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Mycoviruses – the potential use in biological plant protection

Mykowirusy – perspektywy wykorzystania w biologicznej ochronie roślin

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Summary

Biological plant protection is an alternative mean to the chemical pesticides used on a large scale, the use of which carries a great danger for the functioning of living organisms, including humans. Many mycoviruses, which are able to interfere with the host's phenotypic image, have shown great potential in the control of phytopathogenic fungi. The symptoms are composed of the phenomenon of hypovirulence, i.e. the reduction of fungal pathogenicity in relation to the plant. There are known mycoviruses capable of infecting the most important phytopathogens, including *Magnaporthe oryzae*, *Botrytis cinerea*, *Fusarium graminearum* or *Rhizoctonia solani*. This is the basis for continuing research to develop effective antifungal agents.

Key words: phytopathogenic fungi, mycovirus, biological control of crop, fungal diseases, hypovirulence

Streszczenie

Biologiczna ochrona roślin stanowi alternatywę dla wykorzystywanych na masową skalę związków chemicznych, których stosowanie niesie ze sobą duże niebezpieczeństwo dla funkcjonowania organizmów żywych, w tym człowieka. Ogromny potencjał w walce z grzybami fitopatogennymi kryje się w mykowirusach, które są zdolne do ingerowania w obraz fenotypowy gospodarza, ograniczając między innymi tempo wzrostu grzybni, zdolność sporulacji czy wywołując efekt cytolityczny. Powyższe objawy składają się na zjawisko hipowirulencji, czyli obniżenia patogenności grzyba w stosunku do rośliny. Poznane zostały mykowirusy zdolne do infekowania najistotniejszych fitopatogenów, w tym *Magnaporthe oryzae*, *Botrytis cinerea*, *Fusarium graminearum* czy *Rhizoctonia solani*. Stanowi to podstawę do kontynuacji badań, służących opracowywaniu skutecznych preparatów przeciwgrzybiczych.

Słowa kluczowe: grzyby fitopatogenne, mykowirus, biologiczna ochrona roślin, grzybicze choroby roślin, hypowirulencja

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Wstęp / Introduction

Fungi are living organisms whose earliest fossils date back to about 460 million years (Redecker *et al.* 2000), and molecular clock studies suggest an even older metric of more than one billion years (Parfrey *et al.* 2011). This indicates that fungi have appeared on Earth earlier than land plants (the oldest plant fossils are about 420 million years old), and some scientists even suggest that they have allowed colonization of the Earth by the first plants (Redecker *et al.* 2000).

First scientific observations and experiments with fungi, including their germination, are attributed to the Italian scientist Pietro Antonio Micheli, who was named the father of mycology. In 1729 he published a book describing about 1900 species of organisms, 900 of which belonged to fungi. As the precursor of modern mycology, German Anton Antoine de Bary is recognized as the first to prove that fungi are etiological factors of plant diseases, which has been the impetus for the development of phytopathology. Since then until now, knowledge about fungi has developed very dynamically, new species are being discovered as well as remarkable interactions between fungi and other organisms. The aspect of cross-species interactions with fungi is especially gaining increasing interest in practical use in medicine, economy and agriculture. These studies seem to have an indefinite time perspective, because at present there are at least 99 000 species of fungi and FLOs (fungi-like organisms) on our planet, and new taxa (about 1200 per year) are also being rapidly discovered (Kirk *et al.* 2008; Blackwell 2011; Carris *et al.* 2012). This fact makes it prudent to estimate that the total number of fungal species on Earth is approximately 1 500 000 (Hawksworth 2001). This impressive number contains a great variety of heterotrophic organisms representing fungi and fungal-like organisms, now called mycobiote. The unlimited adaptability of mycobiote resulting from their morphology, anatomy, and exceptional physiology provided them with evolutionary success and made them possible to be considered as cosmopolitan and ubiquitous organisms. In all natural ecosystems and agro-ecosystems, their interaction with plants is of particular importance. Most plant-related mycobiote are saprotrophs, causing their debris to decompose, which they use as a source of nutrients (Carris *et al.* 2012). Less than 10% of mycobiote species are capable of colonizing living plants (Knogge 1996) and among these groups are distinguished species that occur with symbiosis (endo- or ectomycorrhizal) plants and parasitic mycobiota (pathogens) (Carris *et al.* 2012). Phytopathogenic mycobiote utilizes nutrients taken from a living host plant, resulting in disease progression in the plant and leading to its death. According to bibliographic data up to now, more than 8000 species of mycobiotes have been found to be phytopathogenic (Ellis *et al.* 2008). There are also known pathogenic fungi (Pier *et al.* 2000), inducing insect zoomycosis (entomopathogens) (Meyling and Eilenberg 2007) and vertebrate dermatoses, including human being (Deangelis *et al.* 2005).

Phytopathogenic fungi, by their effect on the health, quality and quantity of crop yields, have always played an important role in the food economy. It is estimated that up to 70% of plant diseases are caused by phytopathogenic fungi (Carris *et al.* 2012). Integrated plant protection methods commonly used in various plant cultivation mostly limits these losses. However, there are known in history catastrophic examples of the epidemic occurrences of plant diseases that have affected the lives of millions of people. For instance, the Great Famine in Ireland was a period of mass starvation and disease (1845–1850), when *Phytophthora infestans*, which caused potato blight, infected up to one-half of the potato crop in 1845, and about three-quarters of the crop over the next seven years (Clark 2010). The Potato Famine resulted in the death of about 1.5 million and the mass emigration of an equally large group to the United States. Another example is the epidemic of powdery mildew of vine, caused by FLO *Plasmopara viticola*. In the second half of the 19th century, *P. viticola* infected vineyards in western and central Europe, causing huge losses in the vineyards and in consequence, a decline in wine production (Ellis *et al.* 2008). In the 20th century, a number of leaf blight epidemics were recorded, resulting in huge crop and financial losses. It is worth mentioning *Puccinia graminis* f. sp. *tritici* crop infections resulting in the destruction of more than 10 million m^3 of wheat in the United States and Canada and in 1953–1954 only in US causes a loss about $ 365 million (USDA 2017). A list of the 10 most important phytopathogens causing global economic losses has been developed (Dean *et al.* 2012). This list includes, in order: (1) *Magnaporthe oryzae*, (2) *Botrytis cinerea* – the cause of gray mold, (3) *Puccinia* spp. – causes of rust, especially cereal crops, (4) *Fusarium graminearum* – the cause of cereal fusariosis, (5) *Fusarium oxysporum* – the cause of plant tracheomicosis, (6) *Blumeria graminis* – the cause of powdery mildew, (7) *Mycosphaerella graminicola* – the cause of striped septoriosis of wheat leaves, (8) *Colletotrichum* spp. – cause of antracnosis of various plants, (9) *Ustilago maydis* – the root cause of maize, (10) *Melampsora line* – the cause of flax rust. In addition, two phytopathogens were identified: *Phakopsora pachyrhizi* and *Rhizoctonia solani*, which caused respectively soy rust and rhizoctoniosis of various plant seedlings and potato rhizoctoniosis.

The quality of crop plants after harvest is strongly connected with the presence and biochemical activity of phytopathogens producing toxic compounds. Many mycotoxin-producing fungi are common, and often very strongly related to plants, and consequently also to food production. The natural fouling by fungi of the food industry is dominated by three genera: *Aspergillus*, *Fusarium* and

Penicillium. *Fusarium* species are developing pathogens on cereals and other crops, producing mycotoxins during vegetation or just after harvest. The majority of *Aspergillus* and *Penicillium* species, which are also pathogens or plant commensals, are commonly grown on plant products during their drying and storage (Pitt 2000), leading to contamination with mycotoxins. As a result of human or animal consumption of plant products contaminated with mycotoxins, mycotoxicosis may be affected, a toxic effect manifesting as deterioration in health (Peraica *et al.* 1999).

The negative effects of the influence of mycobiotes on the quantity and quality of plant production are forcing them to seek new methods of preventing them. Therefore, the purpose of this paper is to review the literature on the assessment of the potential and effectiveness of mycoviruses as fungistatic or fungicidal agents in biological protection of plants.

Aktualnie stosowane metody przeciwdziałania i zwalczania grzybów fitopatogennych oraz wpływ tych metod na inne organizmy / Currently applied methods of countering and control phytopathogenic fungi and the influence of these methods on other organisms

The occurrence of plant epiphytoses is associated with economic and often sociological consequences such as diseases, famine and population migration. Because of that plant protection with a number of preventive and intervention methods is needed. The most effective preventive methods to eliminate or reduce the presence of phytopathogens in ecosystems are strategies related to (1) good agricultural practice, based on high agrotechnical culture, (2) use of genetically modified plants for resistance to phytopathogenic growth, (3) breeding of resistant varieties and (4) external and internal quarantine regulations (Ellis *et al*. 2008). Interventions are the ability to control phytopathogens with (5) the use of chemicals and (6) biological methods. Possibilities of using genetically resistant cultivars/varieties (3) provide a defense against viral, bacterial, and fungal infections. The necessary condition for registration of new potato varieties is, among others, their resistance to *Synchytrium endobioticum* – the cause of potato canker, a disease that occurred in the first half of the 20th century, and currently has no significant significance. Cultivars resistant to *P. infestans* have been developed to limit the occurrence of the potato late blight. There are known soy cultivars resistant to *Peronospora manshurica*, causing agent of powdery mildew, and various cereal resistant varieties resistant to *B. graminis* (formerly *Erysiphe graminis*), an etiological agent of powdery mildew of cereals and grasses (Ellis *et al.* 2008). Of course, this resistance is not a lasting feature due to the emerging pathotypes of pathogens. The loss of such resistance were reported by the breeders of wheat cultivars resistant to *P. graminis* f. sp. *tritici* when a new strain of *P. graminis* f. sp. *tritici* – Ug99 (in the US nomenclature known as TTKSK) was introduced in Uganda with a potential mutation causing the development of rust on a resistant wheat variety. It has been found that this pathogen rapidly mutated and as many as 13 strains of this phytopathogen within the Ug99 line have been identified as early as 2016, capable of growing on resistant varieties of wheat, which is a real threat to the crop worldwide (Singh *et al.* 2011; Patpour *et al.* 2016).

Prevention and intervention methods related to the use (5) of chemicals are based on: (a) the use of soil fumigants, (b) the application of fungicides during vegetation, and (c) the use of fungicides after the harvest of plant crops.

Unfortunately, the use of chemical plant protection products, including fungicides, presents a great danger to the functioning of living organisms, from microorganisms through plants and animals, to humans. Due to excessive application of fungicides in the vine protection, wine yeast inhibition (Calhelha *et al.* 2006) and photosynthesis in vines have been observed (Saladin *et al.* 2003; Petit *et al.* 2008). In relation to mammals, researchers found problems with sexual differentiation and reproduction in mice (Gray *et al.* 1994; Paro *et al.* 2012), as well as a number of dysfunctions in humans, like neurological diseases, hypospadias, endocrine disorders and increased incidence of cancer (Saracci *et al.* 1991; Blair *et al.* 1993; Kamel and Hoppin 2004). Fungicides and their metabolites enter the body through the skin (USEPA 1992), and may accumulate in fat, liver, thyroid and nervous system (Kamrin 1997). Farmers and others working in plantations where pesticides are used are considered the hazardous group (Saracci *et al.* 1991; Blair *et al.* 1993; Garry *et al.* 2002).

Another undesirable consequence of the use of chemical plant protection products is the production of resistant phytopathogenic pathotypes, which is associated with reduced efficiency and the need to use still new chemical groups. The above problems led scientists to intensify their work on biological plant protection methods which involves maximizing the use of natural processes and dependencies in biocenosis while maintaining homeostasis of the agroecosystem (Campbell 1989).

Algae (Kulik 1995), bacteria including cyanobacteria and actinomycetes (Kulik 1995; Walsh *et al.* 2001; Kim *et al.* 2006a, b; Gonzalez-Franco and Robles-Hernandez 2009), and other types of fungi (Adams and Fravel 1990; Jones *et al.* 2004; Alabouvette *et al.* 2009), also those interacting with hyper-parasitism (Whipps *et al.* 2008) are used in the biocontrol of phytopathogenic fungi. The viruses (mycoviruses) are the least known (Pearson *et al.* 2009), which in view are a very precise weapon that can limit phytopathogen populations and thus protect plant crops from epizootic mycosis. Viruses have great potential for their use against phytopathogenic fungi. Typically, these infections occur in chronic and latent form, but there are species of viruses capable of affecting the host phenotype, leading to hypovirulence, which is reduction of pathogenicity of the fungus against the plant organism (Nuss 2005; Pearson *et al.* 2009; Yu *et al.* 2010; Son *et al.* 2015). An example of hypovirulence is chestnut disease in Europe caused by *Cryphonectria parasitica* and controlled by hypovirulent fungal strains (Heiniger and Rigling 1994).

Mykowirusy grzybów fitopatogennych / Mycoviruses of phytopathogenic fungi

Biological activities of viruses associated with fungi were often speculated about in early observations. The first mention comes from 1936, when Wiebols and Wieringa observe an anomalous lysis in a yeast culture probably due to the presence of lysogenic virus (Wiebols and Wieringa 1936). Suspicions of the action of the virus infecting higher fungi come from 1950. Back then Sinden and Hauser described the degenerative changes of mushrooms recorded in the cultivated mushroom in a mushroom house owned by the La France brothers from Pennsylvania – hence one of the later name of the disease is "La France Disease" (Sinden and Hauser 1950). The infected mushrooms were characterized by distorted sporocarps, and also grew slowly and matured prematurely, resulting in significant crop losses (Son *et al.* 2015). Shortly thereafter, information about similar symptoms came from Europe, Australia and Japan. Suspicions were confirmed in 1962, when Hollings shared information about the research on the relationship between the disease of dieback mushroom (*Agaricus bisporus*) and the presence of viral particles genetic material. Three viral isolates discovered from hymenium were able to infect and cause disease in asymptomatic fungi (Hollings 1962). This discovery laid the foundations for the development of modern mycovirusology.

Viruses capable of using fungal cells for their own development are called mycoviruses (Ghabrial *et al.* 2015). The majority of mycoviral genomes consist of double stranded RNA (dsRNA), while approximately 30% of positively charged single stranded RNA (+ ssRNA) is observed. Studies have shown that mycoviruses infect fungi from all major clusters, such as Chytridiomycota, Zygomycota, Ascomycota, Deuteromycota and Basidiomycota (Son *et al.* 2015).

Up to date, more than 80 species of mycoviruses capable of infecting phytopathogenic fungi have been discovered (Table 1). They were assigned to six families of linear dsRNAs (Chrysoviridae, Hypoviridae, Megabarniviridae, Partiviridae, Reoviridae, Totiviridae), four linear positive ssRNAs families (Alphaflexiviridae, Endornaviridae, Gammaflexiviridae and Narnaviridae), including one family of positive reverse transcriptase ssRNAs (Metaviridae), as well as many species not yet classified to any family with linear and circular genomes built with both RNA and DNA. Based on bibliographic data, a table has been compiled showing the majority of phytopathogenic fungi mycoviruses discovered up to date. It is very promising that there are identified mycoviruses capable of infecting half of the phytopathogenic fungi listed on the register of the 10 most important phytopathogens, including the phytopathogens from the top of the list (*Magnaporthe oryzae* virus 1 and 2, *Botrytis* virus X, *Fusarium graminearum* mycovirus-9, *Fusarium graminearum* dsRNA mycovirus 1, 2, 3 and 4, *Fusarium oxysporum* Skippy virus, *Fusarium oxysporum* chrysovirus 1, *Ustilago maydis* virus H1), as well as significant but not listed *R. solani* (*Rhizoctonia solani* virus 717) (Strauss *et al.* 2000; Howit *et al.* 2006; Voth *et al.* 2006; Yokoi *et al.* 2007; Maejima *et al.* 2008; Yu *et al.* 2009; Sande *et al.* 2010; Darissa *et al.* 2011; Cho *et al.* 2013).

Over the years, through evolution, viruses have developed two ways of transmitting between organisms; intracellular and extracellular transmission, but up to date there is only one example in nature of extracellular transmission (Sande *et al.* 2010; Yu *et al.* 2013).

Transmisja / Transmission

Mycoviruses are mainly spread by vertical transmission, which occurs during the formation of asexual and sexually contaminated spores, where asexual spore is the most effective means of transmission (Sande *et al.* 2010). Transfers can also take place in a horizontal manner, when the hyphae of two fungi fuse resulting in heterokaryon formation (Hollings and Stone 1969; Lhoas 1971; Wood and Bozarth 1973; Van Diepeningen *et al.* 1998). Ability of the mycelium to connect to and exchange of protoplasm is therefore an important element contributing to the spread of infection associated with genetic molecules in populations of fungi occurring in nature (Caten 1972). The ability to carry out mycoviruses between genetically incompatible hyphae is also possible by using a protoplast fusion method in laboratory (Van Diepeningen *et al.* 1998). Using this method it is also possible to transfer viruses among fungi of different species (Van Diepeningen *et al.* 1998). The migration of mycoviruses using protoplast fusions has been observed in phytopathogenic fungi such as *Fusarium poae* (Van Diepeningen *et al.* 2000) and *Rosellinia necatrix* (Kanematsu *et al.* 2010).

Most studies have reported that mycoviruses are not infectious in the classical sense, because the infection can not be initiated by exposure of uninfected fungus to the purified virus particles (Ghabrial 1998). Extracellular infection can be achieved under special experimental conditions primarily through the use of protoplast fusion. Using this method,

Tabela 1. Mykowirusy grzybów fitopatogennych
Table 1. Mycoviruses of phytopathogenic fungi

Genom Genome	Rodzina Family	Rodzaj Genus	Gatunek Species	Genbank Genbank	Źródło Source
1	2	3	4	5	6
ss(+)RNA	Alphaflexiviridae	Sclerodarnavirus	*Sclerotinia sclerotiorum* debilitation associated RNA virus	NC_007415	Xie *et al*. 2006
		Botrexvirus	*Botrytis virus* X	NC_005132	Howitt *et al*. 2006
	Endornaviridae	Endornavirus	*Phytophthora* endornavirus 1	NC_007069	Hacker *et al*. 2005
			Helicobasidium mompa endornavirus 1	NC_013447	Osaki *et al*. 2006
	Gammaflexiviridae	Mycoflexivirus	*Botrytis* virus F	NC_002604	Howitt *et al*. 2001
	Narnaviridae	Mitovirus	*Cryphonectria parasitica* mitovirus 1	NC_004046	Polashock and Hillman 1994
			Ophiostoma mitovirus 3a	NC_004049	Hong *et al*. 1998
			Ophiostoma mitovirus 4	NC_004052	Hong *et al*. 1999
			Ophiostoma mitovirus 5	NC_004053	Hong *et al*. 1999
			Ophiostoma mitovirus 6	NC_004054	Hong *et al*. 1999
	Unclasified		*Diaporthe ambigua* RNA virus	NC_001278	Preisig *et al*. 2000
			Sclerophthora macrospora virus A	NC_005817-..19	Yokoi *et al*. 2003
			Sclerophthola macrospora virus B	NC_004714	Yokoi *et al*. 1999
ss(+)RNA-RT	Metaviridae	Metavirus	*Cladosporium fulvum* T-1 virus	Z11866	Sande *et al*. 2010
			Fusarium oxysporum Skippy virus	L34658	Sande *et al*. 2010
dsRNA	Reoviridae	Mycoreovirus	*Cryphonectria parasitica* mycoreovirus 1	LC019123-..26	Eusebio-Cope *et al*. 2010
			Cryphonectria parasitica mycoreovirus 2	DQ902580	Supyani *et al*. 2007
			Rosellinia necatrix mycoreovirus 3	NC_007524-..36	Osaki *et al*. 2002
	Chrysoviridae	Chrysovirus	*Aspergillus fumigatus* chrysovirus	FN178512-..15	Jamal *et al*. 2010
			Fusarium graminearum dsRNA mycovirus 2	HQ343295-..300	Yu *et al*. 2009
			Fusarium oxysporum chrysovirus 1	EF152346-...48	Cho *et al*. 2013
			Helminthosporium victoriae 145S virus	NC_005978-..81	Ghabrial *et al*. 2002
		Unclasified	*Fusarium graminearum* mycovirus-China 9	HQ228213-..17	Darissa *et al*. 2011
	Partitiviridae	Partivirus	*Aspergillus fumigatus* partitivirus 1	FN376847; FN398100	Bhatti *et al*. 2011
			Atkinsonella hypoxylon virus	NC_003470-..72	Oh and Hillman 1995
			Fusarium solani virus 1	D55668; D556689	Nogawa *et al*. 1996
			Heterobasidion annosum virus	AF473549	Ihrmark 2001
			Ophiostoma partitivirus 1	AM087202-..03	Crawford *et al*. 2006
			Ustilaginoidea virens partitivirus 1	KC469949-..50	Zhang *et al*. 2013
			Verticilium dahliae partivirus 1	KC422243-..43	Feng *et al*. 2013
		Alphapartivirus	*Helicobasidium mompa* virus	AB110979	Osaki *et al*. 2004
		Betapartivirus	*Ceratocystis resinifera* virus 1	NC_010754-..55	Deng and Boland 2007
			Fusarium poae virus 1	NC_030877; NC_003882-..84	Compel and Fekete 1999 Osaki *et al*. 2016
			Rhizoctonia solani virus 717	NC_003801-..02	Strauss *et al*. 2000
			Rosellinia necatrix virus 1	NC_007537-...38	Sasaki *et al*. 2006
		Gammapartivirus	*Aspergillus ochraceus* virus FA0611	EU118277-..79	Liu *et al*. 2008
			Aspergillus ochraceus virus dsRNA1	DQ270031	Kim *et al*. 2006a
			Discula destructiva virus 1	NC_002797; NC_002800-..02	Rong *et al*. 2002
			Discula destructiva virus 2	NC_003710-..11	Rong *et al*. 2002
			Gremmeniella abietina virus MS1	NC_004018-..20	Tuomivirta and Hantula 2003

Tabela 1. Mykowirusy grzybów fitopatogennych – cd.
Table 1. Mycoviruses of phytopathogenic fungi – continued

Genom Genome	Rodzina Family	Rodzaj Genus	Gatunek Species	Genbank Genbank	Źródło Source
1	2	3	4	5	6
		Unclasified	*Fusarium graminearum* dsRNA mycovirus 4	NC_013470-..71	Yu *et al*. 2009
			Botryosphaeria dothidea virus 1	KT372135-..39	Wang *et al*. 2014
			Verticillium albo-atrum partitivirus-1	KJ476945-..46	Cañizares *et al*. 2014
			Rosellinia necatrix partitivirus 3	AB698491	Yaegashi *et al*. 2013
			Rosellinia necatrix partitivirus 4	AB698493	Yaegashi *et al*. 2013
			Rosellinia necatrix partitivirus 5	AB698494	Yaegashi *et al*. 2013
	Totiviridae	Totivirus	*Aspergillus* mycovirus 178	EU289894-..95	Hammond *et al*. 2008
			Aspergillus mycovirus 1816	EU289896	Hammond *et al*. 2008
			Botryotina fuckeliana totivirus 1	NC_009224	De Guido *et al*. 2005
			Helicobasidium mompa V670 L2-dsRNA virus	AB27528-..89	Suzaki 2006b
			Helicobasidium mompa dsRNA virus N10	AB253329	Suzaki 2006a
			Helicobasidium mompa dsRNA virus V169	AB253401	Suzaki 2006a
			Ustilago maydis virus H1	NC_003823	Voth *et al*. 2006
		Victorivirus	*Aspergillus foetidus* slow virus 1	HE588147	Sande *et al*. 2010
			Chalara elegans RNA virus 1	NC_005883	Park *et al*. 2005
			Gremmeniella abietina RNA virus L1	NC_003876	Tuomivirta and Hantula 2003
			Helicobasidium mompa totivirus 1-17	NC_005074-..75	Nomura *et al*. 2003
			Helminthosporium victoriae virus 190S	NC_003607	Huang and Ghabrial 1996
			Magnaporthe oryzae virus 1	NC_006367	Yokoi *et al*. 2007
			Magnaporthe oryzae virus 2	NC_010246	Maejima *et al*. 2008
			Rosellinia necatrix victorivirus 1	NC_021565	Chiba *et al*. 2013
			Sphaeropsis sapinea RNA virus 1	NC_001963	Preisig *et al*. 1998
			Sphaeropsis sapinea RNA virus 2	NC_001964	Preisig *et al.* 1998
		Unclasified	*Fusarium graminearum* dsRNA mycovirus 3	NC_013469	Yu *et al*. 2009
	Hypoviridae	Hypovirus	*Cryphonectria* hypovirus 1	JQ778851-..52 NC_001492	Brusini and Robin 2013 Shapira *et al*. 1991
			Cryphonectria hypovirus 1-EP713	–	Sun *et al*. 2006
			Cryphonectria hypovirus 1-Euro7	–	Sasaki 2009
			Cryphonectria hypovirus 2-NB58	CRPMRNA	Hillman *et al*. 1994
			Cryphonectria hypovirus 3	NC_000960	Smart *et al*. 1999
			Cryphonectria hypovirus 4	NC_006431	Linder-Basso *et al*. 2005
	Megabirnaviridae	Megabirnavirus	*Rosellinia necatrix* megabirnavirus 1/W779	AB512282-..83	Chiba *et al*. 2009
	Unclasified		*Alternaria alternata* virus 1	AB368492;	Aoki *et al*. 2009
			Aspergillus foetidus dsRNA mycovirus	NC_020100-..03	Kozlakidis *et al*. 2013
			Aspergillus foetidus slow virus 2	HE588148	Kozlakidis *et al*. 2013
			Aspergillus foetidus virus satellite RNA	LN614706	Shah *et al*. 2015
			Aspergillus fumigatus tetramycovirus 1	HG975302-..05	Kanhayuwa *et al*. 2015
			Aspergillus mycovirus 341	EU289897	Hammond *et al*. 2008
			Fusarium graminearum dsRNA mycovirus 1 strain DK-21	AY533037	Kwon *et al*. 2007
			Rosellinia necatrix mycovirus 1-W1032/S5	LC061478	Zhang *et al*. 2016
			Rosellinia necatrix mycovirus 2-W1032/S6	LC006253	Zhang *et al*. 2016
			Rosellinia necatrix mycovirus 3-NW10/N10	AB698498	Yaegashi *et al*. 2013
			Sclerotinia sclerotiorum RNA virus L	EU779934	Liu *et al*. 2009
ssDNA	Unclasified		*Sclerotinia sclerotiorum* hypovirulence associated DNA virus 1	KF268025-..28 KM598382-..84	Kraberger *et al*. 2013 Dayaram *et al*. 2015
dsDNA	Unclasified		*Cryphonectria parasitica* bipartite mycovirus 1	NC_021222-..23	Deng *et al*. 2007

purified viral particles belonging to the families of dsRNAs Partiviridae, Totiviriade, Reoviridae and Geminiviridae are able to successfully infect fungal protoplasts of *R. necatrix* (Sasaki *et al.* 2006), *C. parasitica* (Hillman and Suzuki 2004) and *Sclerotinia sclerotiorum* (Yu *et al.* 2010, 2013).

Up to date there is only one exception, which shows extracellular transmission in nature. Yu and colleagues demonstrated, that the viral particles SsHADV-1 (*Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1) can infect hyphae of *S. sclerotiorum* by extracellular way (Yu *et al.* 2013). Compared to experiments with fusion of protoplasts, in this case the infection was possible on intact cells of *S. sclerotiorum*. Based on the results of SsHADV-1 studies, it has been suggested that viral particles are required to infect undamaged cells or fungal protoplasts because naked viral DNA is not infectious (Yu *et al.* 2013). At the same time SsHADV-1-like viruses were recorded in different species of dragonflies, which act like vectors accumulating viruses from their insect prey (Liu *et al.* 2011).

Objawy związane z zakażeniem mykowirusowym / Symptoms related to mycoviral infection

Usually mycoviruses cause latent and chronic infections (Pearson *et al.* 2009; Son *et al.* 2015), but some of them are associated with a variable effect on the phenotype. Mycoviruses were able to coexist in association with their hosts, which could have resulted in the reduction of fungal infections (Van Diepeningen *et al.* 2008). Nonetheless, mycoviral infections that are harmful to fungi have been observed (Nuss 2005; Yu *et al.* 2010).

Mycoviruses interfering with the fungal genotype change their phenotypic image, as shown in the following examples: *Alternaria alternata* – reduced mycelial growth rate, subsidence of airway mycelium, irregular pigmentation, cytolisis (Fuke *et al.* 2011), *F. graminearum*, occurrence of double stranded viral RNA was associated with a reduction in pathogenicity (trials on wheat) and deoxynivalenol production, as compared to wheat infected by samples free of viral RNA (Chu *et al.* 2002), abnormal colony morphology, perythecium developmental defects, growth retardation and sporulation (Lee *et al.* 2014), in turn in *C. parasitica* – reduction of orange pigment production, changes in colony morphology, decreased production of oxalic acid, decreased ability to produce conidia, reduction of sporulation, morphological changes of plant carcinomas and increased or decreased growth rate (depending on viral strain) (Deng *et al.* 2007). The effects of infection such as sporulation reduction or reduced growth rate, are directly related to the phenomenon of hypovirulence, thus the pathogenicity of the fungus is reduced to the plant. This phenomenon is also caused by viruses of other phytopathogenic fungi, like *Diaporthe perjuncta*, *Sclerotinia homoeocarpa*, *Ophiostoma ulmi*, *Ophiostoma novo-ulmi*, *R. solani*, *Helminthosporium victoriae* and *R. necatrix* (Lakshman *et al.* 1998; Hong *et al.* 1999; Preisig *et al.* 2000; Ghabrial *et al.* 2002; Wei *et al.* 2003; Kanematsu *et al.* 2004; Deng *et al.* 2005; Nuss 2005; Wang *et al.* 2014).

Wnioski / Conclusions

Phytopathogenic fungi are an important and current problem in the cultivation of various plants worldwide, and in particular cereal crops. Commonly used chemicals in the form of fungicides pose a threat to the health of many living organisms, including humans, so it is important to find alternative ways to control pathogenic fungi. One of the promising directions is the use of biological plant protection agents. There is a great potential for mycoviruses, with emphasis on the fact that they were isolated from fungi that have the greatest negative impact on many crops. Mycoviral infections are often latent, but some of them affect the phenotype of the fungus. Among the most important changes should be the reduction of sporulation, reduced growth rate, limited mycelial growth or reduction of pigment production. A significant effect of mycoviral infection in the fungal cell is the development of hypovirulence, i.e. the reduction of the pathogenicity of the fungus what was experimentally confirmed in the phytopathogen of the species *F. graminearum*. Reduced dye production has been reported so far in the phytopathogenic fungus *C. parasitica* as well as *A. alternata*.

In conclusion, the discovery of mycoviruses has far-reaching implications, so that over the decades we have learned many mechanisms that should be used as soon as possible in the control against phytopathogenic fungi. For this purpose, further interdisciplinary research in the fields of mycovirology, mycology, genetics, toxicology, and ecology is needed to comprehensively get to know the mycoviruses already identified. It is also expected to discover new species that may have in their genomes indescribable genes, potentially affecting the mechanisms of antifungal activity.

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