

REVIEW PAPER

Pathogens threatening Czech Republic forest ecosystems – a review

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ABSTRACT

In recent years, European forests have been endangered by rising temperatures and more frequent weather extremes. In the Czech Republic, the warm and dry period between 2015 and 2019 led to the weakening of many trees and activation of harmful biotic agents, including fungal and other pathogens. These factors led to the death and decline of many trees and forest stands. The most important pathogens of forest trees in the Czech Republic are *Armillaria ostoyae* (Romagn.) Herink; *A. gallica* Marxm. & Romagn.; *A. cepistipes* Velen.; *A. mellea* (Vahl) P. Kumm; *Heterobasidion annosum* (Fr.) Bref.; *H. parviporum* Niemelä & Korhonen; *H. abietinum* Niemelä & Korhonen; *Ophiostoma novo-ulmi* Brasier; *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya; *Cryptostroma corticale* (Ellis & Everh.) P.H. Greg. & S. Waller; *Eutypella parasitica* R.W. Davidson & R.C. Lorenz; *Cucurbitaria piceae* Borthw.; *Phytophthora alni* species complex; *P. cactorum* (Lebert & Cohn) J. Schröt; *P. cambivora* (Petri) Buisman; *P. cinnamomi* Rands.; *P. plurivora* T. Jung & T.I. Burgess and *P. ramorum* Werres, De Cock & Man in 't Veld. Other important forest tree pathogens with potential for spreading in the Czech Republic in the coming years are *Neonectria coccinea* (Pers.) Rossman & Samuels; *Inonotus* spp.; *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton; *Cenangium ferruginosum* Fr. and *Lecanosticta acicola* (Thüm.) Syd. The effects of most of the above-mentioned pathogens are expected to be similar or greater in the future. Moreover, the introduction of new invasive pathogens cannot be neglected. Measures against dangerous fungal and fungal-like infections should include long-lasting management decisions. It is crucial to strengthen the overall resilience of forest stands by increasing their species, age and spatial diversities; planting site-suitable tree species and focusing on timely interventions against pathogens and the prevention of their spread, all in relation to the integrated pest management plans.

KEY WORDS

climate change, Czechia, drought, forest protection, invasive pathogens

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Received: 29 June 2021; Revised: 19 January 2022; Accepted: 20 January 2022; Available online: 22 March 2022

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Introduction

Fungal pathogens cause significant damage to forest ecosystems worldwide (Stenlid and Oliva, 2016). These pathogens can cause massive economic loss, such as damage caused by *Heterobasidion* root rot, which exceeds 800 million euros in Europe annually (Brunette and Cauria, 2016). Global climate change also has a significant effect on the development of pathogens. It can be a limitation factor in the life cycle of pathogens, and in some cases, worsen their spread. Owing to global climate change, European forests face changes in average climatic factors and increasingly extreme weather fluctuations, such as prolonged drought, storms, floods (Lindner *et al.*, 2008, 2010) and extreme heat (Lorenz *et al.*, 2019). In the Czech Republic, the mean annual temperature during 2015-2019 was approximately 1.3°C higher than the mean annual temperature during 1980-2010. Moreover, the annual total precipitation was 78% in 2015 and 76% in 2018, compared to annual total precipitation during 1980-2010 (ČHMÚ, 2020). These changes lead to an increase in drought frequency as a stress factor, causing a reduction in the assimilation apparatus, which reduces the carbon content in woody plants. This subsequently weakens their resistance to biotic pests (Oliva *et al.*, 2014), including fungal and fungal-like pathogens (Desperez-Loustau *et al.*, 2006). These weather conditions have negatively affected the health of forest stands (Novotný, 2020) and led to the activation of several harmful biotic factors. Overgrowth of bark beetles, combined with the neglect of timely search and sanitation of infested trees, has led to a widespread decay of many stands (Lubojacký and Knížek, 2020). In addition, the damage caused by fungal and other pathogens through primary or secondary participation has increased (Lorenc, 2020b). Moreover, invasive pathogens have massively spread due to the increasing frequency of global trade and transportation. The most important being the timber, wood products, wood packaging and ‘plants for planting’ pathways (Potter and Unquart, 2017). The most significant invasive pathogens that have uncontrollably spread in the Czech Republic in recent years are *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya; *Cryptostroma corticale* (Ellis & Everh.) P.H. Greg. & S. Waller; *Eutypella parasitica* R.W. Davidson & R.C. Lorenz; *Cucurbitaria piceae* Borthw. and *Phytophthora* spp. These, along with other important pathogens and their life cycles, are described in detail below. Some other potential pathogens are also briefly mentioned.

This review aims to summarize the present and possible future pathogens, which can be a significant threat for trees in Czech forests. Presented data about the volume of harvested wood and damaged area from the Czech Republic (MZE, 2015-2021) are based on the data received from forest managers (Knížek and Liška, 2021) and recalculated to represent the whole Czech Republic (MZE, 2021).

Basidiomycete fungal pathogens

The most significant long-term pathogen in Czech forests is honey fungus *Armillaria* spp. The Czech Republic comprises five *Armillaria* species: 1) *A. ostoyae* (Romagn.) Herink, which threatens mainly spruce plantations but can also occur on other conifers and broadleaves; 2) *A. gallica* Marxm. & Romagn., which threatens mainly oak stands but can also occur on other broadleaves and conifers (Jankovský, 2003; Dálya and Sedlák, 2020); 3) *A. cepistipes* Velen., which is predominantly a saprotroph (less often parasite) which occurs on broadleaves and rarely on conifers, mainly in hilly and lower montane beech forests; 4) *A. mellea* (Vahl) P. Kumm., which occurs on broadleaves, including fruit trees and 5) *A. borealis* Marxm. & Korhonen, which is predominantly a saprotroph (rarely a parasite) of both broadleaves and conifers, with no major

economic importance (Jankovský, 2003). *Armillaria* spp. causes severe damage mainly in Silesia and northern and central Moravia. The most endangered plants are monoculture plantations (Dálya and Sedlák, 2020), especially non-native spruce stands (Černý, 1988) on compacted soils, with a lack of nutrients and soil pH values <5 (Lindner *et al.*, 2008). Volumes of harvested spruce wood from salvage cuttings due to *Armillaria* sp. infestation in the Czech Republic were (in m³): 304K in 2020, 210K in 2019, 250K in 2018, 450K in 2017, 731K in 2016 and 423K in 2015 (MZE, 2016-2021). The areas most affected in the long-term are Silesia, North Moravia and South Moravia (MZE, 2016-2021). Research on *Picea abies* (L.) H. Karst. in the Czech part of Silesia in 2015 showed that, among the trees with confirmed honey fungus infections, 56% were infected by *A. ostoyae*, 32% were infected by *A. cepistipes* and 1% were infected by *A. gallica* (Holuša *et al.*, 2018). The symptoms of infestation of woody plants by *Armillaria* spp. include resinous outflow, white rot of wood (mainly in the roots and lower part of the trunk), bottle-thick bases of trunks, light grey-green or yellow-green colouring and subsequent fall-off of needles, the presence of fruiting bodies near infested trees and the presence of brown or black cord-like rhizomorphs on and around the roots (Soukup, 2005). The effect of *Armillaria* spp. increases with higher temperatures and lower precipitation during the growing season (Lindner *et al.*, 2008). Therefore, under the current and future predicted climate conditions, continuing significant damage to woody plants by honey fungus can be expected. Spruce stands have lower pH compared to beech and beech-spruce mixed stands (Cremer and Prietzel, 2017). Therefore, in monocultural spruce plantations, an effective measure can be the planting other tree species (*e.g.*, *Fagus sylvatica*) that increase soil pH, which is less favourable to *Armillaria* species (Holuša *et al.*, 2018). Forest managers should be prepared to convert spruce stands to near-natural forests instead of monoculture plantations (Holuša *et al.*, 2018), as this can significantly reduce the rate of infestation by *Armillaria* spp. as well as other wood-decay fungi (Morrison *et al.*, 2014; Dálya and Sedlák, 2020). Stump removal and root raking are other measures that reduce mortality and can be used in the effort against *Armillaria* spp. (Morrison *et al.*, 2014). Pre-commercial thinning seems to be unnecessary in areas where spruce plantations are highly stressed (Holuša *et al.*, 2018). The most frequent biocontrol agents are based on the fungus *Trichoderma* spp., which may efficiently employ diverse antagonistic mechanisms against fungal plant pathogens (Percival *et al.*, 2011; Chen *et al.*, 2019; Rees *et al.*, 2021).

The second most crucial fungal pathogen causing root rot in the Czech Republic is *Heterobasidion annosum* sensu stricto, which includes three Eurasian species: *H. annosum* (Fr.) Bref.; *H. parviporum* Niemelä & Korhonen and *H. abietinum* Niemelä & Korhonen (Niemelä and Korhonen, 1998). In the Czech Republic, the *H. annosum* species is most common and occurs on many conifers and broadleaves. *H. parviporum* occurs mainly on *Picea* spp. (Sedlák and Tomšovský, 2011) and other conifers, but less on broadleaves (CABI, 2021a). *H. abietinum* occurs only on conifers (Sedlák and Tomšovský, 2011). These pathogens cause the most serious damage in stands on forested former agricultural land. In *P. abies* stands on former pastures and meadows, the primary infection caused through *H. parviporum* spores is dominant, but secondary infection increases with stand age. *H. parviporum* can form large (over 100 m²) territorial clones, causing extensive tree dieback and mortality (Klavina *et al.*, 2021). Symptoms caused by *Heterobasidion* spp. vary depending on the pathogen species involved, the tree species infected, the age and previous use of the forest stand, the soil type, the local climate, and possibly atmospheric pollution. Even so, it is possible to consider the general main symptoms of infestation by *Heterobasidion* spp. to be root rot, subsequent rot of the rhizome of the trunk, and resinous outflow. When disintegration of sapwood starts, the crown begins to thin. Infected trees occur in clusters in the stand and are

highly sensitive to windthrow. Fruiting bodies of *Heterobasidion* spp. grow on roots, stumps, and dead trunks (Soukup, 2011). Climate change towards a milder winter with prolonged periods at temperatures above 5°C can increase the sporulation and infection of *Heterobasidion* spp. (La Porta *et al.*, 2008). Drought can predispose conifers to *Heterobasidion* attack through the reduction of the endogenous defence mechanisms of trees (Lindberg and Johansson, 1992). Therefore, continuing serious damage of conifers by *Heterobasidion* root rot can be expected in the Czech Republic and beyond, because the fungus may remain active in dead stumps and in the root systems for decades. Stumps after thinning can be infected by the pathogen through spores (Pratt and Greig, 1988). Stump removal with the careful removal of all roots is the only effective control strategy against *Heterobasidion* root and butt rots on heavily infested sites (Cleary *et al.*, 2013; Garbelotto and Gonthier, 2013). However, it is an expensive and time-consuming control method that requires the use of machines, making it unsuitable for most forest stands. Potential solutions are chemical and biological control agents (especially biological preparations based on *Phlebia gigantea* [Fr.] Donk.), which were proved to be effective and are recommended for use (Holdenrieder *et al.*, 1998; Klavina *et al.*, 2021). A long-term alternative is to change the tree species composition to a mixture forest, with the use of planting near-natural forests (Worrall *et al.*, 2010).

Ascomycete fungal pathogens

The Dutch elm disease affecting elms (*Ulmus* spp.), caused by the fungus *Ophiostoma ulmi* (Buisman) Nannf., was first recorded in the Czech Republic's present territory (the former Czechoslovakia) in 1932 (Polák, 1932). It spread in the following years, especially in floodplain forests in the lowlands (Kalandra and Pfeffer, 1935). A new and more aggressive species, *O. novo-ulmi* (Brasier, 1991), spread widely in the 1970s (Jančařík, 1976), causing the massive death and disappearance of elms from many areas. The occurrence of *O. novo-ulmi* on elms in the Czech Republic was confirmed by Dvořák *et al.* (2007) using molecular biology methods; the presence of both subspecies *O. novo-ulmi* subsp. *novo-ulmi* Brasier (indigenous in the areas of Ukraine and Moldavia) and *O. novo-ulmi* subsp. *americana* Brasier & S.A. Kirk (indigenous in North America) and its hybrids was recorded. No strain belonged to *O. ulmi* (Dvořák *et al.*, 2007). The spores of both pathogens are mainly spread by subcortical insects, especially *Scolytus* spp. (Příhoda, 1959; Jürisoo *et al.*, 2021). The pathogen's hyphae block the conductive tissues of the host (Příhoda, 1959). The host subsequently defends itself against the penetration of the pathogen and its toxins by forming clumps of accompanying parenchymal cells, which leads to further blockage of the conductive tissues (Jančařík, 1999). During the acute course of the disease, the leaves wither, curl and dry but do not fall off, and the tree dies during one growing season. In some cases, the branches of the infested trees dry from one side of the crown to the centre over many years. The process of dying can take many years, without any symptom (Příhoda, 1959). In recent years, there has been no noticeable increase in the Dutch elm disease in the Czech Republic. Nevertheless, it remains a significant threat. Rising temperatures can favour bark beetles which are vectors of *O. novo-ulmi* (Santini and Faccoli, 2014). However, it is unclear how ongoing climate change will affect elms (Martín *et al.*, 2019) as well as interactions among the fungal pathogen, its insect vectors, and the host trees (Santini and Faccoli, 2014). The most effective measure against this disease is integrated pest management, which lowers the fungal inoculum levels and vector densities. Prompt sanitation is the best single method of containing the disease. Biological protection can also be used via biocontrol products based on *Verticillium albo-atrum* (Postma and Goosen-van de Geijn, 2016). Chemical control, especially fungicides injected pre-

ventively or curatively, play an important role when other methods cannot be implemented (Stipes, 2000). Using non-native, resistant genotypes or material bred with higher field resistance could be used to re-establish European elms (Solla *et al.*, 2005; Martín *et al.*, 2021).

Ash dieback is one of the most concerning and fastest-spreading fungal diseases of woody plants in Europe, including the Czech Republic. The causative agent of ash dieback, the fungus *Hymenoscyphus fraxineus* (anamorph *Chalara fraxinea* Kowalski), was first recorded in the Czech Republic in 2007 (Jankovský and Holdenrieder, 2009), but it has possibly occurred there before. The disease spread from the northeast to the southwest of the country and affected mainly young trees. Nowadays, it occurs in practically the whole of the Czech Republic on both young and old trees (Havrdová and Černý, 2012). In the Czech Republic, *H. fraxineus* attacks the native ash species, *Fraxinus excelsior* L., more often than native *F. angustifolia* Vahl (Havrdová *et al.*, 2016b). Non-native *F. ornus* L. is less susceptible to *H. fraxineus* infection than both native Czech ash species (Queloz *et al.*, 2011). The pathogen is the most serious in plantations with a higher proportion of ash trees – especially in ash-alder alluvial forests, hardwood alluvial forests, riparian stands (Havrdová and Černý, 2012) and urban plantings. Typical symptoms of ash dieback are leaf spots, premature leaf drop, drying of shoots and branches, excessive formation of preventive shoots, secondary crown development (including growth on the trunk), colouring of wood, and necrosis of surface tissues at the base of the trunks and roots (Černý *et al.*, 2016a). Recorded occurrence of ash decline (dominantly due to *H. fraxineus*, less due to other fungal pathogens *e.g.*, *Armillaria* spp. and *Ganoderma applanatum* [Pers.] Pat.) in forests of the Czech Republic were (in ha): 3.5K in 2020, 6K in 2019, 5K in 2018, 4K in 2017 and 4K in 2016 (MZE, 2017-2021). The damage caused by ash dieback increases with tree density, proportion of ash in stands, nutrient and water availability and temperature (Havrdová *et al.*, 2016a). Juvenile trees are more exposed to competition with other vegetation and thus more predisposed to die-off if they are infected by ash dieback (Cech, 2008). In contrast, spore density of *H. fraxineus* decreases with increasing height of the stand (Timmermann *et al.*, 2017) and damage by ash dieback decreases with distance to other ash stands and increasing slope (Havrdová *et al.*, 2016a). Infected trees appear to be more susceptible to other pathogens, especially *Armillaria* spp. (Timmermann *et al.*, 2017). The most significant potential damage areas are warm and wet areas in the Silesia and Western Carpathians (Havrdová *et al.*, 2016a). Due to the rapid spread of *H. fraxineus*, the cultivation of ash trees remains problematic and the establishment of new ash stands is often abandoned. The survival of *H. fraxineus* at temperatures above 35°C is limited; thus, as warming progresses, this pathogen can recede in the warmer regions of Europe (Grosdidier *et al.*, 2018). In the Czech Republic, where such temperatures are still rare (ČHMÚ, 2020), it can be assumed that ash dieback will continue to be a crucial limiting factor to ash growth in the coming years. Thinning for supporting vital ash trees can improve the health status of the stand. All trees with a dead terminal or seriously damaged top part of the crown, with necrosis of the base and a seriously damaged trunk, should be removed. Planting mixed stands rather than monocultures is also recommended. At high humidity sites favourable for *H. fraxineus*, the proportion of ash trees should be low, allowing their replacement by another tree species in the case of ash dieback (Černý *et al.*, 2016a). The use of fungicides is acceptable only for the control of individual valuable trees in the countryside, as well as in urban areas (Rozsypálek *et al.*, 2017) and forest nurseries (Černý *et al.*, 2016a). Models predicting environmental suitability can be useful for making long-term strategic decisions (*e.g.*, identifying areas where future ash regeneration and cultivation may be unsuccessful) (Chumanová *et al.*, 2019).

A possible threat to maples (*Acer* spp.) is the sooty bark disease caused by the fungus *Cryptostroma corticale*. This disease was first recorded in Great Britain in 1945 on *A. pseudoplatanus* L. (Gregory and Waller, 1951), but *C. corticale* was first recorded in North America as a saprotroph on the barks of *A. pseudoplatanus* and *A. saccharum* Marsh. (Ellis and Everhart, 1889). The disease most commonly affects *A. pseudoplatanus* and rarely *A. platanoides* L. (Kelnarová *et al.*, 2016). In the Czech Republic, this disease was first recorded in 2005 on a maple in urban greenery in Prague (Koukol *et al.*, 2014). Subsequently, *C. corticale* was confirmed in the city parks of Prague and the floodplain of the Vltava River (Koukol *et al.*, 2014). Another survey conducted in Prague recorded *C. corticale* in 25% of the 112 surveyed localities, with more frequent occurrence in localities on steep slopes, with higher altitude, with more substantial nitrogen oxide pollution and with a denser network of roads and paths (Kelnarová *et al.*, 2017). The first occurrence of *C. corticale* in Czech forests was documented by Černý *et al.* (2015). However, *C. corticale* probably occurred in the Czech forests earlier and escaped attention due to its largely hidden way of life, occurring in the host tissues without any visible manifestation of the disease (Kelnarová *et al.*, 2016). Recently, infestation by *C. corticale* (accompanied by the ascomycetous fungus, *Prosthecium pyriforme* Jaklitsch & Voglmayr) has been confirmed on *A. pseudoplatanus* in several stands of the Czech forest in North Bohemia (Lorenc, 2020a). In recent years, *C. corticale* has spread in Europe (including the Czech Republic) in response to higher temperatures and repeated periods of drought (Longa *et al.*, 2016). The first symptoms of sooty bark disease include wilting and branch dieback. Later, a greenish-brown stain can be observed in the cross-sections of the trunk. Where the pathogen reaches the bark, subcortical stromata are produced. Ultimately, dark spore masses are visible under peeled, necrotized bark and the dead host remains covered with dark stroma (Gregory and Waller, 1951). Inhalation of large amounts of *C. corticale* spores can cause a hypersensitivity pneumonitis called ‘maple bark disease’ in humans. Persons who have intensive contact with infested trees or wood (*e.g.*, woodman, foresters, sawyers, or paper mill workers) are particularly at risk (Braun *et al.*, 2021). Optimal growth temperature was determined at 25°C (Ogris *et al.*, 2021). *C. corticale* is a mostly weak and opportunistic pathogen, but increases in severity under hot and dry conditions (Ogris *et al.*, 2021). In the event of widespread planting of maples and an increase in summer droughts and temperature, a significant spread of this pathogen in the Czech Republic can be expected. Removing necrotized branches and infested individuals from the stand and ensuring higher air humidity when processing or storing necrotized wood are desirable to prevent the release of spores (Kelnarová, 2015). To avoid contact with *C. corticale* spores, persons working on infested trees or wood should wear personal protective equipment (Braun *et al.*, 2021). It is suitable to replace the removed trees with other species. When planting sycamore maples in new localities, it is necessary to focus on the habitat requirements of the tree species (Kelnarová, 2015). No effective fungicides nor biopreparates against *C. corticale* are available.

Maples are also threatened by the fungus *Eutypella parasitica*, which causes *Eutypella* canker and brown rot of maple heartwood. The pathogen is native to North America and it was first recorded in Europe in 2005 on *Acer pseudoplatanus* in Slovenia (Jurc *et al.*, 2006). In the Czech Republic, it was first recorded in 2015 in Silesia (Černý *et al.*, 2017). Subsequently, it was recorded in natural stands of various ravine and alluvial forests, other natural or commercial forests, riparian stands and open landscapes in the Czech and Polish parts of Silesia. The proportion of infested maples here was found to be 1-50%. The most common host species were *A. pseudoplatanus*, and rarely *A. platanoides* and *A. campestre* L. (Černý *et al.*, 2017). Symptoms of *Eutypella* canker are distinctive oval bark lesions on the trunk. The bark remains in place, except at the oldest part

in the centre. This canker is mainly located on the lower portions of the trunks. White to light cream-coloured mycelial fans of *E. parasitica* are present in the bark, mainly along the advancing edge of the lesions. Fruiting bodies (perithecia) of the pathogen are present on the older parts of the canker (Jurc *et al.*, 2006). Spores of the pathogen are dispersed by wind (EPPO, 2008) and show dissemination for a short distance (Johnson and Kuntz, 1979). A potential problem could be the trade of plants, which can lead to the spread of the disease (EPPO, 2008). *E. parasitica* damages the most valuable sycamore timber and represents a clear risk for maple cultivation (Černý *et al.*, 2017). Extensive areas covering the natural distribution of maples in Europe, including the Czech Republic, are at considerable risk from *E. parasitica* infection (Ogris *et al.*, 2006). Discharge of spores is heavily affected by rain, high humidity, and high temperatures (minimum 4°C, optimum 24–28°C, maximum 36°C), which is important for spore germination and pathogen development (Johnson and Kuntz, 1979). Therefore, areas with a warm and humid microclimate and overgrown stands are particularly threatened (Chumanová *et al.*, 2019). Branches affected by *Eutypella* canker can be pruned, but there is hardly any treatment possible for trunk cankers. In an urban environment, adequate watering and fertilization may help trees to resist infection (EPPO, 2008). No effective fungicides nor biopreparates against *E. parasitica* are available.

Stands of a substitute tree, *Picea pungens* Engelm., especially in the Ore Mountains, are seriously damaged by the *Gemmamyces* bud blight caused by *Cucurbitaria piceae*. The pathogen was first discovered in Scotland in 1906 (Borthwick, 1909). The main host trees of this pathogen are *Picea* spp. and rarely *Abies* spp. (Borthwick, 1909). In the Czech Republic, *C. piceae* was first identified in *P. pungens* in the Slavkovský les Mountains (Western Bohemia) in 1917, but a disease with symptoms corresponding to *Gemmamyces* bud blight had already been observed there in 1909 (Köck, 1918). The widespread death of *P. pungens* due to *Gemmamyces* bud blight began in the Ore Mountains in 2009 (Soukup and Pešková, 2009). Subsequently, *C. piceae* has been commonly observed on *P. pungens* in the Ore Mountains and Jizera Mountains, but lesser plantations of the trees affected by the pathogen are distributed from mountains to lowlands over the whole Czech Republic (Zýka *et al.*, 2018). The pathogen occurs on *P. abies*, in the Ore Mountains, Lusatian Mountains, Šumava Mountains and Kralický Sněžník, but it probably also occurs in other regions (Zýka *et al.*, 2018). The occurrence of *C. piceae* on *P. abies* is low, and infected trees are usually not seriously affected (Soukup and Pešková, 2009). However, a significant increase in the number of trees with a higher proportion of infested buds has been observed in the Ore Mountains since 2014 (Modlinger and Pešková, 2017). The infection occurs during the growing season. The dominant infectious agent is probably conidium, which spreads in humid weather (Černý *et al.*, 2016b). The main symptoms of infestation on *Picea* spp. and *Abies* spp. are twisted shoots and swollen buds, where black stroma with small spherical fruiting bodies appear (Soukup and Pešková, 2009). *C. piceae* is a psychrophile, as indicated by the following cardinal temperatures: 0°C (minimum), 13–18°C (optimum), and 25°C (maximum) (Černý *et al.*, 2016b). Higher damage of *P. pungens* by *Gemmamyces* bud blight has been recorded on sites with higher total precipitation and on moist soils with low nutrients. The opposite effect is observed in higher air temperature and southern exposure (Zýka *et al.*, 2018). However, *C. piceae* has recently moved to warmer, less climatically suitable areas (Černý *et al.*, 2016b). Therefore, it is difficult to predict the occurrence of this pathogen in the Czech Republic in the coming years. In the severely affected Czech *P. pungens* stands, only thinning, gradual suppression of *P. pungens* and change of species composition can be considered. In ornamental plantings with a low disease incidence, the removal of affected twigs, branches and highly affected individuals can be recommended.

For more severe damage, fungicide should be sprayed before or during bud opening, and again during the spore transmission phase. Preventing the introduction of this pathogen to North America, the homeland of the most susceptible *Picea* species (*P. pungens* and *P. engelmannii* Parry ex Engelm) through the inspection or regulation of susceptible plants, is also recommended (Černý *et al.*, 2016b).

Fungal-like pathogens

One of the most serious threats to woody plants are organisms of the genus *Phytophthora*. It is now classified in Oomycetes, in the *Straminipila* lineage within the *Straminipila-Alveolata-Rhizaria* (SAR) eukaryotic supergroup (McCarthy and Fitzpatrick, 2017). *Phytophthora* species can survive under adverse environmental conditions with the use of resting structures (mainly sexual oospores), vegetative chlamydospores and hyphal aggregations (Jung *et al.*, 2018). Soilborne *Phytophthora* species (*e.g.*, *P. alni* species complex; *P. cambivora* (Petri) Buisman; *P. cinnamomi* Rands. and *P. plurivora* T. Jung & T.I. Burgess) infect fine roots, the bark of suberized roots, and the collar region with mobile zoospores under wet soil conditions. Airborne *Phytophthora* species (*e.g.*, *P. ramorum* Werres, De Cock & Man in 't Veld) infect leaves, shoots, fruits and bark of branches and stems with sporangia, that are produced under humid conditions on infected plant tissues and dispersed by rain and wind splash (Jung *et al.*, 2018). Typical symptoms of plants affected by *Phytophthora* spp. are crown thinning, chlorosis and dieback caused by extensive fine root losses and/or collar rot (Jung *et al.*, 2015). In a large-scale study conducted in 732 European nurseries plus 2525 areas in which trees and shrubs were planted, 49 *Phytophthora* taxa were recorded in 91.5% of the nurseries and 66% of the other tested areas (Jung *et al.*, 2015). In the Czech Republic, *Phytophthora* diseases on woody plants and *Phytophthora* diversity were overlooked until 2000 (Černý *et al.*, 2011). The most dangerous invasive *Phytophthora* species for forest trees recorded in the Czech Republic are potentially *P. alni* species complex (Černý *et al.*, 2003), *P. cactorum* (Erwin and Ribeiro, 1996), *P. cambivora* (Černý *et al.*, 2008), *P. cinnamomi* (Černý *et al.*, 2011), *P. plurivora* (Mrázková *et al.*, 2010) and *P. ramorum* (Černý *et al.*, 2011). Between 2006 and 2010, 16 *Phytophthora* species in the Czech Republic were detected on more than 20 investigated woody plants – most frequently *P. alni* species complex, *P. plurivora* and *P. cactorum* (Černý *et al.*, 2011). The most serious invasive *Phytophthora* pathogen on woody plants that has not yet been recorded in the Czech Republic is *P. kernoviae* Brasier, Beales & S.A. Kirk (ÚKZÚZ, 2014–2021). The impact of future changes in temperature and precipitation patterns on the spread and activity of *Phytophthora* remains unknown (Hung *et al.*, 2018). However, due to the interaction between *Phytophthora*-caused fine root losses and droughts, as well as the multicyclic spread of *Phytophthora* zoospores and sporangia under persisting humid conditions, rising temperatures and increased summer droughts, alternating with periods of unseasonal heavy rain, will most likely intensify the root and collar rot incidences (Jung *et al.*, 2018). The control and management of *Phytophthora* pathogens and diseases should mainly focus on the prevention of their introduction and slowing down their spread once they are introduced (Jung *et al.*, 2018). Products based on propamocarb, metalaxyl, fosetyl-Al or dimethomorph can be used against oomycetes, including *Phytophthora* species. Propamocarb and metalaxyl-based products are suitable for soil applications. Potassium phosphonate (phosphite) showed a positive effect on reducing infection pressure, but a major drawback is the need to repeat treatments due to its short shelf life (Hardy *et al.*, 2001; Tynan *et al.*, 2001; Daniel *et al.*, 2005). Phosphite-Al-based fungicide can also reduce *Phytophthora* development and thus mitigate the impact on forest stands (González *et al.*, 2017). Although the success rate of phosphonate use is inversely proportional to the stage of infestation (Gentile *et al.*, 2009), the

efficacy of fosetyl-Al injection against *P. cinnamomi* has been demonstrated (González *et al.*, 2017).

The *P. alni* species complex, which causes *Phytophthora* disease of alders, has spread in Europe since the 1980s and later to the Czech Republic. The pathogen mainly attacks the root neck of trees and causes the mass dying of alders (*Alnus* spp.) (Černý and Strnadová, 2010). The *P. alni* species complex was first identified in 1995 (Brasier *et al.*, 1995) where it was recorded only on alders (Hansen, 2012). The pathogen currently occurs in most European countries (Jung and Blaschke, 2004). In the Czech Republic, it was first isolated from damaged *A. glutinosa* (L.) Gaertn. In western Bohemia (Černý *et al.*, 2003), it occurs on the native alder species, *A. glutinosa* and *A. incana* (L.) Moench. Its occurrence is expected in the whole territory, but mostly in Southern Bohemia (Černý *et al.*, 2010). Within the *P. alni* species complex, there are three known species: *P. × alni*, *P. × multififormis* and *P. uniformis* (Brasier *et al.*, 2004; Husson *et al.*, 2015). Of these, *P. × alni* is the most aggressive and constitutes approximately 88% of the population of the complex (Štěpánková *et al.*, 2013). The main causes of the massive spread of infestation are the transfer of planting material from nurseries (Jung *et al.*, 2007) and spontaneous spread through water-courses (Jung and Blaschke, 2004). The *P. alni* disease of alders has been observed to increase with the mean summer temperature of the river water (Thoirain *et al.*, 2007). *P. × alni* is a thermophile with optimal growth temperature ranges above 22°C (Brasier *et al.*, 1995). On the other hand, high summer temperatures may favour antagonistic microflora populations (Garrett *et al.*, 2011), resulting in unfavourable conditions for *P. × alni* (Aguayo *et al.*, 2014). Low winter air temperatures promote tree recovery because of poor pathogen survival (Aguayo *et al.*, 2014). Extreme drought can accelerate the *Phytophthora* disease process, due to reduced vitality of the host tree (Jung and Burgess, 2009). Depending on the European area, climate change can either enhance or decrease the severity of alder decline (Aguayo *et al.*, 2014). Measures against the *Phytophthora* disease include performing controls and keeping records of the occurrence of the disease, avoiding discharge of the pathogen to water sources and healthy vegetation, and using healthy and controlled material when planting alders. In nurseries, it is possible to change the planted species, change cultivation practices, change the source of irrigation water and use fungicides. In stands, the removal of infested alder trees, replacing alder trees with different plants (even temporarily) and felling downstream in winter, from healthy to damaged stands, is recommended. The infected material should be discarded and working tools and machines should be cleaned (Černý and Strnadová, 2011).

P. cactorum is a well-known pathogen of many plants with both a soil- and an airborne lifecycle (Jung *et al.*, 2018). In the Czech Republic, the pathogen was first recorded on *Fagus sylvatica* L., *A. hippocastanum* L. and *Populus alba* L. as the causal agent of bleeding cankers (Černý *et al.*, 2009). The main host tree of the pathogen in the Czech Republic is *F. sylvatica*, and rarely *Quercus* spp., *Tilia* spp., *Acer* spp., *Larix* spp., *Pseudotsuga* spp., *Abies* spp. or *Picea* spp. (ÚKZÚZ, 2014-2021).

P. cambivora is a soilborne pathogen (Jung *et al.*, 2018) of both conifers and broadleaves (CABI, 2021b), long-established in many European countries (Santini *et al.*, 2013). In the Czech Republic, the pathogen was first recorded on *Castanea sativa* Mill. as the causal agent of ink disease (Černý *et al.*, 2008). The main host trees of the pathogen in the Czech Republic are *Fagus* spp., *Quercus* spp. and *Castanea* spp. (ÚKZÚZ, 2014-2021).

The most feared *Phytophthora* species worldwide is *P. cinnamomi*. It is a soilborne pathogen (Jung *et al.*, 2018) which has a wide range of plant hosts, mainly woody plants. In southwestern Australia, tens of thousands of hectares of *Eucalyptus* forest have been destroyed by the pathogen (Podger, 1972). Within the European trees, *P. cinnamomi* mainly affects *Quercus* spp.

(Bergot *et al.*, 2004). In the Czech Republic, the pathogen was first recorded on *Rhododendron* spp. and *Vaccinium corymbosum* L. (Černý *et al.*, 2011). In case of longer drought periods (Lindner *et al.*, 2008) and higher winter temperatures, expansion of *P. cinnamomi* can be expected (Bergot *et al.*, 2004).

P. plurivora is a soilborne species (Jung *et al.*, 2018) whose isolates were previously routinely identified as *P. citricola* (Jung and Burgess, 2009). The pathogen is native in Europe and has probably spread globally through the nursery trade of diseased plant material (Schoebel *et al.*, 2014). In the Czech Republic, Mrázková *et al.* (2013) isolated *P. plurivora* from 20 hosts, predominantly from *Rhododendron* spp., *Acer* spp., *Quercus* spp., *Fraxinus* spp. and *Tilia* spp. The *P. plurivora* isolates from forest trees were more aggressive towards such trees than isolates from ericaceous ornamental plants. This pathogen is found in a broad range of elevations and environments, including forest and riparian stands, and has potentially become naturalized (Mrázková *et al.*, 2013).

P. ramorum is an airborne species (Jung *et al.*, 2018) with a wide range of both broadleaf and conifer hosts (EPPO, 2021). The pathogen is also a causative agent of Sudden Oak Death (Goheen *et al.*, 2002) and Sudden Larch Death (Brasier and Webber, 2010). In the Czech Republic, *P. ramorum* was first recorded on *Rhododendron* spp. in 2009 (Černý *et al.*, 2011) and subsequently, records of the pathogen came mainly from imports of *Rhododendron* spp. Eradication of the pathogen has been successful and since then, no *P. ramorum* has been recorded in the Czech Republic (ÚKZÚZ, 2014-2021).

Conclusions

The above-mentioned pathogens are just a few potential threats that are well known. Some other important pathogens that can be problematic are *Neonectria coccinea* (Pers.) Rossman & Samuels, *Inonotus* complex, *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton 1980, *Cenangium ferruginosum* Fr. and *Lecanosticta acicola* (Thüm.) Syd. Some of these have caused serious problems (*e.g.*, a combination of drought and pathogens on *Pinus* spp.) and others can present future issues with *Fagus* spp. and *Quercus* spp.

Climate change is likely to have a deep impact on plant – pathogen interactions and represents one of the biggest challenges for the ecological and functional stability of forests in the coming years. Several fungal diseases on trees may become more devastating because abiotic stresses predispose trees to pathogens (La Porta *et al.*, 2008), *e.g.*, *Heterobasidion* spp. (Lindberg and Johansson, 1992) and *Sphaeropsis sapinea* (Vornam *et al.*, 2019). Increasing temperature and moisture positively affect sporulation and dispersal of certain pathogens (La Porta *et al.*, 2008), *e.g.*, *Hymenoscyphus fraxineus* (Havrdová *et al.*, 2016a; Grosdidier *et al.*, 2018). Migration of pathogens triggered by climatic change may increase disease incidence or geographical ranges. New threats may appear either because of a change in tree species composition or because of invasive species (La Porta *et al.*, 2008). Invasive pathogens, *e.g.*, *H. fraxineus* and several *Phytophthora* species, have the potential to radically reshape native woods and forests, (Potter and Unquart, 2017).

It is necessary to make long-lasting management decisions, even if uncertainty about climate change impacts is still large. Forest management requires expert knowledge and enhanced efforts to provide science-based decision support (Lindner *et al.*, 2014). To strengthen the adaptive capacity of temperate forests in Europe, it is recommended to increase tree species richness, increase structural diversity, maintain and improve genetic variation within tree species, increase the resistance of individual trees to biotic and abiotic stress, replace high-risk stands

(especially non-native spruce and pine monocultures in lowlands) and keep the average growing stocks low (Brang *et al.*, 2014). Forest adaptation can include intermixing of native and non-native tree species as well as non-local genetic strains, which can adapt better to future climate conditions (Bolte *et al.*, 2009). *Picea abies* and *Pinus sylvestris* L. will likely become unprofitable and, consequently, their abundance in Central European lowland forests during the anticipated climate change will significantly decrease. *Fagus sylvatica* and *Quercus robur* L. may endure in large parts of Central Europe. Potential alternative tree species, such as *Quercus ilex* L., *Pinus nigra* J.F. Arnold, *P. halepensis* Mill., *P. pinaster* Aiton and *Castanea sativa* can be considered a meaningful replacement of locally declining tree species (Buras and Menzel, 2019). However, the introduction of new species has a risk of uncontrolled spread (Lombardero *et al.*, 2008).

The phenotype, and hence phenotypic maladaptation, evidently plays a significant role in a tree disease. Biotic factors are key in limiting the capacity of trees to use all their potential phenotypic plasticity and plastic responses. We still know little about the physiological mechanisms behind phenotypic tree resistance (Stenlid and Oliva, 2016). The biggest problem is that we do not know how pathogens kill trees, because it is a complex process. Pathogens can establish a large array of interactions with the host with differing physiological consequences. Our understanding of how pathogens kill trees is often misled due to an interaction with other abiotic factors that lead to the killing of trees.

The most cost-effective measurement against both native and invasive species is to prevent their establishment. Regional and international regulatory programs that can restrict the predictable pathways of pathogens can be useful tools (Hansen, 2008). Specifically, it is important to manage imported plant material, control the seeds and planting material in forestry, ensure timely application of suitable chemical preparations or bio-preparations in forest nurseries (preventively and in case of pathogen attack), apply adequate watering, plant individual tree species in suitable habitats, ensure timely removal of infested plants or their parts and plant interventions, creating less suitable conditions for the pathogens.

Authors' contribution

F.L., M.S. – manuscript preparation; F.L., M.S. – manuscript corrections.

Conflicts of interest

There is no conflict of interest.

Acknowledgements

The authors would like to thank Scribendi Inc. for quick English proofreading.

Funding source

This review was supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0118.

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STRESZCZENIE

Patogeny zagrażające ekosystemom leśnym Republiki Czeskiej – przegląd

W związku z globalnymi zmianami klimatycznymi obserwuje się zmiany średnich wartości czynników klimatycznych (zwłaszcza wzrost temperatur) oraz nasilające się ekstremalne wahania pogodowe. W Republice Czeskiej ekstremalne upały i długotrwała susza w latach 2015-2019 doprowadziły do zwiększenia częstotliwości redukcji aparatu asymilacyjnego i w konsekwencji osłabienia odporności roślin drzewiastych na czynniki biotyczne, w tym patogeny grzybowe i grzybopodobne. Ponadto nastąpiło masowe rozprzestrzenianie się patogenów inwazyjnych w związku z rosnącą częstotliwością importu gatunków egzotycznych. Celem pracy jest podsumowanie wiedzy na temat obecnych oraz potencjalnych patogenów, które mogą być istotnym zagrożeniem dla drzew w czeskich lasach.

Armillaria ostoyae (Romagn.) Herink, *A. gallica* Marxm. & Romagn., *A. cepistipes* Velen. i *A. mellea* (Vahl) P. Kumm powodują białą zgniliznę drewna. Najgroźniejszym gatunkiem jest *A. ostoyae* w lasach świerkowych na Śląsku oraz północnych i środkowych Morawach, przy czym coraz większy wpływ na zachorowania mają wysokie temperatury i niższe opady w okresie wegetacyjnym. *Heterobasidion annosum* (Fr.) Bref., *H. parviporum* Niemelä & Korhonen i *H. abietinum* Niemelä & Korhonen powodują białą zgniliznę drewna, głównie na drzewach iglastych na zalesionych gruntach porolnych, szczególnie w latach suszy i łagodnych zim.

Ophiostoma novo-ulmi Brasier, powodująca holenderską chorobę wiązów, rozprzestrzeniła się w latach 70. i wyparła *O. ulmi* (Buisman) Nannf. *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya powoduje zamieranie jesionów. Wcześniej patogen ten występował głównie na młodych drzewach w regionie północno-wschodnim, a obecnie jest spotykany na całym terytorium, zarówno na młodych, jak i na starszych drzewach w jesionowo-olszowych lasach łągowych, liściastych lasach łągowych, drzewostanach łągowych i miejskich plantacjach rodzimych *F. excelsior* L. i *F. angustifolia* Vahl. Największe możliwości wyrządzenia znacznych szkód występują w ciepłych i wilgotnych miejscach. *Cryptostroma corticale* (Ellis & Everh.) P.H. Greg. & S. Waller powoduje chorobę kory klonów, zwłaszcza na *A. pseudoplatanus* L., i jest obserwowana w Czechach na drzewach miejskich od 2005 roku, a w lasach od 2015 roku. Rozprzestrzeniła się ona w związku z letnimi suszami i wysokimi temperaturami. *Eutypella parasitica* R.W. Davidson & R.C. Lorenz powoduje raka i brunatną zgniliznę drewna klonu i jest obserwowana w Czechach od 2015 roku, głównie na *A. pseudoplatanus* na Śląsku. Preferuje ona tereny o wilgotnym mikroklimacie oraz przegęszczone drzewostany. *Cucurbitaria piceae* (Borthw.) powoduje zarazę pąków i występuje głównie w Rudawach, gdzie w 2009 roku rozpoczęło się powszechne

zamieranie nierodzimych świerków *Picea pungens* Engelm. Preferuje miejsca wilgotne, o niskiej temperaturze powietrza.

Grzybobodobne organizmy rodzaju *Phytophthora* powodujące zgniliznę korzeni były niedostrzeżone aż do końca XX wieku. Potencjalnie najbardziej niebezpiecznymi inwazyjnymi gatunkami *Phytophthora* dla czeskich lasów są: *P. alni* sensu lato, *P. cactorum* (Lebert & Cohn) J. Schröt., *P. cambivora* (Petri) Buisman, *P. cinnamomi* Rands., *P. plurivora* T. Jung & T.I. Burgess oraz *P. ramorum* Werres, De Cock & Man in 't Veld. Rosnące temperatury i nasilające się letnie susze na przemian z okresami niesezonowych ulewnych deszczy mogą potencjalnie nasilać występowanie zgnilizny korzeni i szyi korzeniowej.

Długotrwałe decyzje gospodarcze, oparte na wiedzy specjalistycznej, powinny obejmować środki zapobiegające niebezpiecznym infekcjom powodowanym przez grzyby i organizmy grzybobodobne. W celu wzmocnienia zdolności adaptacyjnej lasów strefy umiarkowanej w Europie zaleca się zwiększenie różnorodności gatunkowej, strukturalnej i genetycznej drzew, utrzymanie niskich średnich zasobów drzewostanu oraz wymianę drzewostanów wysokiego ryzyka (zwłaszcza świerkowych i sosnowych na nizinach). Najbardziej opłacalne środki zapobiegania osiedlaniu się gatunków inwazyjnych obejmują kontrolę materiału roślinnego, sadzenie poszczególnych gatunków drzew w odpowiednich siedliskach, odpowiednie nawadnianie i terminowe leczenie lub usuwanie chorych roślin bądź ich części.