=4	*n*=4	*n*=2	*n*=2	*n*=2	*n*=2	*n*=2
NR	3.16													
IR	6.31	10.51												
R1	11.09	11.16	1.89											
R2	11.49	11.27	5.63	0.57										
R3	9.52	10.92	13.70	14.16	6.77									
R4	6.22	8.40	11.44	11.72	10.72	1.55								
R5	5.35	7.83	11.88	12.12	10.40	7.36	5.30							
R6	12.86	12.81	7.96	5.40	15.58	12.99	13.29	6.09						
R7	11.49	12.02	8.19	7.52	14.09	11.75	12.16	9.57	0.73					
R8	11.07	11.61	7.83	6.93	13.79	11.41	11.84	9.02	6.34	2.56				
R9	10.43	11.23	8.05	7.99	12.64	10.96	11.18	9.93	8.60	8.38	0.30			
R10	8.06	9.96	11.92	12.04	9.78	9.42	8.83	13.31	12.35	11.99	11.28	3.50		
R11	8.74	10.11	10.44	10.41	12.35	10.05	10.13	11.96	11.04	10.62	10.15	10.60	1.20	
R12	10.25	10.70	4.20	5.67	13.13	10.68	11.10	7.49	7.64	7.28	7.45	11.30	9.73	2.90

and I). NADC34-R2 strains were submitted from Iowa (8/9). NADC34-R3 strains were mainly submitted from Iowa (5/8). NADC34-R4 to R12 (excluding R7) were predominantly found in New York. In China, eight recombinant strains falling into IR or R3 were found across five provinces. The highest share is in Sichuan (3/8), followed by Heilongjiang (2/8, IR), Jilin (1/8, IR), Liaoning (1/8, IR), and Taiwan (1/8, R3) (Appendices H-c and I). This distribution may reflect the high density of pig farming and the presence of numerous research institutions in these regions (Zhang *et al.* 2025). Most NADC34-like PRRSV recombinant patterns (R1–R12, excluding R7) exist in the USA, with R1, R2, and R3 as the top three patterns. R3 initially appeared in 2014, with four additional cases in 2017. Subsequently,

R2 emerged in 2017 (*n*=9) but was not detected thereafter. Then, R1 appeared in 2018 (*n*=19) at a relatively high frequency and was detected again in 2021 at a similarly high frequency. Other recombinant patterns were less frequently observed, primarily between 2020 and 2021. In China, one NADC34-R3 strain was identified in Taiwan in 2018. We sought to identify potential intermediate recombinants. However, their temporal distribution suggests they are not obligatory evolutionary intermediates.

As shown in Appendix J, NADC34-like PRRSV strains increased significantly from 2014 to 2021. The USA remains the primary country where these strains are prevalent, accounting for the highest proportion (80.68%, 142/176), followed by China (17.05%, 30/176). Recombinant strains (56.82%, 100/176) are now predominant over non-recombinant strains (43.18%, 76/176). Among the recombinant strains, NADC34-R1 strains constitute the largest proportion (20.45%, 36/176) of the analyzed strains and are exclusively found in the USA.

In summary, whole-genome analysis revealed significant genetic diversity and recombination patterns among NADC34-like PRRSV strains in the USA, China, and South Korea. Distinct from previous studies that focused solely on the USA (Kikuti *et al*. 2021) or China (Zhang *et al.* 2025), this study provides a comparative international analysis. A key insight is the identification of a temporal shift in recombination hotspots in Chinese strains (from structural proteins to ORF1a), contrasting with the persistent circulation of the NADC34-R1 recombinant lineage in the USA. However, a direct link between recombination and virulence remains unclear. The predominance of NADC34-R1 strains in the USA suggests their role in localized outbreaks. Continued surveillance and in-depth analysis are crucial for developing targeted intervention and control strategies, providing valuable insights for future PRRSV prevention.

Acknowledgements

This work was supported by the National Natural Science Foundation of China-CGIAR (32361143511), the Jiangsu Innovative and Entrepreneurial Talent Team Project, China (JSSCTD202224), the 111 Project D18007, and the Priority Academic Program Development of Jiangsu Higher Education Institutions, China (PAPD).

Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Ethical statements

Not applicable.

Appendices associated with this paper are available at https://doi.org/10.1016/j.jia.2026.01.006

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