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Ophiostomatoid fungi (Ascomycota: Ophiostomataceae) associated with bark beetles and their possible economic impact in forests and timber production

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Abstract

Ophiostomatoid fungi are commercially and economically important group of fungi in forestry and timber production. This group is represented by several genera of Ascomycetes with common morphological characteristics, although with distinct taxonomy and phylogeny. Several genera of ophiostomatoid fungi have been considered synonymous solely based on morphological similarities as a result of an adaptation to insect dispersal. Ophiostomatoid fungi cause considerable economic losses in the forestry and timber production due to sap stain and vascular wilt diseases. The threat of introduced ophiostomatoid fungi is increasing with the global timber trade and loose control measurements. An overview of the taxonomy, ecology, concept of association (mutualism/symbiosis) and the economic importance of ophiostomatoid fungi are provided.

Key words: ophiostomatoid fungi, taxonomy, morphology, vector dispersal, diseases, forest

Ofiostomatoidne glive (Ascomycota: Ophiostomataceae) na podlubnikih in njihov možni gospodarski vpliv na gozdove in lesno proizvodnjo

Izvleček

Ofiostomatoidne glive so komercialno in gospodarsko pomembna skupina gliv za gozdarstvo in za proizvodnjo lesa. To skupino predstavlja več rodov Ascomycetes, ki imajo veliko enakih morfoloških značilnosti, vendar različno taksonomijo in filogenijo. Več rodov ofiostomatoidnih gliv je bilo štetih kot sinonim na podlagi morfološke podobnosti, ki je rezultat prilagoditve vektorskemu raznosu. Ofiostomatoidne glive povzročajo velike gospodarske izgube v gozdarstvu in lesni proizvodnji, ker povzročajo obarvanje beljave in bolezni prevodnih elementov dreves. Nevarnost vnosa ofiostomatoidnih gliv se veča z globalno trgovino z lesom in z ohlapnimi ukrepi nadzora trgovine. Prikazana sta pregled taksonomije, ekologije, koncept asociacije (mutualizem /simbioza) in gospodarska pomembnost ofiostomatoidnih gliv.

Ključne besede: *ofiostomatoidne glive, taksonomija, morfologija, raznos z vektorji, bolezni, gozdovi*

1 Introduction

1 Uvod

Many scientists throughout the world emphasize the importance of the fungi group commonly named ophiostomatoid fungi. This name is derived from one member of the group *Ophiostoma* sp. (Ophiostomataceae). Ophiostomatoid fungi are an artificial group of many morphologically similar genera of the phylum Ascomycota, including important tree pathogens and tree sapstain agents (blue stain fungi).

Sanitary felling or salvage cuttings are usually prescribed as an important forestry protection measures to improve the condition of forest stands that have incurred tree mortality caused by biotic and abiotic factors (JURC *et al.* 2003, GRODZKI *et al.* 2004). The increasing number of sanitary felling, which draws attention to tree health in forests, is raising scientists' concerns about climate change and its related phenomenon, such as bark beetle outbreaks and fungi association with insects and trees.

The purpose of this article is to clear the confusion around ophiostomatoid fungal taxonomy and phylogeny, followed by the description of the influence this group of fungi has on the forest and consequently on the timber industry. We will also touch the topic of the influence of the environmental changes, either global warming or global wood trade, on the ophiostomatoid fungi. Finally, the purpose of this article is to draw the conclusion about possible solutions to mitigate the influence of ophiostomatoid fungi.

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2 Taxonomy of the ophiostomatoid fungi

2 Taksonomija ofiostomatoidnih gliv

Ophiostomatoid fungi are artificial group of fungi based on common morphology. The genera in this group are *Ophiostoma* Syd. & P. Syd., *Ceratocystis* Ellis & Halst., *Ceratocystiopsis* H.P. Upadhyay & W.B.Kendr., *Grosmannia* Goid. as well as related asexual fungi in the genera *Leptographium* Lagerb. & Melin, *Pesotum* J.L. Crane & Schokn., *Sporothrix* Hektoen & C.F. Perkins, *Hyalorhinocladiella* H.P. Upadhyay & W.B. Kendr., *Thielaviopsis* Went, *Chalara* (Corda) Rabenh., *Graphium* Corda (WINGFIELD / SEIFERT / WEBBER 1993, KIRISITS 2004, REPE / JURC 2009).

Ophiostomatoid fungi from the phylogenetic species concept are presented next. The two most distinctive genera of ophiostomatoid fungi are *Ophiostoma* and *Ceratocystis*, both of which are taxonomically and phylogenetically distinct. They belong to different orders of the Ascomycota (SAMUELS 1993, WINGFIELD *et al.* 2006b). *Ophiostoma* and *Ceratocystis* as well as *Ceratocystiopsis* and *Grosmannia* are morphologically similar, though phylogenetic studies based on rDNA analyses proved that ophiostomatoid fungi are polyphyletic. They place *Ophiostoma* in the monophyletic group, not closely related to *Ceratocystis* (HAUSNER *et al.* 1993, OKADA *et al.* 1998, WINGFIELD *et al.* 2006a). *Ophiostoma* is phylogenetically classified in Ophiostomataceae, class Ophiostomatales, Sordariomycetidae, Sordariomycetes, Ascomycota, Fungi (KIRK *et al.* 2008). *Ceratocystis* is a genus belonging to the Ceratocystidaceae family, Microascales, Hypocreomycetidae, Sordariomycetes, Ascomycota, Fungi (KIRK *et al.* 2008). *Grosmannia* and *Ceratocystiopsis* are distinct from *Ophiostoma*, according to the multigene phylogenies research by Zipfel and collaborators and are placed in Ophiostomatales (ZIPFEL *et al.* 2006).

Here the differences between ophiostomatoid fungi based on morphology and sexual and asexual stages are presented. The genera differentiation in the group of ophiostomatoid fungi can be implemented on the basis of their sexual stages. These produce a great variety of anamorphs, even within one species (MALLOCH / BLACKWELL 1993). *Ceratocystis* species have a *Thielaviopsis* asexual stage used for *Chalara*-like anamorphs (SEIFERT 2006). The asexual stages of *Ophiostoma* belong to a variety of hyphomycetes genera; mycelial anamorphs: *Sporothrix, Hyallorhinocladiella, Pesotum. Hyalorhinocladiella* conidium development is annellidic (percurrent) with delayed secession giving rise to an illusion of sympodial development (BENADE / WINGFIELD / WYK 1995). The distinction between *Hyalorhinocladiella* and *Sporothrix* based on morphology is not clear because intermediate forms between the two genera exist (BENADE / WINGFIELD / WYK 1995, AGHAYEVA *et al.* 2004). *Pesotum* is a synnematous anamorph previously known as *Graphium*, now separated from *Graphium* (Microascales) based on variations in conidium ontogeny (OKADA *et al.* 1998). Conidium development is always exogenic by apical wall building (SAMUELS 1993, KIRISITS 2004). Similarly, *Ceratocystiopsis* spp. have *Hyalorhinocladiella* and *Sporothrix* anamorphs without *Pesotum* and *Leptographium* states (SAMUELS 1993, KIRISITS 2004, ZIPFEL *et al.* 2006). *Leptographium* is a macronematous anamorph of *Grosmannia* (SEIFERT 2006) (Table 1).

Distinction between anamorph genera is based on variations in the conidiophore structure and in patterns of conidial development (BENADE / WINGFIELD / WYK 1995, OKADA *et al.* 1998, JACOBS / WINGFIELD 2001).

Ceratocystis and *Ophiostoma* have almost indistinguishable teleomorphs, but quite different asexual forms (KIRK *et al.* 2008). Nevertheless, they can also be distinguished through other characteristic. *Ophiostoma* species are tolerant of high concentrations of the antibiotic cycloheximide and are characterized by the presence of cellulose, rhamnose and chitin in their cell walls (SAMUELS 1993, JACOBS / WINGFIELD 2001). In comparison to them, *Ceratocystis species* do not have cellulose in their cell walls and are sensitive to antibiotics (SAMUELS 1993). *Ophiostoma* species primarily grow on woody plants while *Ceratocystis* species grow on a wide variety of herbaceous and woody plants in temperate and tropical zones (SIX 2003). *Ceratocystis* species more commonly cause plant diseases than *Ophiostoma* species (SIX 2003). Some known destructive pathogens from *Ceratocystis* genera include *C. fagacearum* (Bretz) J. Hunt, *C. fimbriata* Ellis & Halst., *C. platani* (J.M. Walter) Engelbr. & T.C. Harr. (≡*C. fimbriata* f. *platani* C. May & J.G. Palmer), *C. courelescnes* (Münch) B.K. Bakshi. However, *O. ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier are important deconstructive *Ophiostoma* pathogens. They are more commonly known as Dutch elm disease, responsible for epidemics on elm trees in Europe and North America.

Table 1: The teleomorph and its anamorph of ophiostomatoid fungi (known genera)

Preglednica 1: Spolni in nespolni stadiji ofiostomatoidnih gliv (poznani rodovi)

Teleomorph	**Anamorph**
Ceratocystis	*Thielaviopsis* (*Chalara*)
Grosmannia	*Leptographium, Pesotum*
Ophiostoma	*Sporothrix* *Pesotum* *Hyalorhinocladiella* *Graphilbum, Phialocephala*
Ceratocystiopsis	*Hyalorhinocladiella, Sporotrix*

3 Morphological characteristics of the ophiostomatoid fungi

3 Morfološke značilnosti ofiostomatoidnih gliv

The ophiostomatoid fungi are classic 'spore drop' fungi, producing slimy masses of spores at the tops of long stalks (WINGFIELD / SEIFERT / WEBBER 1993, WINGFIELD / SEIFERT 2006b). They are superficially morphologically similar (WEBBER / BRASIER 2001).

They have the following general characteristics. Ascocarps are globose to subglobose or flask-shaped. They are dark, hyaline or lightly coloured in whole or in part. They have ostiolum (perithecial) or are entirely closed (cleistothecial). They usually have long necks, possibly terminated with fringes of ostiolar hyphae (UPADHYAY 1981, KIRK *et al.* 2008). The asci are borne irregularly throughout the centrum and are clavate and subspherical, spherical or fusiform. They deliquesce early in the development of the ascospores and lack croziers. Ascospores are hyaline, usually unicellular (sometimes bi-cellular with a medium septum) and are variable in shape (UPADHYAY 1981, WINGFIELD / SEIFERT / WEBBER 1993, KIRISITS 2004, KIRK *et al.* 2008). In many species, the ascospores have a multilayered wall that appears as a gelatinous sheet under light microscopy (UPADHYAY 1981, KIRK *et al.* 2008). Ascospores exude through the long neck at the apex into a mucilaginous droplet (UPADHYAY 1993).

Conidiophores morphology may be very variable. There are considerable differences, as described before, between genera in ophiostomatoid group in the asexual stages, regarding their conidiophore structure and the way conidia grow (JACOBS / WINGFIELD 2001). Conidiophores can be large, mononematous with pigmented stipes. They can also be micronematous – a typical characteristic of the *Sporotrix* genus, less differentiated, with little or no pigmentation, and yeast-like budding. Some of the species produce synnematous conidiophores (HARRINGTON 1992). Conidia are often round, cylindrical or oval (SIX 2003).

Similar ascocarps of *Ceratocystis, Ophiostoma, Ceratocystiopsis*, and *Grosmannia* were independently developed owing to their adaptation to insect dispersal (HARRINGTON 1993, SIX 2003, KIRISITS 2004, WINGFIELD / SEIFERT 2006b).

4 Vector dispersal

4 Prenos z vektorji

Some ophiostomatoid fungi are arthropod associated particularly with bark beetles (Coleoptera: Curcolionidae: Scolytinae) which commonly act as vectors. Bark beetles are economically significant pests that can cause enormous economic losses in forestry. They are typical dendrobionts and primarily colonize conifer trees. They are phloeophagous (i.e. they colonize phloem and cambial layers) or xylomycetophagous (i.e. they feed on mycelium in their galleries, which can be bored 12 cm deep in wood) (JURC 2008). The bark beetles increase their potential of colonizing their hosts by symbiotic association with microorganisms, particularly with fungi (RIVERA *et al.* 2007). They are associated with a wide variety of fungi (HARRINGTON 1993, SIX 2003, NOVOTNY / JANKOVSKY 2005), but predominantly with fungi from the ophiostomatoid group (SIX 2003). This association is assumed to worsen damages or can even cause the death of the tree (SIX 2003, LEE 2006, LINNAKOSKI *et al.* 2008a). Beetles are carrying fungi spores on specialized structures called mycangium, or most commonly freely on beetles' bodies. They can also be eaten and passed through the digestive tract (HARRINGTON 1993, SOLHEIM 1993, PAINE *et al.* 1997, LEE 2006).

The morphological similarity of the orders in the ophiostomatoid group is based on adjustment to vectors, since many depend on their host for dissemination (SIX 2003). Their sexual fruiting structures have long necks on which there are sticky masses of spores that easily adhere to the bodies of passing insects and are transferred to new substrates (KIRISITS 2004, JANKOWIAK 2005, WINGFIELD / SEIFERT 2006b). In addition, their asexual states often have long stalks bearing sticky conidia suitable for dispersal with insects. Consequently, fungi are introduced into the tree during the beetles attack process (PAINE / RAFFA / HARRINGTON 1997).

The vector relationship with insects is a strategy that makes both genera effective, as well as often causing major economic damage to the forest and crops (WINGFIELD / SEIFERT 2006b). Some authors (HARRINGTON 1993, PAINE / RAFFA / HARRINGTON 1997, SIX 2003, PAINE 2006) support the idea that beetle and fungus association is primarily mutualistic. In fact, they range from mutualistic to commensal, and from facultative to obligate (SIX 2006). Obviously, the fungus benefits from being dispersed. The fruiting structures of the perfect and imperfect states of ophiostomatoid fungi present adaptations to vector dispersal (HARRINGTON 1993). Beetle species may benefit from the association with fungi by feeding on them (SIX 2003, HARRINGTON 2005). Fungi constitute a good nutrition source for them, providing them with sterols, B vitamins, nitrogen and readily digestible carbohydrates (HARRINGTON 2005). An additional benefit for bark beetle may be that fungi growing in sapwood reduce the moisture content of trees to a level suitable for successful beetle brood development (LEE 2006). The association with fungi may be beneficial for insects, as it limits the impact of potentially detrimental fungi, and also since fungi contribute to the host tree death through mycelial penetration of host tissue, toxin release, interactions with performed and induced conifer defences, or even through the beetle's and fungi's combined action during colonization (PAINE / RAFFA / HARRINGTON 1997, PAINE 2006). However, not all the fungi are pathogenic to the host trees. Moreover, mostly weak pathogens are isolated from the most aggressive bark beetles (PAINE / RAFFA / HARRINGTON 1997).

Mycangium

Fungus adaptation is visible in mucilaginous masses of spores on long stalks, whereas the bark beetles adaptation to fungi transmission are constituted by structures on the beetle's body, special pits, and sacs (the so-called mycangia) (HARRINGTON 1993, SIX 2003). In the narrow sense, mycangia are specialized structures in the beetle's integument associated with glands or secretory cells that are used for the storage, transport, and transmission of fungi (KIRISITS 2004, HARRINGTON 2005). Mycangium in a broadest sense can also refer to pits and setae along with deeper pockets acting as fungal repositories. Nevertheless, they are not known to be associated with glands (SIX 2003). Not all bark beetles possess mycangium in its narrow sense (HARRINGTON 2005). Economically, the most important damaging bark beetle on Norway spruce in Slovenia and Europe, *Ips typographus* (L.) (JURC *et al.* 2006, JURC 2004), does not have mycangia with glands and secretory cells, but possesses pits on the pronota and elytra (FURNISS / SOLHEIM / CHRISTIANSEN 1990, SOLHEIM 1993).

5 Diseases caused by ophiostomatoid fungi

5 Bolezni, ki jih povzorčajo ofiostomatoidne glive

Most of ophiostomatoid fungi species are competitive saprophytes or weak parasites, commonly found on woody plant tissues (HARRINGTON 1993). The tree influence should be considered in order to understand relationships between bark beetle and fungi. They cannot be discussed individually, since they represent integrated complexes (LEE 2006). Trees defend themselves against bark beetles and pathogens with diversified mechanisms. Suberized and lignified periderm derivates, sclerified cells or cell layers represent static defence (FRANCESCHI 2000). In conifer trees, the most common ophiostomatoid fungi hosts (KIRISITS 2004, LINNAKOSKI 2008), defence strategies include constitutive mechanical and chemical defence reactions and induced defence reactions (HUDGINS / FRANCESCHI 2004, TEIZ /ZEIGER 2006). Constitutive defence involves the initiation of wound periderm, traumatic resin duct formation as well as concentric layers of polyphenolic parenchyma and sclerenchyma (FRANCESCHI *et al.* 2000, TEIZ / ZEIGER 2006, URBANEK KRANJC 2009). Inducible defence systems include secondary resin synthesis, production of new phenolics and protein-based chemical defence (HUDGINS / FRANCESCHI 2004, TEIZ /ZEIGER 2006, URBANEK KRANJC 2009). A few days after the first attack the resistance throughout the tree increases, which is known as systemic acquired resistance (TEIZ /ZEIGER 2006).

Ophiostomatoid fungi have often been associated with plant diseases, such as vascular stain diseases and sap stain on host trees. In some cases, they are thought to aid their vectors in killing host trees. Some are capable of overcoming the resistance of a healthy host tree (GIBBS 1993). However, they usually do not kill healthy trees, but reduce the value of timber and facilitate the stress in trees. Ophiostomatoid fungi occur in both conifers and hardwood trees.

Sap stain or bluestain

Sap stain is defined as a blue-black discoloration of sapwood caused by deeply penetrating fungi that are not causing decay (GIBBS 1993, SEIFERT 1993). These fungi are disseminated by the beetles to appropriate habitats. They colonize insect galleries and adjoining bark sapwood, causing a disorder called sap stain (JANKOWIAK 2005, LINNAKOSKI *et al.* 2008). The pigment responsible for the stain is usually considered to be a fungal melanin (SEIFERT 1993) in the fungal cell walls. The colour of the hyphae cell walls is brown, but due to the light interference the discoloration appears grey, black or blue (MAČEK 2008). The mycelium grows in parenchyma cells, rarely in tracheids. They are generally unable to penetrate wood cell walls, but pass from cell to cell through border pits (SEIFERT 1993, MAČEK 2008). The wood does not lose its strength or its technical value because cell walls are not decaying, since bluestain fungi do not posses wood decaying enzymes (MAČEK 2008). Regardless, the loss of aesthetic worth makes the timber value decrease, thus causing significant financial losses to the timber industry. The sapstain is caused by numerous *Ceratocystis* and *Ophiostoma* species; listed herewith are the ones that are proven to cause wood discoloration: *O. piceae, O. piliferum, O. pluriannulatum, O. minus, C. coerulescens* (WEBBER / BRASIER 2001), *C. fimbriata, C. fagacearum* (JURC 2001a, 2001b).

Vascular wilt diseases

Many species of ophiostomatoid associated with bark beetles have been shown as pathogenic to conifers, when artificially inoculated into seedlings or trees. They are regarded as an important aid to stem-feeding bark beetles in killing mass-attacked trees (HARRINGTON 1993). The most aggressive tree pathogens are those causing vascular wilt diseases (KIRISITS 2004). They are disseminated by insect vectors or abiotic agents. They infect the vascular system of living trees, leading to water transport disruption and finally tree death (HARRINGTON 1992, KIRISITS 2004). The most recognized vascular wilt disease is Dutch elm disease that is caused by *O. ulmi* and *O. novo-ulmi* associated with *Scolytus* spp. (WEBBER / BRASIER 2001). They caused huge epidemics in Europe and North America in the 20th century.

Stain pathogens

The action of sapstain pathogen, often in association with insects, leads to a suppression of the host's resistance mechanisms, the death of the phloem, and extensive invasion and staining of the wood (WEBBER / BRASIER 2001). Some of sapstain fungi are highly pathogenic and associated with specific bark beetles. One of the common associate of *Ips typographus* on Norway spruce tree is *Ceratocystis polonica*. Together they cause widespread damage to spruce (WEBBER / BRASIER 2001). According to SOLHEIM (1993), *C. polonica* is the only species that can be isolated from the wood after the bark beetle attack and is found at the leading edge of fungal penetration into the wood.

The stain pathogens that cause diseases are considered a threat to the economical role of forests and timbers (MAČEK 2008). Ophiostomatoid fungi (regularly together with bark beetles) influence, damage and cause premature trees death at all stages of development, which prevents the realization of forest functions; often requiring salvage cuttings and affects forest management. Too early (non-intentional) cuttings decrease wood increment per area unit (MAČEK 2008). The consequently high amount of wood on the market causes a drop in wood prices (KOŠIR / KRČ 2007).

Direct economic impact on the forests is related to the reduced efficiency of production, because of the vascular wilt diseases and vascular stain pathogens. Often, economic losses result from the depreciation of wood caused by bluestain fungi.

It is worth considering the potential of the ophiostomatoid fungi to become a serious pest in changed or new environments. Global trade in living coniferous host plants, logs and wood products raises a significant risk of introducing pathogens into new environments. Ophiostomatoid fungi, currently causing only minor sapstain, may potentially become serious vascular stain pathogens on allied host species in new parts of the world if introduced there (GIBBS 1993). The cases of previous introduction of non-native invasive organisms into new environments show severe outbreaks with economic and ecological disruption in forests (TKACZ 2001). One of the most severe examples, the pandemics of Dutch elm disease, has already been mentioned in this paper. The risk is high since the host population in the new environment has little or no resistance to pathogen. Therefore, an epidemic may occur if the environmental facts are favourable. In addition, insect associations provide rapid local dispersal (SLIPPERS / WINGFIELD 2006).

Even if the damage is presently on a small scale, predicted environmental changes at various levels may trigger new threats at larger scales or areas (KAMATAA *et al.* 2002, KAUSERUD *et al.* 2009). Ophiostomatoid fungi are becoming a serious economic problem on Norway spruce in recent years; previously, they were documented as a major problem mainly on pines (FRIEDL 2004).

6 Possible solutions to mitigate the influence of ophiostomatoid fungi on forests

6 Možne rešitve za omilitev vpliva ofiostomatoidnih gliv na gozdove

The most important strategy is the strengthening of the plant protection system in Slovenian Integrated Forest Protection with administrative, executive and inspectorial tasks. Selected harmful organisms, which in the future might negatively influence forest health, must be intensively investigated. The organization and mode of work of reporting, diagnostic and prognostic service for forests must be strengthened, as well as the tasks concerning threatening harmful organisms to forests (JURC 2006).

Abroad, the use of fungicide against ophiostomatoid fungi is implemented where the damage is significant; for example to fight Dutch elm disease. Fungicides are used to control sapstain at the time before wood processing. Fungicide-based sapstain control methods are either not possible for all markets or problematic because of their broad spectrum of action. In forestry, the use of fungicide is also not advisable since they are not ecologically suitable (ACT ON FORESTS 1993). The environmental impact resulting from pesticide usage has prompted the search for alternative approaches to sapstain control (HELD *et al.* 2003).

One potential solution may be breeding trees for disease resistance i.e. phenotypic selection or genetic improvement of forest trees. This is suitable for long-term control, but there is doubt because of the trees' long development; the resistance also may change from young to adult trees. The second obstacle is that fungi can change in virulence (DWINELL 2001). The breeding of disease-resistant trees for years is often pointless since in the meantime fungi behaviour or virulence may change. It could be useful for the extension plantations, but not for the natural forests.

Wood-staining fungi colonize green wood at the harvesting site and during storage and transportation (SCHROEDER 2001). Bluestain development depends on timber storage time and specific bluestain fungi environmental conditions. An interesting study was made in Austria (FRIEDL 2004) on Norway spruce, in which a model was developed to estimate the maximum storage time – from felling to the occurrence of discoloration – on the logs caused by bluestain fungi. The model is based on the parameters: season of harvest and mean daily air temperature. With the help of proper models, the necessary storage time could be estimated before bluestain appears; economic loss could be lower if the wood is processed before that time. In Austria, they estimated the maximum storage time: 3 to 4 weeks during the summer, and 15 weeks during the winter.

Possible solutions can be altering the ophiostomatoid fungi, the transformation of fungal genome, developing strains that cannot cause sapstain or that cannot perform one or more of their life tasks. However, this is even a more difficult and complex task to perform than breeding trees for disease resistance. Moreover, it is dangerous to implement genetically altered specimen in to the environment. According to the Directive on the deliberate release into the environment of genetically modified organisms (GMO) (2005), a case-by-case environmental risk assessment should always be carried out prior to a release. It should also take due account of potential cumulative long-term effects associated with the interaction with other GMOs and the environment.

The use of albino strains of *Ophiostoma* species has been suggested as a potential biological control strategy for sapstain (FARRELL *et al.* 1993). Effective albino agents on sapstain should be able to colonize the substrate quickly and resist any displacement by sapstain fungi (SCHROEDE *et al.* 2002). These strains do not synthesize the melanin-like hyphal pigments of common sap-staining fungi (HELD *et al.* 2003). In research done in New Zealand, many albino isolates of *O. floccosum, O. piceae* and *O. pluriannulatum* were effective in stopping the problematic fungi from staining wood chips and were fast growing and colourless when grown unchallenged on wood chips. Selected albino isolates of *O. pluriannulatum* were used in two field trials in New Zealand to control sapstain. Several strains were found to significantly reduce dark sap stain as compared to the untreated control logs (HELD *et al.* 2003).

To extract nitrogen from an organic form as proteins and amino acids and to sustain their growth on wood, sap-staining fungi produce several extracellular proteases. HOFFMAN / BREUIL (2004) made a study of disrupting the gene encoding the enzyme for extraction from these protein resources. After the disruption of the gene, the growth of the fungus on organic nitrogen and wood was reduced.

Another important finding was that the amount and form of nitrogen available in trees could influence the growth of sap-staining fungi. As the levels fluctuate with the season, this information may help identify high- and low-risk periods for harvesting logs (HOFFMAN / BREUIL 2004).

Appropriate precautions and strict control over the import of plants, wood material and products should be implemented. With global trade growth, the risk of movement and new potential ophiostomatoid fungi pathogens grows. Specific quarantine requirements are recommended. Control is achieved through chemical treatment and kiln drying (WEBBER / BRASIER 2001).

7 Conclusion

7 Zaključek

Fungi from the ophiostomatoid group are ubiquitous in forests around the world and thus in Slovene forests as well. They are very commonly associated with bark beetles and woody plants. They occur both on coniferous and deciduous trees, most significantly on conifer trees of the northern hemisphere. The taxonomy of the species in this group was uncertain for a long time, but it became now clearer with comprehension surveys and molecular methods. New discoveries indeed clarify the phylogenetic relations between fungi. However, the phylogenetic status of many genera and its relationships with other teleomorph and anamorph has still not been explained. Moreover, not enough is known about anamorph – teleomorph relations, which should help to understand fungi biology.

Ophiostomatoid fungi cause vascular wilt diseases and sap stain, both contributing to economic losses in forestry sector. The wood industry relies on the production of high quality products in order to remain competitive and profitable. The aesthetic quality of wood is often compromised by sap stain wood-inhabiting fungi reducing its economic value. Because of the pathogens and pests, the amount of sanitary felling increases. It is necessary to find an appropriate solution against bluestain and vascular wilt disease. Efforts should be concentrated on finding inexpensive solutions to fight these disorders. Additional endeavour should thus be made to find an environmentally friendly sustainable solution. A crucial point is to understand the fungal biology and consequently the disease development in order to fight the diseases.

The risks of forest trees damages caused by ophiostomatoid fungi increase with ecological changes and their introduction to new environments. A serious problem is posed by global trade as it causes a blending of species around the world. The second risk is climate change and with it new, perhaps favourable, conditions for pathogens. The possible behaviours of different fungi in different ecological conditions should be researched. Fungi impacts on the forestry and timber production in a changed environment could be predicted with these researches.

However, solutions to fight negative ophiostomatoid fungi effects can be time and means consuming. None of the solutions considered in this paper can be constantly economically or environmentally acceptable. The damage that one species may cause and the expenses for the control implementation always have to be taken into consideration.

Although a significant amount of research has been done in this field, ophiostomatoid fungi should be studied in various conditions in the future; their role in the bark beetles ecology and pathogenicity on trees should also be considered. The vector dissemination of fungi to appropriate habitat is an important issue. The research efforts on the various dissemination vectors as well as on the fungi – beetle – tree complex could also be enhanced.

Finally the organization and mode of work of reporting, diagnostic and prognostic service for forests in Slovenia must be strengthened as well as the tasks concerning threatening harmful organisms to forests, which include ophiostomatoid fungi.

8 Summary

8 Povzetek

Glive znane pod skupnim imenom ofiostomatoidne glive, sestavljajo skupino različnih rodov iz debla Ascomycota. Ti rodovi so *Ophiostoma* Syd. & P. Syd., *Ceratocystis* Ellis & Halst., *Ceratocystiopsis* H.P. Upadhyay & W.B.Kendr., *Grosmannia* Goid., kakor tudi nespolne oblike *Leptographium* Lagerb. & Melin, *Pesotum* J.L. Crane & Schokn., *Sporothrix* Hektoen & C.F. Perkins, *Hyalorhinocladiella* H.P. Upadhyay & W.B. Kendr., *Thielaviopsis* Went, Chalara (Corda) Rabenh., *Graphium* Corda.

V preteklosti so bile na osnovi morfoloških in ekoloških znakov in po doktrini morfološkega koncepta vrste omenjene skupine uvrščene v skupen rod. S pomočjo genetskih analiz rDNA in v skladu s filogenetskim konceptom vrste lahko ugotovimo, da sestavljajo več različnih rodov oziroma si niso niti v bližnjem sorodstvu. *Ophiostoma, Grosmannia* in *Ceratocystiopsis* so uvrščene v red Ophiostomatales, *Ceratocystis* v red Microascales. Rodovi v ofiostomatoidni skupini so si morfološko podobni. Askokarpi imajo kroglast spodnji del in navadno podaljšan vrat, vrh katerega so lahko resice oziroma ostiolarne hife (peritecij). Skozi ostiolum se izločajo askospore v lepljivih kapljicah. Konidiofori so lahko sestavljeni iz posameznih hif (mononematous) ali več hif (synnematous). Normalno so to visoke steljke, na vrhu katerih so konidiogene celice, ki jih pokriva sluzasta masa konidijev. Glive s takšnimi plodišči so prilagojene raznosu spor z vektorji, najpogosteje hrošči. Predvidevamo, da je odvisnost od prenosa z žuželkami razlog za njihovo morfološko podobnost sicer taksonomsko oddaljenih rodov.

Ofiostomatoidne glive se najpogosteje pojavljajo na lesnatih rastlinah in so lahko vzrok za številne bolezni. Največjo gospodarsko škodo povzročajo na iglavcih severne poloble. Za poznavanje biologije ofiostomatoidnih gliv je pomemben tritrofični odnos med glivo, hroščem in gostiteljskim drevesom. Hrošči, predvsem pa podlubniki (Scolytinae), prenašajo glivne trose na svojem telesu, v posebnih mešičkih in vdolbinicah na telesu ali specializiranih strukturah z žlezami, ki se imenujejo mikangiji (micetangij). S trosi gliv se hrošči tudi prehranjujejo in jih z iztrebki prenesejo na novega gostitelja. Odnos med glivo in hroščem je ugoden za oba, posledično pa lahko povzroča veliko gospodarsko škodo na drevesih. Glive, ki jih ob napadu v drevo prinesejo hrošči, na drevesu povzročajo obarvanja beljave (glive modrivke), bolezni prevodnega sistema gostiteljskega drevesa in pomagajo svojim vektorjem uničiti drevo. Obarvanje beljave povzroča micelij glive, ki raste v parenhimskih celicah. Hife ne prodirajo skozi celično steno, saj ne proizvajajo encimov za razgradnjo komponent celične stene, ampak se razraščajo v medceličnih prostorih. Tako tehnična vrednost lesa ni zmanjšana, zmanjšana je njegova estetska vrednost, kar povzroča veliko gospodarsko škodo. Bolezni prevodnega sistema so za drevo nevarne in so dodaten dejavnik sušenja dreves povezan s podlubniki. Glive okužijo prevodni sistem vitalnega drevesa, kar povzroči prekinitev transporta vode, hranil in nastalih asimilatov ter rezultira v sušenju drevesa. Najbolj znana bolezen prevodnega sistema brestov je holandska brestova bolezen, ki jo povzročata glivi *O. ulmi* in *O. novo-ulmi*, ki ju prenašajo beljavarji (*Scolytus* spp.).

Ofiostomatoidne glive pomenijo nevarnost v spremenjenih ali novih okoljih. Glive, ki trenutno ne povzročajo večje škode v gozdovih in gozdnih produktih, bi s spremembo klime ali s prenosom v novo okolje (trgovina z lesom in lesnimi proizvodi) lahko postale pomembni patogeni.

Ofiostomatoidne glive skupaj s podlubniki spremenijo in poškodujejo prevodna tkiva dreves, čemur sledi prekinitev transporta snovi in končno prezgodnjo odmiranje dreves v vseh razvojnih stopnjah. Zato ofiostomatoidne glive vplivajo na vse funkcije zdravega gozda, poveča se pogostost sanitarnih sečenj in posledično se spremeni gospodarjenje z gozdovi. Predlagamo več rešitev za blaženje posledic vpliva ofiostomatoidnih gliv. Najpomembnejša strategija je razširitev sistema za varstvo rastlin v slovenskem integralnem varstvu gozdov. Podrobno je treba preučiti škodljive organizme, ki bi v prihodnosti lahko povzročili veliko škode. Fungicidi v slovenskem gozdarstvu niso priporočljivi in so ekološko neustrezni. Poiskati moramo ustreznejše rešitve. Ena je vzgajanje oziroma selekcija dreves, ki bi bili odporni na škodljivce in patogene. Pri razvoju obarvanja lesa, ki ga povzročajo glive, sta ključna čas poseka dreves in hitrost spravila po poseku. Študije so pokazale, da s posekom v zimskem času in hitrim spravilom in predelavo lahko preprečimo obarvanje, saj se le-to pojavi na mestu poseka, med skladiščenjem in prevozom lesa in sicer v 3-4 tednih v poletnem času in v 15 tednih v zimskem času. Zaradi povečanega transporta in prenosa patogenih in asociacijskih gliv v druga območja je nujen strog nadzor nad uvozom rastlin in lesnega materiala. Možna rešitev je uporaba biološke kontrole gliv modrivk v lesu z genetskimi različicami gliv, ki jih taksonomsko uvrščamo v ofiostomatoidne glive, vendar le-te ne povzročajo obarvanja lesa ali bolezni prevodnega sistema gostiteljev, so pa konkurenčne drugim ofiostomatoidnim glivam.

Kako prepoznati negativne vplive obravnavane skupine gliv na sestoje in kako pravočasno preprečiti sušenje sestojev, ki jih le-te še dodatno povečujejo? Potrebno je nadaljnje preučevanje ofiostomatoidnih gliv v različnih razmerah, raziskati njihovo vlogo v ekologiji podlubnikov in patogenosti do dreves. Pospešiti je treba raziskave na področju sprememb okolja in posledično sprememb vpliva ofiostomatoidnih gliv na gozdove. Vse morebitne ukrepe integralnega varstva gozdov, ki bi sledili

novim spoznanjem, bo nujno pretehtati v kontekstu multifunkcionalnosti gozda in gospodarnosti.

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