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Lelliottia nimipressuralis (Carter 1945) Brady et al. 2013 as the causative agent of bacterial wetwood disease of common silver fir (*Abies alba* mill.)

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Abstract

In recent decades, in many regions of the planet, there has been a widespread deterioration in the health condition and dieback of dark coniferous forests, caused by the combined action of various stress factors of biotic and abiotic origin. Forests with the participation of species of the genus *Abies* Mill. are particularly prone to degradation and dieback. The aim of the research is to study the symptoms of bacterial wetwood disease of *Abies alba* in the Ivano-Frankivsk region (state enterprise 'Kutske forestry') and to determine the anatomical, morphological and cultural properties of the pathogen. Some of the common symptoms of the disease include cracks and ulcers on the trunks with exfoliated rhytidome and exudate secretion, massive development of epicormic shoots, saturated xylem and phloem, wet rot with a characteristic odour of fermentation and pathological nucleus.

Based on the syntaxonomic analysis of fir forests, an attempt has been made to identify the objective causes that lead to excessive development of phytopathogens and dieback of *Abies alba*. Our research established that the primary cause of dieback of *Abies alba* Mill. forests is a systemic, vascular–parenchymal disease known as bacterial wetwood of fir, which affects all plant tissues at all stages of ontogenesis. We isolated and experimentally confirmed that the causative agent of the disease is a phytopathogenic bacterium *Lelliottia nimipressuralis* (Carter 1945) Brady et al. 2013, which also causes bacterial wetwood in many species of forest woody plants, and also studied its common morphological, physiological and biochemical properties.

Key words

dieback, aetiology, J. Braun-Blanquet method, pathogenesis

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Introduction

The dieback of forests is currently an important point of discussion of the world scientific community (Sano et al. 1995). The prevailing assumption is that the dieback is closely associated with the ongoing climate change (Dale et al. 2001; Lebourgeois et al. 2010; Pinto et al. 2007; Stoyko 2009; Jactel et al. 2012; Yavorovs'kyy 2015; Shvydenko et al. 2018; Zhang et al. 2018), the development of pathogenic organisms of different systematic and functional affiliations (Gvozdyak et al. 2012; Goychuk et al. 2020b), the natural changes in the biotopes (Levanic 1997; Schelhaas et al. 2003; Pinto et al. 2008; Kobal et al. 2015), forest management practices (Kalutsky 2008; Kulbanska 2015; Meshkova et al. 2018) or complex causes (Gašperšić 1967; Manko and Gladkova 2001; Elling et al. 2009).

Abies (Mill.) species, including common silver fir (*Abies alba* Mill.), are known to be particularly susceptible to dieback. As a result of exposure to the combined action of abiotic and biotic factors, inclding parasitic environmental factors in different parts of Europe, Asia, North America and Japan, there is dieback of forest stands with the participation of common silver fir (Manko and Gladkova 2001).

In the Spanish Pyrenees, the dieback is associated with the spread of fungal white rot caused by *Heterobasidion annosum* and *Viscum* L. species (Oliva and Colinas 2010). In Ukraine, polymerase chain reaction (PCR) analysis of total DNA from fir trunk wood identified two genera of phytopathogenic fungi, including *Fusarium* sp. and *Heterobasidion parviporum* Niemelä & Korhonen (Pogribnyy et al. 2018). Polish researchers have also suggested the mycotic aetiology of common silver fir dieback (Sierpinski 1981). The causative agent *Phytophthora citricola* Sawada (synonym of *Phytophthora cactorum* var. Applanata Chester) was isolated from seedlings of common silver fir in forest nurseries in Poland (Orlikowski et al. 2004).

The dieback may also be caused by acid rain, parasites or bacterial pathogens, bark beetle, and so on (Cherpakov 2012; Goychuk et al. 2020c). Deterioration of the health condition of common silver fir stands in Bulgaria is associated with mistletoe infestation (Rosnev and Petkov 1994).

A serious problem of Croatian forestry (since the 19th century) was the mass mortality of common silver fir (so-called 'dieback of silver fir'), which is manifested by mass dieback, loss of vital energy and reduced growth rates of trees. The phenomenon of fir extinction is associated with a number of causes of abiotic and biotic origin (Seletković et al. 2008; Ugarković et al. 2009).

An extensive syntaxonomic research of forest communities involving *Abies alba* Mill. to determine the causes of deterioration and death has been recently conducted in Ukraine (Soroka et al. 2019). The excessive removal of beech tree components from natural fir forests was shown to be the root cause of the massive dieback of *Abies alba* in Ukrainian Carpathians. Improper silvicultural practices changed the ecosystem balance on a massive scale, including soil characteristics, the composition of grasses and mosses, micro and mycobiota, and so on. The changes in mycorrhizal and soil mesofauna, commonly antagonistic to *Abies alba* pathogens, resulted in the overall reduction of fir immunity and resistance to diseases. It has been shown that pure coniferous forests are usually the foci of dieback. It has also been stated that secondary pathogens, such as *Heterobasidion annosum* (Fr.) Bref. (1888), *Armillaria mellea* Vahl., *Climacocystis borealis* (Fr.) Kotl. & Pouzar (1958), bark beetles and a number of microxylotrophs, are not the cause of the disease, but they merely inhabit a free ecological niche in the modified biocenosis (Soroka et al. 2019).

The studies on phytobacteriological aspects and their relation to the dieback of fir forests are scanty. The first information about the 'wetwood disease' of coniferous species dates back to 1934 (Lagerberg 1934), and the first report of bacterial wetwood of deciduous species of the family Ulmaceae dates back to 1945 (Carter 1945). Typical symptoms of bacterial wetwood of some species of the genus *Abies* have now been reported in the USA, Japan and Europe, including *Abies nordmanniana* Spach (Shcherbin-Parfenenko 1963), *Abies sibirica* Ledeb. (Cherpakov 2012), *Abies nephrolepis* Maxim. (Cherpakov 2012), *Abies alba* Mill., *Abies balsamea* (L.) Mill., *Abies concolor* (Gord. Et Glend.) Lindl. ex Hildebr., *Abies grandis* (Dougl. ex D. Don) Lindl., *Abies lasiocarpa* (Hook.) Nutt., *Abies amabilis* (Dougl.) ex Forbes, *Abies procera* Rehd., *Abies magnifica* A. Murr., *Abies magnifica* var. *shastensis* Lemm. (Ward and Pong 1980; Cherpakov, 2012) and *Abies sachalinensis* (Schmidt.) Mast.

In 1963, A.L. Shcherbin-Parfenenko described a bacteriosis called 'bacterial wetwood' caused by the gram-negative bacterium *Erwinia multivora* Scz.-Parf. (Shcherbin-Parfenenko 1963), which was later found in many coniferous tree species by other authors (Rybalko and Gukasyan 1986; Shalovilo et al. 2011; Cherpakov 2012). According to researchers, *Erwinia multivora* and a very close species of *Erwinina carotovora* Jones can be attributed to one species.

In contrast, *Erwinia multivora* and *Enterobacter nimipressuralis* are different species with different symptoms of development (Cherpakov 2017). In general, the bacteriosis of tree species differs well in symptoms from fungal and viral infections: it is characterised by spring and autumn activity, rapid spread to conductive tissues and sudden focal dieback of trees (Jacobi 2009; Goychuk et al. 2020a, 2021).

The aim of the research is to study the symptoms of bacterial wetwood disease of *Abies alba* in the Ivano-Frankivsk region (state enterprise 'Kutske forestry') and to determine the anatomical and morphological and cultural properties of the pathogen.

Material and methods

The research was carried out in the forests of the state enterprise Kutske forestry and adjacent territories of the Ivano-Frankivsk region. According to geobotanical zoning, the research region is located within the Pokut-Bukovyna spruce–fir–beech and spruce–beech–fir forests, the sub-district of dark coniferous–beech watershed forests, the district of beech forests of the Ukrainian Carpathians (Golubec 2003; Plikhtyak 2019). According to forest zoning, the objects of research were within the forest region of the Outer Carpathians with beech and dark coniferous–beech forests, mountain Carpathian district, forestry region of the Ukrainian Carpathians (Hensiruk 1964).

Geobotanical and forestry descriptions of vegetation and flora inventory, sampling of wood, forest floor, bark, cones and seeds, mycothalluses of pathogenic and mycorrhizal macromycetes for laboratory studies were performed. In the process of research, 17 model trees of *Abies alba* from II (weakened) and III (very weakened) categories of condition were cut down. One hundred and twenty samples were taken for microbiological research; 39 bacterial isolates were isolated. Moist spruce–fir–beech forests were the predominant types of forest conditions within the sample plots.

The phytocenotic features of groups and macroscopic features of individual fir plants, which could pre-diagnose the pathogen without complex laboratory tests, were outlined based on the ecological–floristic classification of vegetation and the method of J. Braun-Blanquet (1964).

For bacteriological analysis, common silver fir wood samples with typical signs of bacterial wetwood disease were used. In particular, the material of the affected wood (on the border with externally healthy tissue) was selected for bacteriological analysis. Bacteriological analysis was performed by homogenising the plant material, followed by a culture test in Petri dishes on agar nutrient media and growing under thermostat conditions at 28ºC for 4–5 days. In the process of conducting experimental studies (for the purpose of a detailed analysis of the characteristics of bacteria), microbiological inoculation was carried out in test tubes on agar media. Bacteria were Gram stained and tested for oxidase and protopectinase. Oxidase-negative isolated bacteria were investigated for their identification; their properties were studied and compared with the collection strain *Erwinia nimipressuralis* 8791 and the properties of bacteria listed in the Identifier of Bacteria (Brenner et al. 2005). Morphological, cultural and biochemical properties of bacterial isolates were determined according to generally accepted methods (Klement et al. 1990; Patyka et al. 2017) and using the API 20E test system and the test system NEFERMtest24 MikroLaTEST®, ErbaLachema.

The pathogenic properties of the isolates were tested *in vivo* and *in vitro* by artificially infecting the vegetative organs (including shoots) of common silver fir, as well as test and indicator plants, with a bacterial suspension with a titer of 108–109 cells/ml cells × ml^{-1}. Also, according to Koch's postulates, the bacterium was reisolated by artificial infection and compared with the original strain.

Latin names of higher plant species are given by The Plant List (http://www.theplantlist.org), of mycobiota by Index Fungorum (http://www.indexfungorum.org) and of microbiota by List of Prokaryotic names with Standing in Nomenclature (http://www.bacterio.cict.fr/e/erwinia.html). The degree of tree damage was determined by categories (Sanitary rules in the forests of Ukraine 2016).

Results

Massive dieback of *Abies alba* covers large areas and all age categories of forests. The identification of the causes of dieback was based on several groups of traits. The first evidence of the development of a bacterial infection in forests with the participation of common silver fir was obtained in 2016. During reconnaissance surveys of stands with the participation of fir in the Pestinskoye forest division in January 2016, from 12% to 20% of dead trees were identified. In March, this number varied within 30–50%, and by the end of summer, up to 60–70% of *Abies alba* of older age was found. So, the dieback of the trees manifested itself sharply and in a short period of time after the dry summer of 2015, which was the first evidence of the development of a bacterial infection. It was also found that forests with the participation of *Abies alba* are formed mainly on brown soils, the genesis of which is associated with the predominance of atmospheric precipitation over evaporation. Such soils are characterised by deep seasonal moisture and short-term seasonal freezing, which also played a role in dry 2015. Phytosociological studies have shown that the highest degree of infection of *Abies alba* by bacteriosis and secondary mycopathogens is inherent in forests with a modified species composition. The highest percentage of infected fir trees was found in the forests of the association *Dentario glandulosae-Fagenion* Oberd. et Müller 1984, of which beech was selected by selective felling. Fir, which grows in natural cenoses of the *Abieti-Piceetum (montanum)* Szaf., Pawł. et Kulcz. 1923 em. J. Mat. 1978, is practically unaffected (Soroka et al. 2019).

The next visual examination of the affected fir stands revealed the second group of evidence – macroscopic signs of bacterial wetwood disease, which was confirmed by laboratory studies. The symptomatology of bacterial wetwood disease in fir is similar to its manifestation at other woody plants (Cherpakov 2012, 2017; Goychuk et al. 2020b; Kulbanska et al. 2021). These signs include the following morphological and anatomical signs and structural modifications of the affected *Abies alba* trees:

– dieback develops from the upper part of the crown, which may indicate the spread of the inoculum, including wind;
– cracks and ulcers form on the trunks with exfoliated rhytidome, abundant protrusions of exudate appear, the primary bark and phloem are exposed, and in 2 years, the wound meristem appears (Fig. 1A, 1B);
– in the middle of hot summer, the bases of the trunks remain wet, which indicates a blockage of the xylem flow in the trunk (Fig. 1C);
– trees have a characteristic 'hedgehog appearance' due to the massive development of epicormic shoots that die during several vegetative periods (Fig. 1D);
– in the later stages of the disease, secondary pathogens – *Heterobasidion annosum* Fr. Bref. (1888), *Phellinus hartigii* (Allesch. & Schnabl) Pat. 1903, *Armillaria mellea* (Vahl.) P. Kumm. 1871, *Climacocystis borealis* (Fr.) Kotl. & Pouzar, 1958 and xylophagous insects – appear (Fig. 1D2);
– on the cross-section of the trunks, noticeable changes in anatomical structures appear: watery xylem and phloem, areas of wet rot with a characteristic odour of fermentation, pathological nucleus;
– the wood of the affected trees is very heavy and practically impossible to process due to tracheal obstruction and very high humidity.

It is known that a whole complex of microorganisms from the genera *Clostridium, Erwinia, Edwardsiella, Klebsiella, Lactobacillus, Xanthomonas, Agrobacterium, Acinetobacter, Bacillus* and *Pseudomonas* (Shink et al. 1981) are isolated from the affected wetwood. However, only *Erwinia multivora* and *Erwinia carotovora* cause tissue maceration, which gives a symptomatic picture of bacterial wetwood disease (Cherpakov 2015).

For bacteriological analysis, common silver fir wood samples with typical signs of bacterial wetwood disease were used (Fig. 2).

Bacteria that formed grey, translucent colonies with a slightly wavy edge were isolated from the affected tissues of common silver fir and used in further experiments (Fig. 3).

The selected colonies of bacteria were similar to the colonies of the collection strain of the causative agent of bacterial wetwood disease *Erwinia nimipressuralis* 8491 (Fig. 4).

In the course of the research, it was found that common silver fir isolates, as well as the collection strain

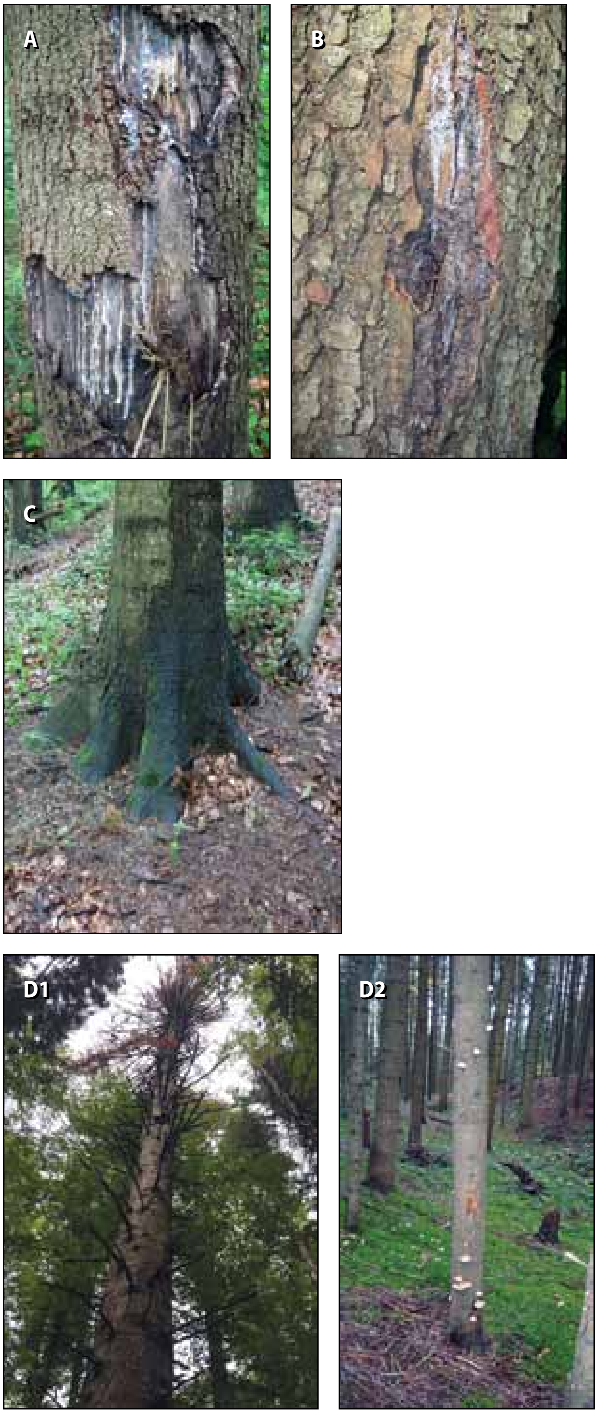

Figure 1. Macro-signs of bacterial wetwood disease in *Abies alba*:A – cracks and exudate on rhytidome; B – ulcer formed with exposed secondary phloem and wound meristem (callus); C – wet base of the trunk; D1 – dieback of epicormic shoots; D2 – settlement of secondary pathogens

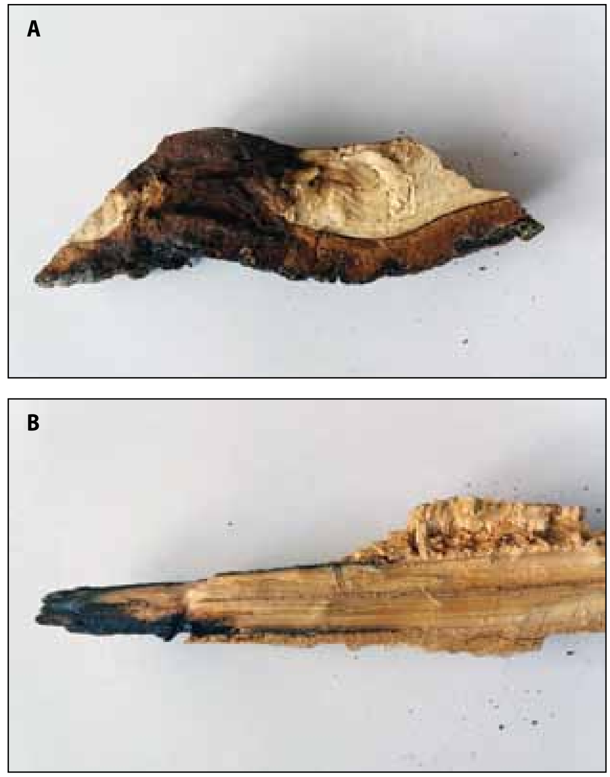

Figure 2. Wet ulcer on the trunk, under the bark of which dark brown affected areas of wood were found against the background of healthy light-coloured wood – A and affected (as if burned) vessels of the sapwood part of the knot – B

Erwinia nimipressuralis 8791, were gram-negative motile rods (Fig. 5).

The studied bacteria were facultative anaerobes, using glucose in both aerobic and anaerobic conditions. All studied bacterial isolates did not form gelatinase and pectinase (not able to cause a rot of potato pieces).

Characteristics of bacteria from type a lesion (Fig. 2): Bacteria were Gram stained and tested for oxidase. Four isolates from type 1 lesion (grey zone) were oxidase negative (Tab. 1).

Studies of the biological properties of the isolated bacterial samples were performed using two test systems – NEFERMtest24 MikroLaTEST (Figs 4 and 5, Tab. 1) and ARI 20 E test system (Fig. 6, Fig.7, Tab. 2) – in order to determine more characteristics of bacteria required for their identification.

Vials 1, 4, 7 – control, growth of bacteria in aerobic conditions; vials 2, 3, 5, 8 – growth of bacteria under a layer of oil (anaerobic conditions)

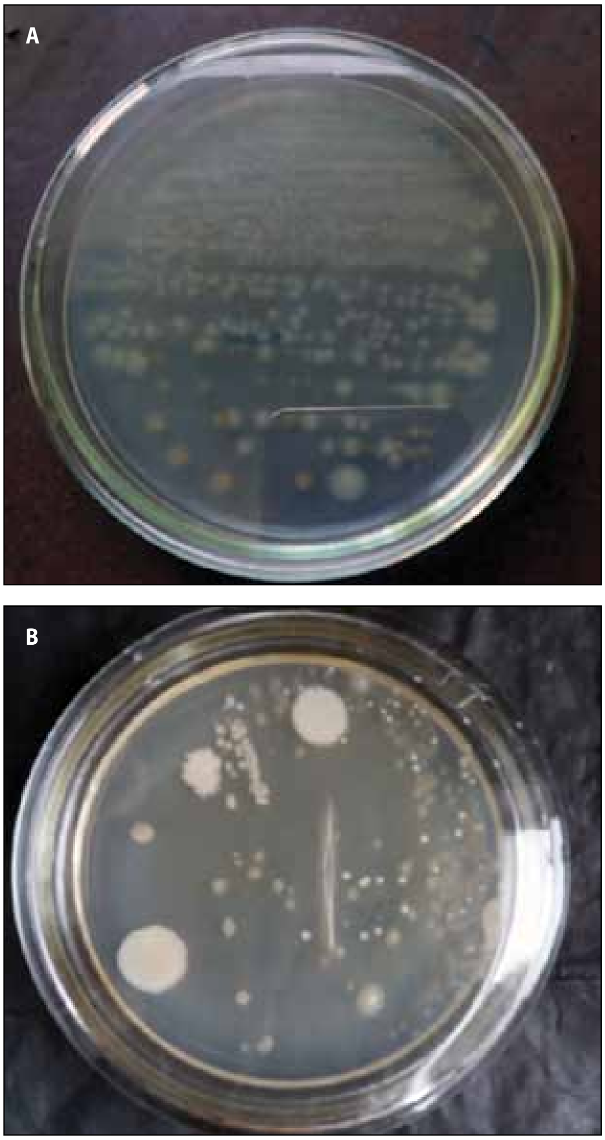

Figure 3. Bacterial colonies on potato agar isolated from common silver fir

It was found that the isolated bacteria do not use lactose and glucose (anaerobically), like bacteria of the genus *Pseudomonas*. But the isolated bacteria are oxidase positive and cannot be phytopathogenic (Gvozdyak et al. 2012). These bacteria reduce nitrates and give the Voges–Proskauer reaction, similar to bacteria of the genus *Pectobacterium (Erwinia),* but according to the set of studied characteristics, they cannot be attributed to *Pectobacterium (Erwinia)* because they do not use glucose anaerobically.

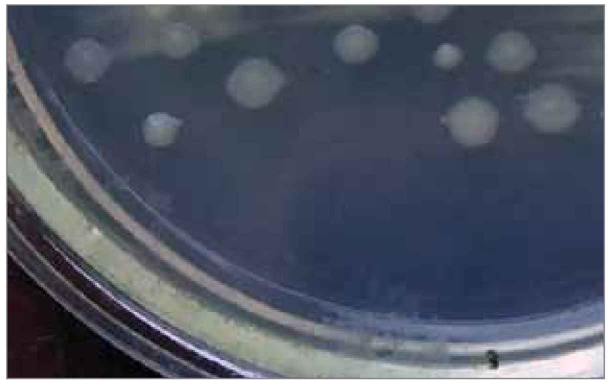

Figure 4. Colonies of the collection strain *Erwinia nimipressuralis* 8791 on potato agar

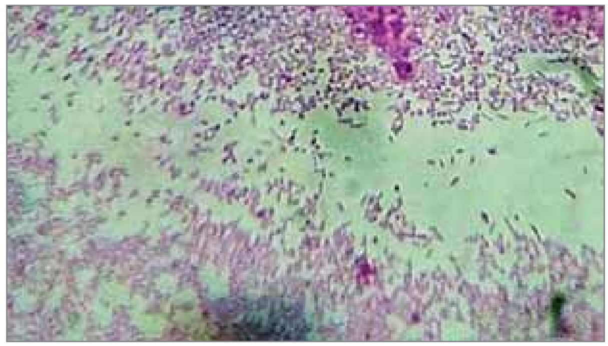

Figure 5. Cells of the causative agent of bacterial wetwood disease of common silver fir under a light microscope

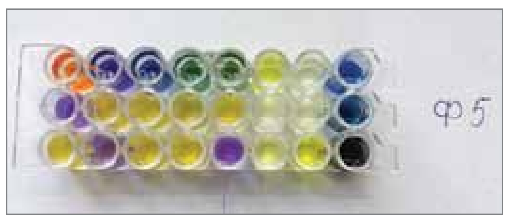

Figure 6. Characteristics of F5 isolate which were determined by using the NEFERMtest24 MikroLaTE test system

Figure 7. Growth of bacterial isolates on glucose medium (anaerobic) using the NEFERMtest24 MikroLaTEST®, ErbaLachema test system

Table 1. Physiological and biochemical properties of isolates fromwooden samples of fir (affection of type a) by using the TNEFERMtest24 MikroLaTEST®, ErbaLachema test system

Symbol	Test	Isolates from fir (4)
OXI	Oxidase	+
URE	Urease	+
ARG	Arginine	+
ORN	Ornithine	+
LYS	Lysine	–
AAM	Acetamide	+
βGL	β-Glucosidase	+
NAG	N-acetyl-β-D-glucosamididase	–
SCI	Simpson citrate	+
LAC	Lactose	–
MAN	Mannitol	+
TRE	Trehalose	+
XYL	Xylose	+
ARA	Arabinose	+
αGA	α-Galactosidase	–
βGA	β-Galactosidase	–
MAL	Malonate	+
GAL	Galactose	+
MLT	Maltose	–
CEL	Cellobiose	+
SUC	Saccharose	+
INO	Inositol	–
γGT	γ-Glutamyl transferase	+
PHS	Phosphatase	+
ESL	Esculin	+
	Glucose (anaerobic)	–

Thus, bacteria isolated from the internal tissues of fir are not pathogens of bacterial wetwood, but are saprotrophic bacteria.

Characteristics of isolates from type b lesions (Fig. 2)

Identification of two isolates was performed by comparing their characteristics with the collection strain *Erwinia nimipressuralis* 8791 and the properties of bacteria listed in Bergey's manual of systematic bacteriology (Tab. 3, Fig. 8).

Table 2. Physiological and biochemical properties of fir isolates (affection of type a, Fig. 2) (test system API 20 E)

Tests	Bacterial isolates
Yellow pigment	–
Reduction of nitrates	+
Formation of H_2S	–
Formation of indole	–
β-galactosidase	–
Arginine dehydrolase	+
Lysine decarboxylase	+
Ornithine decarboxylase	+
The use of citrate	+
Urease	–
Tryptophan deaminase	+
Voges–Proskauer reaction	+
Gelatinase	+
The use of glucose (anaerobic)	–
Mannitol, inositol, sorbitol, rhamnose, saccharose	–
Melibiose, amygdalin, arabinose	–

Table 3. Morphological and biochemical properties of isolates from fir

Tests	Bacterial isolates	*Erwinia nimipressuralis* 8791
1	2	3
Gram's staining	–	–
Yellow pigment	–	–
Oxidase	–	–
Reduction of nitrates	+	+
Formation of H_2S	–	–
Formation of indole	–	–
β-Galactosidase	+	+
Arginine dehydrolase	–	–
Lysine decarboxylase	–	–
Ornithine decarboxylase	+	+
The use of citrate	+	+
Urease	–	–
Tryptophan deaminase	+	+
Voges–Proskauer reaction	+	+
Gelatinase	–	–

1	2	3
Pectinase activity	–	–
The use of: Glucose (anaerobic)	+	+
Mannitol	+	+
Inositol	–	–
Sorbitol	–	–
Rhamnose	+	+
Melibiose	+	+
Amygdalin	+	+
Arabinose	+	+

Note: + presence of properties, – absence of properties, n/d – no data.

Figure 8. Characteristics of isolate 11 using API 20E test system

The bacteria do not use inositol and sorbitol and do not form indole and hydrogen sulphide (H_2S), but are able to reduce nitrates. They lack arginine dehydrolase and lysine decarboxylase, but β-galactosidase and ornithine decarboxylase are present

Discussion

According to the set of studied characteristics, bacterial isolates isolated from common silver fir are similar to the collection strain *Erwinia nimipressuralis* 8791 and the properties listed in Bergey's manual of systematic bacteriology for *Erwinia nimipressuralis*. According to the literature and own research, the causative agent of bacterial wetwood disease of coniferous trees is the bacterium *Erwinia nimipressuralis* (Carter 1945) Brenner et al. 1988, which is proposed to be referred to the newly created genus as *Lelliottia nimipressuralis* (Carter 1945) Brady et al. 2013 (Brady et al. 2013).

Therefore, isolates of bacteria from the affected samples of common silver fir, identified based on morphological, physiological and biochemical properties as *Lelliottia nimipressuralis* (Carter 1945) Brady et al. 2013 (Brady et al. 2013), obsolete name – *Enterobacter nimipressuralis* (Carter 1945) Brenner et al. 1988 (Cherpakov 2017; Alizadeh 2017; Khodaygan et al. 2011; Liu and Tang 2016), are the causative agent of bacterial wetwood disease.

A number of assumptions have been made about the causes of this phenomenon, including climate change and hydrothermal stress, invasive infectious agents and pests, but currently, each of the theories needs scientific confirmation (Gvozdyak and Yakovleva 1979; Patyka and Pasichnik 2014; Goychuk et al. 2020c).

Conclusions

Based on the studies of white fir stands within the Ukrainian Carpathians, we claim that the disease we have identified is systemic, vascular–parenchymal bacteriosis, known as bacterial wetwood disease of fir, which affects all tissues of plants and generative organs at all stages of ontogenesis.

The common manifestations of bacterial wetwood disease of common silver fir include the formation of separate foci of lesions, characterised by defoliation and death of annual shoots. Other symptoms may include bark cracks and deformation, dark mucous with an odour of butyric acid fermentation, necrotic wet wounds, epicormic shoots on the trunks and so on.

Summarising the obtained results, we can conclude that the most common and harmful component of the pathogenic microflora isolated from the lesion of common silver fir is bacteria, which, according to morphological, physiological and biochemical properties, are identified by us as *Lelliottia nimipressuralis* (obsolete name *Enterobacter nimipressuralis* (Carter 1945) Brenner et al. 1988), the causative agent of bacterial wetwood disease of fir.

In the course of experimental studies during artificial infection with *Lelliottia nimipressuralis* isolate, similar natural symptoms of damage to the organs of *Abies alba* (cracks and ulcers on trunks with exfoliated rhytidoma and pronounced exudative discharge) were revealed, as well as the formation of necrotic wounds on indicator plants, which was confirmed as a result of *in vivo* experiments and *in vitro* conditions. Doing so allows for developing better and more precise treatment plans for countering bacteriosis as part of an integrated forest management strategy.

Other research methods must be involved in the search for the root causes of the disease, particularly, phytocenotic, which allows revealing both the degree of alteration of forest coenosis and the direction of destructive and regenerative processes in it.

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