GENETIC PREDISPOSITIONS OF COMMON ASH TO THE ASH DIEBACK CAUSED BY ASH DIEBACK FUNGUS

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The paper reviews information on ash dieback, a serious disease of common ash and its causing agent ash dieback fungus *Hymenoscyphus fraxineus*. This paper covers biology and genetics of the causing agent. Main emphasis is given to the genetic predisposition of the tolerance to the disease. Strong genetic control of the infection-tolerance opens the possibility for selection of hyposensitive trees for the establishment of seed orchards, which will produce offspring with improved tolerance to *H. fraxineus*.
Keywords: disease tolerance, *Fraxinus excelsior*, *Hymenoscyphus fraxineus,* resistance

INTRODUCTION

Since the mid of the 1990s, common ash (*Fraxinus excelsior* L.) has been severely stricken by the novel dieback disease, which was attributed to a synergic effect of various fungal pathogens at the beginning (LYGIS *et al*., 2005; PRZYBYL, 2002). The dieback was first reported on common ash in northeastern Poland in the 1990s (KOWALSKI, 2006; PRZYBYL, 2002) and since then it has spread rapidly over the most of its natural range.

The causing agent of the disease was first time recognized by KOWALSKI (2006), which asexual morph he named as a novel species *Chalara fraxinea* Kowalski based on the detailed morphological studies. After the molecular characterization of the ITS region, the fungus was

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classified into the fungal genus *Hymenoscyphus* (KOWALSKI and HOLDENRIEDER, 2009b). The same authors found the sexual stage of *C. fraxinea* morphologically identical with the species *Hymenoscyphus albidus* (Gillet) W. Phillips which is native and widespread in Europe but known to be a saprophyte on ash leaves. Further study, based on a detailed characterization of DNA sequences gained from apothecia or cultures collected from various regions of Central Europe (QUELOZ *et al.*, 2011), showed that *H. albidus* is an aggregate of two clearly delimited species that are indistinguishable morphologically. The species which occurs in regions without ash dieback was considered to be the genuine *H. albidus*. The other one, which asexual morph was already known as *C. fraxinea*, (QUELOZ *et al.*, 2011), was denominated as *Hymenoscyphus pseudoalbidus* Queloz *et al*. Later, it was renamed towards *Hymenoscyphus fraxineus* (Kowalski) Baral, Queloz and Hosoya (BARAL *et al.*, 2014). *H. pseudoalbidus* is still accepted as its synonymic name.

The short history of rapid expansion and high intensity of the ash dieback epidemic in Europe shows clearly that *H. pseudoalbidus* is an invasive alien organism (QUELOZ *et al.,* 2011; HUSSON *et al.,* 2011). According to available data, European countries where this disease was recorded most recently are Serbia (KEČA *et al.*, 2017) and Montenegro (MILENKOVIĆ *et al.*, 2017). The species was shown to have been introduced from Eastern Asia (ZHAO *et al.*, 2012; GROSS *et al.*, 2014). Their study based on morphological and genetic characteristics of the species showed that the species is naturally found in East Asia, where it was previously described by HOSOYA *et al.* (1993) as *Lambertella albida* (Gillet) Korf where it was found on petioles of *Fraxinus mandshurica* (Rupr.) in Japan. At the same host species, the fungus was found in Korea, China, Far East Russia, and on *Fraxinus rhynchophylla* (Hance) in Korea (GROSS *et al.*, 2014), but on the Asian ash species there have been reported no symptoms typical for European ashes, colonized by the fungus. *Fraxinus mandshurica* and *F. chinensis* (Rox.) with their natural occurrence in Japan and China are even considered as resistant, which also suggests that *H. fraxineus* originating from these areas (ZHENG and ZHUANG, 2014).

Life cycle of Hymenoscyphus fraxineus

The entire life cycle of *H. fraxineus* is completed on *Fraxinus* leaves (GROSS *et al.*, 2014). Ash dieback fungus is overwintering in infected last year's petioles, found at the forest floor. At the beginning of summer apothecia start to form in these petioles. The apothecia release ascospores that are then spread by wind which facilitates the transmission of infection to long distances (KOWALSKI and HOLDENRIEDER, 2009a). Exceptionally, apothecia may occur on root collars of young plants which are dead due to the infection (KIRISITS *et al.*, 2012).

Sporulation is most intense at the beginning of the summer, but it may occur in the spring and autumn as well. On the other hand, fructification is highly dependent on favorable climate conditions (HIETALA *et al.*, 2013).

At the end of summer, small necrotic lesions start to develop on ash leaves, at points where ascospores were landed previously (GROSS *et al.,* 2014). These lesions gradually spread to the petioles, causing drying of leaves and leading to premature leaf fall in late summer (FREINSCHLAG, 2013).

Subsequently infection is spread in the woody parts of the plant (phloem and xylem). By the time the infection spreads so that sapwood and cambium cells are infected, a rapid wilting of whole shoots and branches is recorded (SCHUMACHER, 2007, 2011)

Genetics of Hymenoscyphus fraxineus

ZHAO *et al*., (2012) showed that *Lambertella albida* is the same species as *H. pseudoalbidus* (a synonymic name *of H. fraxineus)* by means of the comparison of species-specific DNA markers including ITS regions, rDNA, CAL and translation elongation factor EF1-α. In their comparative population-genetic study, GROSS *et al*., (2012) showed considerably higher genetic diversity of *H. fraxineus* in its natural range in Japan in comparison than in Europe. Following GROSS *et al.,* (2014), this observation confirms the origin of *H. fraxineus* in Eastern Asia. In general, more information is available about the structure of European population of *H. fraxineus* than about its native Far-Eastern populations. However BENGTSSON *et al*., (2012) detected high genotypic diversity but only limited allelic richness (the majority of loci are only bi-allelic in European *H. fraxineus)* and almost zero interpopulation differentiation ($F_{ST} \leq 0.028$) by means of the microsatellite DNA markers. Also, GROSS *et al*., (2012) presented similar conclusions when compared two big population samples from Germany. Limited allelic richness of European *H. fraxineus* obviously results from the genetic drift – the Founder´s Effect – due to the limited initial number of parent genotypes which gave rise to current population of the pathogen (BENGTSSON *et al*., 2014). The both aforementioned authors also find the high genotypic diversity a proof of the outcrossing mating system and subsequent spreading of the fungus by ascospores.

Genetic similarity of populations in the centre and periphery of infection spreading, along with nearly equal proportions of heterothalic and homothalic genotypes, demonstrate the existence of random mating and exlude initial clonal population structure of the fungus (GROSS *et al*., 2012). Contrary to it, the Europe´s native *Hymenscyphus albidus* is homothalic (GROSS *et al*., 2012). It does not form anamorphs (KIRISITS *et al*., 2013) what results in its lover genotypic diversity (QUELOZ *et al*., 2011).

Regarding the variation in the virulence of European population of *H. fraxineus*, no differences were detected between the different isolates (BAKYS *et al.*, 2009; KOWALSKI and HOLDENRIEDER, 2009a). On the other hand, significant differences were observed in the set of 10 isolates (genotypes) of the species in the rate of establishment and spreading of leaf necroses on the host individuals of *F. excelsior* and *F. angustifolia* (SCHWANDA and KIRISITIS, 2016). Similar results were presented also by MATLAKOVA (2009), PIRIBAUER (2013), and GROSS and SIEBER (2015).

The genome-wise analyses showed the existence of an array of genes encoding for cell-wall degrading enzymes which are typical of necrotrophic fungi. However, infections of Manchurian ash in the native range of *H. fraxineus* do not result in the necrosis. Hence, while necrotrophy clearly prevails when *H. fraxineus* infects a susceptible host, the hemibiotrophy is typical of it on a natural (original) host species. The mechanism switching this change of behavior is not known up to now (GROSS *et al*., 2014).

Genetic predisposition of tolerance and susceptibility in the host species

Host tree species are trees from the genus *Fraxinus* (KOWALSKI and HOLDENRIEDER, 2009a). All three european ash species are found as suscpetible to the disease, mainly common ash (*F. excelsior)* and narrow-leaved ash (*F. angustifolia*), which are highly susceptible (KIRISITS *et al*., 2009). Manna ash (*F. ornus)*, was found to be less susceptible to the disease – moderately susceptible (KRAUTLER and KIRISITS, 2012).

F. excelsior is clearly the most susceptible species to the disease. This could cause major problems, not only in forestry, where the species is significantly represented, but also in the urban landscape and greenery (PAUTASSO *et al.*, 2013)

Apart from european ash species, symptoms of the disease were found on ash species native to America, including: *F. americana* L., *F. pensylvanica* (Marshall) and *F. nigra* (Marshall). DRENKHAN and HANSO (2010) found in Estonia in their experiment with introduced ornamental ash species black ash (*F. nigra*) as a highly susceptible, green ash (*F. pensylvanica*) moderately susceptible, while white ash (*F. americana*) and Manchurian ash (*F. mandshurica*) were less affected. *F. mandshurica* is ash species native to China, Korea and Japan where *H. fraxineus* was found as a harmless, saprophyte fungus, causing no damage at local ash population.

Intensity of ash dieback depends on the age of host trees, density of their population, location, microclimate, genetic factors as well as the presence of other parasitic and opportunistic organisms (KOWALSKI, 2006; KIRISITIS and CECH, 2009), Although, *H. fraxineus* attacks all age classes of *F. excelsior* trees, much greater damage and mortality was observed in young trees due to the infection in comparison to adult trees (PLIŪRA *et al.*, 2011). Also, trees in forest stands are much more affected due to better microclimate conditions and prevalence of secondary fungi such as *Armillaria* ssp., especially *A. gallica* (Marxm. and Romagn.) and *A. cepistipes* (Velen.) which are commonly found on root collar of infected ash trees (ENDERLE *et al.*, 2013). These fungi usually colonize cambium at the tree bases, which results in a gradual tree death (LYGIS *et al.*, 2005; KIRISITS *et al.*, 2009; BAKYS *et al.*, 2011).

Ash dieback fungus *H. fraxineus* is a novel species to Europe and thus any phylogenetic contact between it and common and narrow-leaved ash can barely been assumed. The existence of genetic predispositions of the susceptibility-tolerance to the infection by *H. fraxineus* was observed particularly in the common ash. Related observations provide even the hope for preserving common ash particularly in the northern and central part of its natural range severely haunted by the ash dieback disease. Heritable differences in the intensity of ash dieback were first detected in the common-garden experiments with provenances representing different source population (PLIŪRA *et al.*, 2011; METZLER *et al.*, 2012; ENDERLE *et al.*, 2013; HAVRDOVÁ *et al.*, 2016), progenies (MCKINNEY *et al.*, 2011; PLIŪRA *et al.*, 2011; LOBO *et al.*, 2015) as well as in the clonal tests (STENER, 2007, 2013; MCKINNEY *et al.*, 2011; FREINSCHLAG, 2013). Tolerance (hyposensitivity) to the infection was revealed in some ash individuals in spite of the invasiveness of *H. fraxineus* to Europe, which is native to Far-East Asia, with which European ash species thus have not been in a phylogenetic contact (in a contact for many generations, at least).

The strong genetic basis of tolerance to the ash dieback caused by *H. fraxineus* was first reported by STENER (2007) from two replicate seed orchards in southern Sweden, in which the values of broad sense heritability ranged from 0.29-0.40 for the overall vitality and 0.28-0.52 for the damage of shoots.

At the population level, PLIŪRA *et al.*, (2011) found 2 to 4 fold difference in the survival rate, and 50% in the health condition among populations in the provenance experiment including common ash provenances from Ireland, France, Belgium, Germany, Czech Republic and Lithuania. The survival rate and health condition of local Lithuanian provenances was by 50-73% better and their growth 20% better in comparison with the provenances from Central and Western Europe. However, when only populations from a geographically limited range in

Denmark were compared KJÆR *et al.*, (2012) found no major neither significant differences between them. In the single plot provenance experiment in the Czech Republic HAVRDOVÁ *et al.*, (2016) confirmed the role of source population (provenance) of forest reproductive material and less intensive infection of *H. fraxineus* in higher altitude (mountain) provenances.

In the experiment with ash in Poland PACIA *et al.*, (2017) studied *F.excelsior* genome, using nuclear and chloroplast molecular markers within different vitality classes of trees. The study revealed a lack of colleration between aforementioned classes of trees, as well as their nuclear and chloroplast genetic differentiation.

However, they found the heterozygosity (Ho) value to be significantly different between different vitality classes of trees (classes 2 and 3). The highest heterozygosity was found among the most damaged trees (class 3). The most healthiest class of trees (0+1), was not statistically different in any genetic parameter, though.

The broad sense heritability estimates (H^2) for the health condition were estimated on the seed orchard clones of common ash replicated at 2 sites by STENER (2007; 2013) in Sweden and by MCKINNEY *et al.*, (2011) in Denmark. The both studies focused on the seed orchard clones of common ash replicated at 2 sites in either of the countries, and earned almost consistent values of H^2 equal to 0.25-0.54 in Sweden and 0.28-0.52 in Denmark.

In the experiment with half-sib families from Ireland, Belgium, Germany, Czech Republic and Lithuania, PLIŪRA *et al.*, (2011) detected relatively high narrow-sense heritability (h^2) values for the ash dieback associated with infection by *H. fraxineus*: 0.60-0.92 at the age of 4 and 0.40-0.49 at the age of 8 years. In the experiment with 101 half-sib progenies from 14 Danish source populations replicated at 2 plots, KJÆR *et al.*, (2012) reported similar values of h^2 of 0.37-0.52 for the crown damage scores attributable to *H. fraxineus*. After the paternity of progenies within the aforementioned experiment was verified, LOBO *et al.*, (2015) revealed the correlation coefficient between parents and their progenies as high as 0.85 in average crown damage due to natural infection, and 0.73 in the average necrosis development after controlled inoculation. This study proved thus strong heritable control and indicates that both crown damage estimates and bioassay based on controlled inoculations have the potential of becoming fast and cost-effective tool for individual estimation of the ash dieback susceptibility.

The high narrow-sense heritability and low level of genotype by environment interactions suggests a potential for recovery of natural ash populations haunted by the dieback. Bulk of genetic variation for susceptibility to the infection by *H. fraxineus* lies within populations and is manifested by substantial differences in the susceptibility among the families and clones.

The infection-tolerance appears to be of quantitative and not of qualitative nature where action of few resistance genes in the host may trigger undesirable co-evolution of the pathogen KJÆR *et al.*, (2012). High to catastrophic mortality and decreased population density could be expected, however, in the first generation(s) following the outburst of the ash dieback. PLIŪRA *et al.*, (2011) reported only 2.8% infection-tolerant individuals in their international experiment. MCKINNEY *et al.*, (2011) reported similar proportion of 2 to 5% of hyposensitive individuals from the Danish progeny experiment. KJÆR *et al.*, (2012) estimates that only 1% of native trees have the potential of producing offspring with expected crown damage less than 10% under the present disease pressure.

For the identification of perspective hyposensitive genotypes of common ash, KOWALSKI *et al.*, (2012) identified 2 DNA markers of resistance. Using the molecular-genetic

technique based on the comparison of transcriptomes of susceptible and tolerant ash individuals, HARPER *et al*., (2016) made the whole set of DNA and RNA markers available for the identification of perspective ash-dieback tolerant individuals.

Large effective population sizes will therefore be required then to avoid genetic bottlenecks in the both natural adaptation-oriented management and also breeding of the ash. Fortunately, *F. excelsior* trees have been reported to connect even in a fragmented landscape through pollen flow (BACLES and ENNOS, 2008). The overall effect on future population structure will probably vary substantially between landscapes depending on a priori species density and type of landscape management (KJÆR *et al*., 2012). In order to maintain sufficiently large population of survivors of the ash dieback, indiscriminate elimination of all ash individuals irrespectively of their health condition needs to be avoided in the thinning and reconstruction of forest stands affected by the ash dieback irrespectively of their health condition.

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GENETIČKE PREDISPOZICIJE OBIČNOG JASENA NA NAPAD GLJIVE
Hymenoscyphus fraxineus

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Izvod

U radu su date informacije o ozbiljnoj bolesti jasena koju izaziva gljiva *Hymenoscyphus fraxineus*. Prikazana je biologija i genetika ovog izazivača bolesti. Glavni akcenat je dat genetskoj predispoziciji tolerancije na ovu bolest. Jaka genetička kontrola infekcije-tolerantnosti otvara mogućnost odabira manje osetljivih genotipova za zasnivanje rasadnika u kojima će se proizvoditi sadnice sa povećanom tolerantnošću na *H. fraxineus*.