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## The chestnut blight fungus for studies on virus/host and virus/virus interactions: From a natural to a model host

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## ABSTRACT

The chestnut blight fungus, *Cryphonectria parasitica*, is an important plant pathogenic ascomycete. The fungus hosts a wide range of viruses and now has been established as a model filamentous fungus for studying virus/host and virus/virus interactions. This is based on the development of methods for artificial virus introduction and elimination, host genome manipulability, available host genome sequence with annotations, host mutant strains, and molecular tools. Molecular tools include sub-cellular distribution markers, gene expression reporters, and vectors with regulatable promoters that have been long available for unicellular organisms, cultured cells, individuals of animals and plants, and certain filamentous fungi. A comparison with other filamentous fungi such as *Neurospora crassa* has been made to establish clear advantages and disadvantages of *C. parasitica* as a virus host. In addition, a few recent studies on RNA silencing vs. viruses in this fungus are introduced.

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## Introduction

It is believed that there exist at least 1.5 million fungal species on the globe that include over 100,000 identified species and those unidentified or unreported (Hawksworth, 1991). Viruses are found in all major groups of fungi (Ghabrial and Suzuki, 2009; Pearson et al., 2009), and the International Committee on Taxonomy of Viruses now lists ~80 definitive species ([http://talk.ictvonline.org/files/ictv\\_documents/m/msl/4911.aspx](http://talk.ictvonline.org/files/ictv_documents/m/msl/4911.aspx)). This number in reality should be far higher. It is reasonable to assume that a vast number of unrecognized fungal viruses (mycoviruses) make up a nano-world in the kingdom Fungi. In fact, viruses were found in a few to several tens of percent of field fungal isolates when they were screened (Arakawa et al., 2002; Ikeda et al., 2004; Jiang et al., 2014). Among the enormous number of fungi, there are only a limited number of them are studied that are of economical, agricultural, medical, technological or purely scientific

importance. Of them, only a few are studied as virus hosts one of which is the chestnut blight fungus, *Cryphonectria parasitica* (Murrill) Barr. Chestnut blight attracts great attention mainly from interconnected factors as an important plant pathogen and as a virus host (Hillman and Suzuki, 2004). Here, we overview properties of the chestnut blight fungus as a model filamentous fungus for studies of virus/host and virus/virus interactions. Readers are also referred to other related elegant reviews (Dawe and Nuss, 2001, 2013; Nuss, 2005; Turina and Rostagno, 2007; Wickner, 1996). Although *C. parasitica* also has been a research subject in the biological control of a plant pathogenic fungal disease involving fungal viruses (Heiniger and Rigling, 1994; Milgroom and Cortesi, 2004), this is not the scope of this paper.

### Chestnut blight and *C. parasitica*: a brief overview

Chestnut trees occupied a large portion of the forest canopy. The trees provided shelter for a variety of wildlife, and were utilized for its hard-quality lumber, and sources for tannins, wood, fuel, and edible nuts. Common existence of chestnut trees was greatly involved in the life of people in North America and Europe, and had deeply taken root into the culture. Thus, this crop was considered of great economic and ecological importance. However, the introduction of chestnut blight

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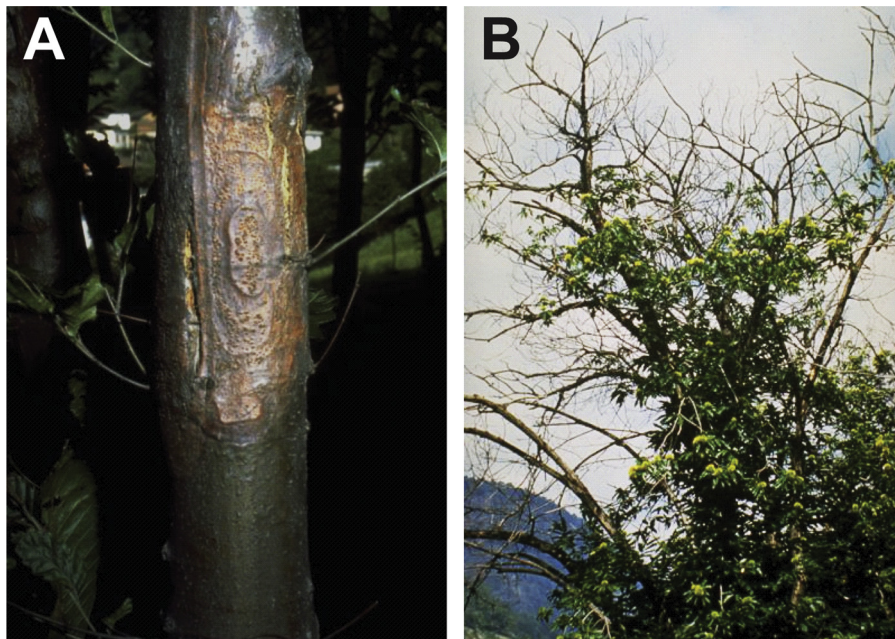
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**Fig. 1.** Naturally occurring chestnut blight. (A) Virulent canker naturally induced by the chestnut blight fungus on a European chestnut tree (*Castanea sativa*). A European chestnut tree with die-back symptoms. These pictures are courtesy of Dr. Daniel Rigling at Swiss Federal Institute for Forest, Snow and Landscape Research WSL.

disease caused by the ascomycetous fungus, *C. parasitica* to the United States and Europe in the 20th century from East Asia (most likely from Japan) resulted in destruction of the chestnut trees in those areas (Anagnostakis, 1982; Griffin and Elkins, 1986; Milgroom et al., 1996). The causal agent, *C. parasitica*, enters host trees from wound sites. The disease exhibits sunken canker in the stem of the affected tree that continues to expand and penetrate, thus, demolishing the cambium layer (Fig. 1A). Diseased trees often show die-back symptoms (Fig. 1B) and are eventually killed. This fungus develops fan-shaped formation of mycelia in the cambium and bark of the host. Success of this pathogen to perpetuate itself is through the multitude of conidia (asexual spores) and ascospores (sexual spores) loaded in cankers, which act as effective propagules for dispersal and continuity of the disease cycle (Fig. 2). These propagules, dispersed by wind, rain, insects, or small animals, germinate and develop into a network of interconnected hyphae (mycelia). Matured mycelial strands then give rise to new progenies (conidia) emanating either directly from the somatic hyphae or specialized conidiogenous cells, often borne on hyphal branches (conidiophores). Regardless of tree age during the onset of disease, the upper part of the infection site starts to senesce showing wilted leaves and, at times, partial death of tree. This is a typical symptom of blight, hence the name of the disease. Due to the breadth of its destruction, chestnut blight is considered as one of the three most destructive tree diseases of the world along with Dutch elm disease and white pine blister rust (Tainter and Baker, 1996). For the detailed pathology of this fungus, see previous papers (Anagnostakis, 1987; Roane et al., 1986).

The fungal pathogen *C. parasitica* belongs to the phylum Ascomycota, subphylum Pezizomycotina, class Sordariomycetes, order Diaporthales, and family Cryphonectriaceae (Gryzenhout et al., 2006). As do most filamentous ascomycetes, each *C. parasitica* isolate has haploid nuclei with a single mating type either *MAT-1* or *MAT-2* (McGuire et al., 2004). Sexual crossing occurs only between the different mating types. Results of cytological and molecular karyotyping (Eusebio-Cope et al., 2009) of the standard wild-type (WT) strain, EP155, demonstrated the chromosome number of this fungus to be nine (Fig. 3) and a rough estimate of its genome as 50 mega base pairs (Mb). A group of researchers led by Donald L. Nuss initiated a genome

sequence project of this fungus in 2007 and the Joint Genome Institute (JGI, United States Department of Energy) released the assembly version 2.0 of the whole genome shotgun reads of *C. parasitica* for public use <http://genome.jgi.doe.gov/Crypa2/Crypa2.home.html>. With its scaffold sequence bases total size of 43.9 Mb, a total of 11,609 genes were structurally and functionally annotated in the latest version. This number is close to the estimated 10,000 protein-coding genes contained in the approximately 40-Mb in seven chromosomes of *Neurospora crassa*, orange bread mold, a relative of the chestnut blight fungus and the best-characterized fungus among filamentous fungi (Galagan et al., 2003). Furthermore, a large-scale transcriptome data set is available (Dawe et al., 2003; Shang et al., 2008).

#### *C. parasitica* as a model filamentous fungus for virological studies

Early eukaryotic model organisms can be represented by *Saccharomyces cerevisiae* (baker's yeast), *Musa musculus* (mouse), *Drosophila melanogaster* (fruit fly), *Caenorhabditis elegans* (nematode), and *Arabidopsis thaliana* (thale cress). Properties common to these include their small body and genome sizes, short generation time and easy propagation, available genome sequences with well-established annotations, available techniques for gene manipulation, and useful biological resources and molecular tools. Findings with model organisms can be applicable for more important organisms, i.e., humans, livestock, and crops. During the past decade, the number of eukaryotes for which genome sequences were determined has grown, and many of them fulfill aforementioned criteria. The chestnut blight fungus also meets most criteria expected of a model virus-host organism as described below. *C. parasitica* is reminiscent of *Nicotiana benthamiana* in biological tractability as a virus host to many viruses (Bombarely et al., 2012; Goodin et al., 2008). As discussed below, like *N. benthamiana*, (tobacco plant) *C. parasitica* has some disadvantages over other better-established model organisms, but has great advantages as a virus host. Comparison of the two organisms in this regard will be discussed in the forthcoming 60th Anniversary Special Issue of Virology.

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