The authors of Zhang et al. 34:1446–1449 (2021) retracted this article because the initially reported genome assembly of NAFU1 was contaminated. This article was retracted on 28 November 2022, and the correction of the NAFU1 genome assembly at NCBI will be made in the future.

Genome Sequence Resource for *Erysiphe necator* NAFU1, a Grapevine Powdery Mildew Isolate Identified in Shaanxi Province of China

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Abstract

Erysiphe necator is an economically important biotrophic fungal pathogen responsible for powdery mildew disease on grapevine. Currently, genome sequences are available for only a few *E. necator* isolates from the United States. Based on the combination of Nanopore and Illumina sequencing technologies, we present here the complete genome assembly for an isolate of *E. necator*, NAFU1, identified in China. We acquired a total of 15.93 Gb of raw reads. These reads were processed into a 61.12-Mb genome assembly containing 73 contigs with an N₅₀ of 2.06 Mb and a maximum length of 6.05 Mb. Combining the results of three gene-prediction modules (i.e., an evidence-based gene modeler [EVIDENCEModeler], an ab initio gene modeler, and a homology-based gene modeler), we predicted 7,235 protein-coding genes in the assembled genome of *E. necator* NAFU1. This information will facilitate studies of genome evolution and pathogenicity mechanisms of *E. necator* and other powdery mildew species through comparative genome sequence analysis and other molecular genetic tools.

Genome Announcement

Powdery mildew caused by ascomycete fungi in the order Erysiphales is an important and widespread disease of numerous plant species, including wheat, barley, bean, rose, rubber, tomato, strawberry, and grape (Braun and Cook 2012; Wu et al. 2018). The Eurasian grape, *Vitis vinifera* L., is the most widely cultivated and economically important fruit crop in the world. However, the Eurasian grape is susceptible to many oomycete and fungal diseases, including downy mildew caused by *Plasmopora viticola*, gray mold caused by *Botrytis cinerea*, and powdery mildew caused by *Erysiphe necator* (Gadoury et al. 2012; Gessler et al. 2011). Among these three types of pathogens, *E. necator* does not require specific humidity and temperature conditions for infection (Dry et al. 2010); therefore, powdery mildew is the most frequent disease of grapevines in many areas. *E. necator* can infect all green tissues of a grapevine. As in other plants, grapevine leaves infected by powdery mildew often

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Keywords

Erysiphe necator, genome, genomics, grapevine, powdery mildew

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show reduced photosynthesis and suffer from premature senescence and abscission (Han et al. 2016). Even a low-level infection can reduce the quality of berries, which may affect the flavor of wine and table or raisin grape berries. Severe infection can cause berry cracking and dropping, or even result in significant loss of harvest (Gadoury et al. 2003; Qiu et al. 2015). Despite its importance, relatively little information is currently available regarding pathogenicity mechanisms of *E. necator* as well as other powdery mildew pathogens. Apart from the genetic intractability of all powdery mildew fungi, the lack of well-assembled genomes for the identification of key effectors of host-adapted powdery mildew species, sub-species, or isolates also hinders mechanistic studies of powdery mildew.

To date, the whole-genome sequences of five isolates of *E. necator* (Branching, C-strain, e1-101, Lodi, and Ranch9) have been reported. There are apparent sequence differences among the genomes of the five powdery mildew isolates with different genetic and geographical backgrounds (Jones et al. 2014). Another report indicated that there is sequence polymorphism between isolates from different regions and hosts in the eastern United States, let alone when the U.S. isolates are compared with those from southern France and Italy (Brewer and Milgroom 2010; Frenkel et al. 2012). Viticulture has a long history in China and there is rich wild grapevine germplasm (Gao et al. 2016) in many different regions of China. It is conceivable that the long-time grapevine–powdery mildew coevolution must have shaped the genomes of powdery mildew pathogens in these regions. Hence, obtaining the whole-genome sequence of a grapevine powdery mildew isolate identified in China would provide valuable sequence information for future investigation of host adaptation of powdery mildew in different regions.

Here, we report the genome sequence of an *E. necator* isolate NAFU1, which was isolated from *Vitis vinifera* 'Rizamat', Shaanxi Province, China and maintained on the susceptible grapevine cultivar Thompson Seedless (Gao et al. 2016). Spores *E. necator* NAFU1 were collected from infected leaves of grapevine at 10 to 15 days postinoculation using a small vacuum and used for genomic DNA extraction using the cetyltrimethylammonium bromide method (Feehan et al. 2017). Approximately 12 µg of pure DNA with an average size of 20 kb was used for genome sequencing by the Oxford Nanopore and Illumina technologies. The genome sequences of *E. necator* NAFU1 were assembled by using a combination of short reads (approximately 6,657,136,974 bp) generated by Illumina sequencing (NOVA-Seq6000 platform, PE150, read length = 150 bp, paired-end reads) and long reads (approximately 13,268,751,137 bp) by Oxford Nanopore sequencing (PromethION) performed at Biomarker Technologies (Beijing, China). In total, 13.27 Gb of Nanopore long reads, representing approximately 217× coverage of the *E. necator* NAFU1 genome, and 6.66 Gb of Illumina NOVASeq6000 short reads (approximately 109×) were generated. The Nanopore reads of low quality and less than 2,000 bp were filtered out. NECAT was used to assemble the Nanopore subreads after filtering, and Pilon was used to correct the assembled sequences using the second-generation sequence data (Koren et al. 2017; Walker et al. 2014).

The final genome assembly of *E. necator* NAFU1 is 61.12 Mb in length with 48.5% GC content. The assembly contains 73 contigs with an N₅₀ length of 2.06 Mb (the longest contig length is 6.05 Mb) and 98.3% benchmarking universal single-copy ortholog (BUSCO) completeness (based on 1,315 conserved Ascomycota orthologs). This indicates that the whole-genome assembly of *E. necator* NAFU1 is of high quality, which ensures accurate prediction of the protein-coding genes in its genome. Genscan (Burge and Karlin 1997), Augustus v2.4 (Stanke and Waack 2003), GlimmerHMM v3.0.4 (Majoros et al. 2004), GeneID v1.4 (Blanco et al. 2007), and SNAP (version 2006-07-28) (Korf 2004) were used for ab initio gene prediction, and GeMoMa v1.3.1 (Keilwagen et al. 2016) was used for homology-based gene prediction. Finally, EVIDENCEModeler v1.1.1 (Haas et al. 2008) was used to integrate the above two methods to obtain 7,235 protein-coding genes. In total, 7,235 protein-coding genes were predicted, with an estimated BUSCO completeness of 96.7% and average length of protein-coding gene of 2,169 bp. The sequence features of the genome assembly of *E. necator* NAFU1 and other isolates are shown in Table 1. A comparison with the assembled genomes of other isolates (Jones et al. 2014) suggests a much deeper sequence depth and higher genome coverage, with fewer contigs, than for that of *E. necator* NAFU1.

To ensure a successful infection on their host plants, fungal pathogens produce a suite of carbohydrate-active enzymes (CAZymes) to digest polysaccharides of the plant cell wall and send hundreds of secreted effector proteins into the host cell to suppress plant immunity (Adachi et al. 2020; Yin et al. 2012). To assess the size of the CAZymes of *E. necator*

Table 1. Sequence features of the genome assembly of *Erysiphe necator* NAFU1 and other isolates

Genomic feature	NAFU1	C-strain	Lodi	Ranch9	Branching	e1-101
Sequencing platform	Nanopore	Illumina MiSeq	Illumina HiSeq	Illumina HiSeq	Illumina HiSeq	Illumina HiSeq
BioSample	SAMN17620199	SAMN02803834	SAMN02803901	SAMN02803894	SAMN02803892	SAMN02803896
BioProject	PRJNA695796	PRJNA247407	PRJNA248904	PRJNA248903	PRJNA248900	PRJNA248902
Total assembly size (bp)	61,122,667	52,505,057	49,793,988	49,465,130	50,658,153	49,942,550
Coverage	217x	76x	42x	24x	29x	42x
GC content (%)	48.5	39.0	38.9	38.8	38.5	38.8
Number of contigs	73	8,584	8,093	8,274	11,631	7,601
Maximum contig length (bp)	6,053,329	–	–	–	–	–
Contig N ₅₀ (bp)	2,063,233	16,949	13,724	13,213	12,413	15,756
Contig N ₉₀ (bp)	822,440	–	–	–	–	–
Contig L ₅₀	9	895	1,073	1,099	1,195	935
Total protein-coding genes	7,235	6,484	–	–	–	–
BUSCO (%) ^a	98.3	–	–	–	–	–
Transfer RNAs	244	–	–	–	–	–
Ribosomal RNAs	76	–	–	–	–	–
Secretome ^b	453	422	–	–	–	–
Effectorome ^c	196	150	–	–	–	–

^a BUSCO: benchmarking universal single-copy ortholog completeness.

^b Secretome: proteins have signal peptide but without a transmembrane domain.

^c Effectorome: predicted by software EffectorP.

NAFU1, genes encoding such enzymes were predicted by the webtools at the CAZymes database. In total, 327 CAZyme genes were predicted in the genome of *E. necator* NAFU1. These CAZymes belong to five superfamilies, including 138 (42.2%) glycosyl hydrolases, 96 (29.35%) glycoside transferases, 53 (16.2%) carbohydrate esterases, 26 (7.95%) enzymes with auxiliary activities, and 14 (4.28%) other carbohydrate-binding proteins. To identify candidate genes encoding secreted proteins, SignalP v3.0 (Bendtsen et al. 2004) was used for the prediction of an N-terminal signal peptide and TMHMM (Krogh et al. 2001) was used for the prediction of transmembrane domains. In total, 453 genes in the genome were predicted to encode secreted proteins that contain a signal peptide but no transmembrane domains. Using EffectorP (Sperschneider et al. 2018), 41 genes were predicted to encode candidate effector proteins in the genome of *E. necator* NAFU1.

The availability of the genome sequence of *E. necator* NAFU1 will facilitate intraspecific as well as interspecific comparative genome analyses of powdery mildew fungi for investigating how they have coevolved with their respective plant hosts in different habitats. One future study we hope to conduct is to assess the impact of resistance from various wild Chinese grapevines on the effector repertoire of *E. necator* NAFU1 in comparison with *E. necator* originating in the United States and Europe.

Data Availability

The *E. necator* NAFU1 genome has been deposited at the DNA Data Bank of Japan/European Nucleotide Archive/GenBank database under the accession number JAF-BAW000000000 (BioProject PRJNA695796 and BioSample SAMN17620199). The version described in this article is version JAFBAW010000000.

Author-Recommended Internet Resource

CAZymes database: <http://www.cazy.org>

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