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REVIEW PAPER

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SITE CONDITIONS FOR DECLINE OF ASH STANDS IN EUROPE

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ABSTRACT

Introduction. The process of European ash dieback emerged in 1992 in northeastern Poland. By 2012, the disease had spread throughout Europe. Two trends have been dominant in studies aiming to find an explanation for this phenomenon. One referred to the ecology of the species and abiotic conditions, while the other consisted in research concerning phytopathology and fungal genetics of *Hymenoscyphus fraxineus*, which is considered to be the main cause of ash dieback.
Aim and materials. The paper aims to review results of current research related to the influence of habitat conditions on European ash dieback. The material was based on a review of journal articles and documents from various European countries as well as studies carried out in Poland.
Conclusion. The review indicates that ash dieback is an extremely complex phenomenon, requiring further detailed research to confirm the observations showing diversification of the health state of European ash in various habitat conditions. The moisture content of habitats, soil conditions and species composition in the stand should be considered as particularly important.

Keywords: European ash dieback, habitat conditions, forest site type, soil moisture

INTRODUCTION

The first reports concerning the decline of ash stands came in 1992 from the north-eastern part of Poland, from the Borki and Czerwony Bór Forest Districts, the Regional Directorate of the State Forests in Białystok (Gil et al., 2006). Similar symptoms were also described in the Wielkopolska, Lubelszczyzna and Pomerania regions (Stocki, 2001a). This marked a turning point in the search for the causes of this phenomenon, as it was found that the disease is not contained in small areas and is not connected solely with local conditions. In the next several years after the presentation of the first reports on the disease symptoms the disease appeared in 86.5% forest districts with ash stands (Bielawska, 2006; Zachara et al., 2007). In the years 1995–1996 the same symptoms were reported in northern Lithuania (Juodvalkis and Vasiliauskas, 2002; Vasaitis, 2012). Over 30 thousand hectares were affected by the disease. The area of ash stands dropped from 50 800 ha in 1995 to 36 300 ha in 2011 (Douglas, 2012). In 2002 their decline was observed e.g. in Sweden (Barklund, 2005), in 2003 in Denmark (Thomsen et al., 2007), in the Czech Republic (Jankovský and Holdenrieder, 2009; Vacek et al., 2015), in Belarus (Timmermann et al., 2011), in 2004 in Slovakia (Longauerová et al., 2017), while in 2005 in Austria (Keßler et al., 2012). The rate of disease spread was estimated at 20–30 km/year in all directions (Key Scientific…, 2012), while in Sweden the disease covered the entire range of European ash of over 900 km within as little as 4 years (Current state…, 2012). In 2012 the disease reached Great Britain and Ireland (All-Ireland Chalara…, 2013; Worrel Raport, 2013). What is more,

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disturbing symptoms were also described in narrow-leafed ash (*F. angustifolia* Vahl.; Kirisits et al., 2009; Keča et al., 2017). Those symptoms were different, primarily because of a lesser intensity of the disease, less frequent incidence of necroses and their smaller length on the main shoots (Hauptman et al., 2012). Later observations showed high resistance of manna ash (*F. ornus* L.) (Kirisits and Schwanda, 2015) and ashes introduced in Europe (Drenkhan and Hanso, 2010).

The decline of ash stands was initially associated with a combination of several adverse factors, including e.g. soil salinity, excess nitrogen, late frost, prolonged water stagnation, lowered groundwater tables as well as changes in substrate acidity (Stocki, 2001a; 2001b). When the disease symptoms started to appear increasingly often in stands showing no signs of changes in the abiotic factors, research focused on biotic threats, particularly fungal, viral and bacterial diseases. In 2006 a new species of fungus, *Chalara fraxinea* (Kowalski, 2006), was described as the one found solely on dying tissue of ash trees. Phytopathological analyses identified it as the main causal agent of ash dieback in Europe (Bakys, 2013; Kowalski and Holdenrieder, 2009; Timmermann et al., 2011). Further analyses of the teleomorph of this fungus resulted in its renaming to *Hymenoscyphus fraxineus* (Baral et al., 2014). To date research has not shown a definite origin of this fungus. It is assumed that the dieback of ash stands in Europe is a result of repeated accidental introduction of a pathogenic fungus from Eastern Asia or its mutation (Drenkhan et al., 2014; Timmermann et al., 2011; Vasaitis, 2012).

AIM AND MATERIALS

The aim of this paper is to present current knowledge on habitat conditions promoting dieback of European ash in Europe. The review was based on available source materials, including scientific papers and official documents monitoring the status of European ash in selected European countries. The discussion focuses on the aspects related to habitat conditions, which in the opinion of many authors may have a significant effect on dieback of this species.

HABITAT ASPECTS OF THE DISEASE IN LITERATURE SOURCES

Forest site type and species composition of stands

Studies concerning dieback of European ash have focused on the analysis of the species composition and evaluation of the tree health condition depending on the occupied forest site type. Results of analyses conducted in Austria and Switzerland showed that the highest degree of tree dieback is observed in flood plain habitats with ash as the dominant species in the species composition. A high seedling mortality rate was recorded both in forest nurseries and in natural regeneration (Kirisits et al., 2011). It was found that the intensity of the disease is affected by the correlation of habitat factors directly influencing the biology of the fungus and the production of spores infesting healthy trees. The most important factors include the species composition of stands and the number of ashes growing in the immediate vicinity (Cech, 2008; Keßler et al., 2012). However, a study conducted by Bakys (2013) showed no relationship between tree stocking and disease development. In Czechia and Slovakia symptoms of dieback were found most frequently in young stands in habitats located in river valleys (Douglas, 2012). Similar observations were reported from Great Britain and Ireland. The first outbreak sites in those countries were recorded in forest nurseries and they were associated with nursery material imported directly from continental Europe (Rapid asessment…, 2012; Turczański, 2016). Those reports indicated that the greatest potential threat to European ash is found in flood plain habitats along riparian alluvial zones and in deciduous forests with the dominance of ash in the species composition (All-Ireland Chalara…, 2013; NFI…, 2013; Worrel Raport, 2013).

In Poland the disease has spread throughout the country and has affected ashes of all age classes, while the intensity of symptoms in stands has not been uniform. This diversity depends, among other things, on the age of trees, provenance, regeneration method, form of admixture and forest site type (Dmyterko et al., 2003; Gil et al., 2006; Kowalski and Łukomska, 2005; Kowalski and Czekaj, 2010; Kowalski et al., 2012). According to Kowalski and Czekaj (2010), problems with identification of a definite effect of the

occupied forest site type on the condition of trees may have caused a failure to present definite management indications facilitating breeding of healthy ash stands. Dieback symptoms have been recorded in all habitats occupied by that species. The greatest intensity was reported in moist habitats, in artificially regenerated stands (Kowalski and Łukomska, 2005) and those at the age up to 20 years (Gil et al., 2006; Kowalski et al., 2012). Results of questionnaires collected from almost 90% forest districts showed that ash dies mainly in the habitats optimal for this species, i.e. moist broadleaved forest, riparian forest and ash-alder swamp forest. Moreover, a trend was observed indicating the best health condition of trees in habitats theoretically disadvantageous for ash (mesic broadleaved forest, mesic mixed broadleaved forest) with a mixed species composition and at the absence of considerable soil moisture content (Bielawska, 2006; Gil et al., 2006; Zachara et al., 2007). The above observation is consistent with the results of recent studies conducted in the central Wielkopolska region (Turczański et al., 2020a) and research conducted in Hungary, which showed the lowest percentage of diseased trees recorded in habitats with a mixed species composition (Koltay et al., 2012; Szabó, 2009).

Habitat moisture content and soil conditions

It is reported in literature on the subject that the presence of water in the soil is a major factor affecting the condition of European ash. Lowering and fluctuations in groundwater levels lead to disturbed water relations in trees, which as a consequence results in increased susceptibility to secondary pathogens (Dobrowolska et al., 2011). Studies on the main causal agent for dieback of ash stands, i.e. a fungus *H. fraxineus*, show that high moisture content and its fluctuations promote development of the pathogen and increase the probability of infection (Kirisits et al., 2011; Kowalski et al., 2012; Vacek et al., 2015). Very few studies have investigated this aspect in more detail. Observations conducted in Europe indicate the role of this aspect jointly with the other elements constituting the habitat, providing brief statements based on analyses performed in the course of phytopathological studies. Results suggest that the highest percentage of diseased trees is found in optimal habitats, at an abundance of water in the soil and at high precipitation levels, particularly in the summer (Cech, 2008; Douglas, 2012; Keßler et al., 2012; Kirisits et al., 2011). Studies carried out in Serbia and Slovenia showed that disease intensity is greater in habitats with higher humidity, lower temperatures and no direct access of sunlight. Moreover, some authors reported that in the future the warmer and drier continental climate may lead to a reduction of this disease in the Balkans (Hauptman et al., 2012; Keča et al., 2017; Ogris et al., 2009). In Ukraine significant differences were recorded in dieback of European ash in various habitats. Weather conditions, flooding and high humidity were identified as factors promoting increased intensity of the disease and infection spread (Davydenko and Meshkova, 2017). The negative effect of moisture content on the fungal infection was recorded first of all in cyclically flooded sites, with high groundwater levels (Vacek et al., 2015). In Germany the greatest intensity of dieback symptoms was reported in habitats with high soil moisture contents, at the simultaneous presence of *Armillaria* fungi and *H. fraxineus* (Kirisits et al., 2011). It was found that the development of fungal apothecia may be limited by very dry environmental conditions (Holdenrieder, 2012). This finding is confirmed by some studies conducted in various parts of the European continent. In stands growing in Finland it was shown that under dry conditions the fungus spread is much slower, as in order to sporulate this species requires at least two years with high moisture levels (Douglas, 2012). In Hungary more frequent cases of infection were recorded in areas exposed to frost and with high soil moisture contents. The lowest percentage of diseased trees was observed in dry habitats (Koltay et al., 2012; Szabó, 2009). Similar results were reported from Latvia. The lowest percentage of dieback in regeneration stands was recorded in habitats with dry and mineral soils – over 76% healthy trees, while on moist soils this percentage did not exceed 54% (Pušpure et al., 2017; Vasaitis, 2012).

Results of analyses conducted in Poland are consistent. Ash dies mainly in moist and flood plain habitats (Dmyterko et al., 2005; Zachara et al., 2007). The highest percentages of dying and damaged trees were recorded in sites exposed to cyclical fluctuations of groundwater levels – in drained ash-alder swamp forests and flood plain forests (Turczański et al., 2020a).

It is one of the factors resulting in increased susceptibility of trees to secondary pathogens and as a consequence leading to increased dieback rates (Schütt, 1981). What is more, analyses of edaphic conditions indicate the highest rate of ash dieback in habitats, where the organic matter content exceeds 7.5%, while the soil pH of the humus horizon exceeds 7.0 (Turczański et al., 2020b).

CONCLUDING REMARKS

The presented review shows that ash dieback is an extremely complex phenomenon, requiring further thorough studies in order to confirm diversification of the health status of ash trees growing under various habitat conditions. The need for further research on the subject is confirmed by observations recorded in Poland and worldwide, indicating diversification of the health status of trees in some habitats. Certain studies refer to attempts at correlating disease intensity with natural conditions; however, the presented data are too general and refer to the determination or simply presentation of forest site type, species composition and admixture types based on forest habitat surveys of individual forest districts. Nevertheless, even in terms of solely forest site types this indicate the complexity of this disease and it highlights the need to broaden our knowledge in this respect to provide insight into dieback of ash stands. Within one forest site type we may distinguish various soil types and subtypes, moisture content variants, types and levels of water contents in the habitat, soil horizon reaction, soil grain size composition or mineral contents. Additionally, in view of the complexity and variability of habitat structure in sites occupied by European ash significant differences may appear even within a single compartment. In many cases ash is an admixture or accounts for a small percentage of trees within larger compartments ascribed a specific forest site type, soil type and subtype or moisture content variant based on the whole subcompartment, compartment or – in the case of soils – several compartments. These characteristics may vary greatly, constituting microhabitats directly affecting the condition of the stand and forest floor vegetation cover.

Summing up it needs to be stated that the habitat, particularly the species composition of the stand, moisture content and soil conditions, may be a major aspect affecting the rate of European ash dieback. The above-mentioned elements seem to be markedly correlated with the results of analyses for biology of the fungus *H. fraxineus* as well as observations of disease symptoms, which particular intensity is found under moist conditions and in habitats optimal for ash. This review also indicates that habitat moisture content and the related soil conditions may be particularly significant, as they may be factors limiting or promoting dieback of ash stands. A considerable effect on the presence of European ash in the forest structure may also be related to a decrease in precipitation totals, particularly in the early spring, and the lowering of groundwater levels. Adverse moisture content conditions may predispose some ash trees growing in moist habitats to accelerated dieback. In such a situation the fungal disease in combination with climate change may have a negative effect on the presence of this species in the flora of Polish forests. On the other hand, ashes currently growing in mesic habitats, characterised by the absence of marked fluctuations in soil moisture content at the rhizosphere, with the groundwater level below 1.8 m, may be exposed to much milder changes. As a consequence, ash trees growing in less advantageous habitats may retain a good health condition. Within the next decade or two the health status of ash trees and their regeneration needs to be closely monitored also in mesic forest sites and even in mesic mixed broadleaved forests, in which microhabitat conditions advantageous for growth of European ash may consequently develop.

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SIEDLISKOWE UWARUNKOWANIA PROCESU ZAMIERANIA DRZEWOSTANÓW JESIONOWYCH W EUROPIE

ABSTRAKT

Wstęp. Proces zamierania jesionu wyniosłego (*Fraxinus excelsior* L.) zaobserwowano po raz pierwszy w 1992 roku w północno-wschodniej Polsce. Do 2012 roku choroba rozprzestrzeniła się w całej Europie. Wśród prac poszukujących przyczyn wyjaśnienia zjawiska dominują dwa trendy. Pierwszy dotyczy ekologii gatunku i warunków siedliskowych, drugi – badań z fitopatologii i genetyki grzyba *Hymenoscyphus fraxineus*, który jest uznawany za główną przyczynę zamierania gatunku.

Cel i materiały. Celem pracy było ukazanie dotychczasowej wiedzy na temat uwarunkowań siedliskowych procesu zamierania jesionu wyniosłego w Europie. Przegląd wykonano na podstawie publikacji oraz oficjalnych dokumentów monitorujących stan gatunku w wybranych krajach Europy.

Konkluzje. Analiza literatury pozwoliła stwierdzić, iż problem zamierania jesionu jest zjawiskiem niezwykle złożonym, wymagającym dalszych szczegółowych badań w celu potwierdzenia obserwacji wykazujących istnienie dywersyfikacji stanu zdrowotnego jesionów w różnych warunkach siedliskowych. Za szczególnie istotne należy uznać wilgotność siedliska, warunki glebowe oraz skład gatunkowy drzewostanu.

Słowa kluczowe: zamieranie jesionu wyniosłego, warunki siedliskowe, typ siedliskowy lasu, wilgotność gleby