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ORIGINAL PAPER

Scolytus spp. associated with elms with symptoms of Dutch elm disease in Poland and the reproductive potential of *Scolytus multistriatus* (Marsham, 1802) (Coleoptera, Curculionidae, Scolytinae)

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ABSTRACT

Dutch elm disease is caused by a species of *Ophiostomatales* (*Ascomycota*), namely *Ophiostoma ulmi*, *O. novo-ulmi* and *O. himal-ulmi*. These pathogens are transmitted by elm bark beetles (Coleoptera, Scolytinae: *Scolytus* spp., *Pteleobius* spp., and *Hylurgopinus rufipes*). This disease has devastated the native population of elms in Europe, North America, and New Zealand. Dutch elm disease was first reported in Poland in 1927 and since, it has been the most frequent cause of tree dieback. The process of tree colonization by species from the genus *Scolytus* was observed in selected experimental sites in Northern, Central and Western Poland. A total of four tree colonizing species were found including: *Scolytus scolytus*, *S. multistriatus*, *S. pygmaeus*, and *S. ensifer*. Among them, *S. scolytus* and *S. multistriatus* were reported in the greatest numbers and highest frequency. The reproductive potential was determined for *S. multistriatus*. A very high mortality of the young generation was recorded (86% and 89%), which did not limit the spread of the disease. Preferences for tree colonization and location of feeding grounds were investigated in the case of *S. multistriatus*. No correlation was found between the stem diameter and the number of maternal galleries, whereas a correlation was observed between the stem diameter and the obtained reproduction index [*Ri*]. It was highest for sections of trees with diameters of 10-17 cm.

KEY WORDS

beetles, DED, elms, feeding galleries, reproductive success, *Scolytus*, *Ulmus*

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Introduction

It has been 100 years when the dieback of trees from the genus *Ulmus* was first observed in Holland (Spierenburg, 1921). During that period, the disease which was damaging elms spread throughout Europe, Asia and North America. The disease is caused by *Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier (Brasier, 1991; Mańka, 2005; Łakomy *et al.*, 2016; Jüriso *et al.*, 2019) as well as *Ophiostoma himal-ulmi* Brasier & M.D. Mehrotra (Brasier and Mehrotra, 1995) whose vectors are insects from the genus *Scolytus*. These beetles contribute to the spread of Dutch elm disease (DED) by infecting successive trees during juvenile feeding. Vectors of DED primarily include five species of the genus *Scolytus*, *i.e.*, *Scolytus scolytus* (Fabr.), *S. multistriatus* (Marsh.), *S. schevyrewi* Semenov, *S. kirschi* Skalitzky and *S. laevis* Chapuis (Webber, 1990; Hansen and Somme, 1994; Six *et al.*, 2005; Solheim *et al.*, 2011; Jacobi *et al.*, 2013; Jankowiak *et al.*, 2019). A frequently identified vector is also *S. ensifer* (Eichh.) (Marković *et al.*, 2011) as well as other elm bark beetles that transmit the disease. The vector of *Ophiostoma novo-ulmi* is also *Pteleobius vittatus* (F.), and sporadically *Hylesinus crenatus* (F.) on *Fraxinus excelsior* (L.) and *S. intricatus* (Ratz.) on *Q. robur* L. (Jankowiak *et al.*, 2019). Recently, Jürisoo *et al.* (2021) showed that *Xyleborinus saxesenii* Ratz. and *Xyleborus dispar* (F.) are also vectors of *O. novo-ulmi*. In North America, one of the main vectors of elm disease is *Hylurgopinus rufipes* (Eichh.) (Pomerleau, 1947; Strobel and Lanier, 1981). Phoretic mites accompanying *Scolytus* beetles may also be vectors of the disease (Moser *et al.*, 2010). Nevertheless, the greatest role in disease transmission is ascribed to *S. scolytus* (Anderbrant and Schlyter, 1987). This species may have also been the most frequent vector of the disease in the Holocene leading to a marked decline in the elm population (approx. 5000 years) (Girling and Greigb,1985; Clark and Edwards, 2004).

Ophiostomatales are also commonly associated with *Scolytus* that breed on non-elm tree species (Kirschner, 1998; Kirisits, 2004). For example, recently Jankowiak *et al.* (2019) documented that 13 taxa belonging to *Ophiostomatales* were associated with *S. intricatus* on oaks *Q. robur* in Poland. Among them were *Ophiostoma quercus* (Georgev.) Nannf. and one unknown *Sporothrix* species named *Sporothrix* sp. 9, as the main fungi associated of this beetle species. *S. ratzeburgi* Jans. is considered to be the primary vector for *Ophiostoma karelicum* Linnak., Z.W. de Beer & M.J. Wingf. found in birch *Betula pendula* Roth in Finland, Norway, Russia (Linnakoski *et al.*, 2008, 2009), and Poland (Jankowiak *et al.*, 2019). In addition, *Graphilbum fragrans* (Math.-Käärik) Z.W. de Beer, Seifert & M.J. Wingf., *Leptographium betulae* R. Jankowiak, B. Strzałka & Linnak., *O. quercus*, and *Sporothrix fusiformis* (Aghayeva & M.J. Wingf.) Z.W. de Beer, T.A. Duong & M.J. Wingf. were found to be associated with this beetle species in Poland.

It is well known that phloem- and wood-dwelling beetles are also commonly associated with various species of ascomycetes of the genus *Geosmithia* (*Hypocreales*) (Kolařík *et al.*, 2004). In Poland, *Geosmithia flava* M. Kolařík, Kubátová & Pažoutová, *G. ulmacea* Pepori, M. Kolařík, Bettini, Vettraino & Santini, and *Geosmithia* sp. 5 are commonly found in association with *P. vittatus*, *S. scolytus*, and *S. multistriatus* (Strzałka *et al.*, 2021).

The most important role in the transmission of this fungus and thus the spread of the Dutch elm disease is played by two species which are the larger elm bark beetle *S. scolytus* and the smaller European elm bark beetle *S. multistriatus* (Webber, 1990; Martín *et al.*, 2004; Santini and Faccoli, 2014, Jankowiak *et al.*, 2019). For this reason, it is essential to determine the reproductive potential of these insects, since the numbers of these species determines the speed of disease spread.

In Poland, the spread of DED has been observed since the late 1920s (Mańka, 2005). Similarly, as throughout Europe, the disease is caused by two fungal species from the genus *Ophiostoma* (*O. ulmi* and *O. novo-ulmi*) (Guździoł *et al.*, 2004; Łakomy *et al.*, 2016). This disease is of considerable importance in forests as well as a major factor affecting tree health in urban, park, and in-field plantings. In Southern Poland, a positive effect of DED was shown to be an increase in dead wood resources as reproduction sites of Rosalia longicorn *Rosalia alpina* (L.) and a threatened beetle species from the family Cerambycidae (Bartnik *et al.*, 2015).

This study aimed to show which species from the genus *Scolytus* are found most frequently on dying elms with symptoms of DED and to determine the reproductive potential of one of the most frequently associated species, *S. multistriatus*.

Materials and methods

Observations were conducted at ten locations situated in Northern, Western and Central Poland within dense forest complexes and on trees in parks and along roadside avenues (Fig. 1, Table 1).

The bark beetles colonizing elms at each site were identified based on observed feeding galleries and insects caught in window (barrier) traps which did not employ pheromones. Triangular flight interception traps with an area of 3,800 cm^2 were hung on trees that had symptoms of DED. Ethylene glycol was used as a preservative, and traps were checked every three weeks during the growing season.

Additionally, studies were conducted on the reproductive potential of *S. multistriatus*. For this purpose, two locations were selected that differed in terms of the intensity of the disease. One location in Kazimierz was characterized by a highly advanced progression of the disease (which guaranteed maximal colonization of trees by elm bark beetles), while the other location in Kórnik was established where the disease process was starting. The site with the greatest incidence of the disease was selected based on an evaluation of the condition of each *Ulmus* tree at the site (18-30 trees/site) according to the following 5-degree scale:

'0' – healthy tree; no disease symptoms,

'1' – weakened tree; disease symptoms start to appear in the form of drying leaves,

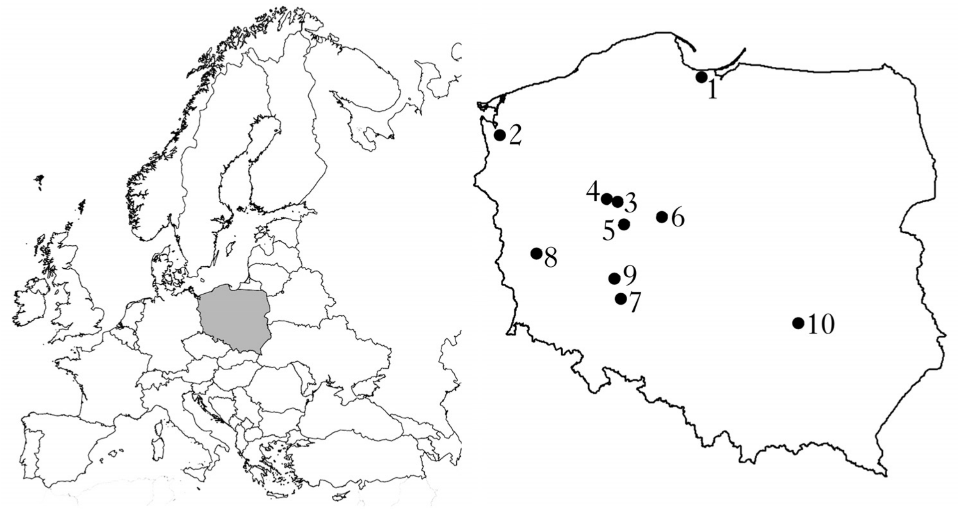

Fig. 1.
Distribution of experimental sites (numbers as in Table 1)

‘2’ – dying tree – stage 1; visible disease symptoms in the form of dying leaves and dying branches,
‘3’ – dying tree – stage 2; visible disease symptoms in the form of dead branches and easily flaking bark,
‘4’ – dead tree.

In a plot of the most advanced disease process (only the location in Kazimierz), studies were conducted to determine the hypothetical maximal fecundity of the main DED vectors. For this purpose, five dead trees were randomly selected and examined after felling.

The degree of their colonization was determined on the basis of the feeding galleries. For this purpose, trees after felling were divided into sections of approx. 1 m in length (Table 3). Diameters were measured at mid-length of the sections and in each of them the number of feeding galleries, the length of maternal galleries and the number of larval galleries were recorded.

Table 1.
Species from the genus *Scolytus* reported in the study

Experimental site no.	Location	GPS guidance	Elm species	Location	*Scolytus* species
1	Jantar	N54°20'1.32" E19°0'19.08"	*Ulmus laevis*	stand	*Scolytus scolytus*
2	Szczecin	N53°26'16.88" E14°33'45.78"	*Ulmus laevis*	roadside avenue	*Scolytus scolytus*
3	Złotniki	N52°28'37.05" E16°48'53.86"	*Ulmus laevis*	roadside avenue	*Scolytus scolytus*, *Scolytus multistriatus*
			Ulmus minor	roadside avenue	*Scolytus multistriatus* *Scolytus pygmaeus*
4	Kiekrz	N52°29'12.88" E16°48'08.91"	*Ulmus laevis* *Ulmus minor*	roadside avenue roadside avenue	*Scolytus scolytus*, *Scolytus multistriatus* *Scolytus multistriatus* *Scolytus ensifer*
5	Kórnik	N52°14'38.99" E17°05'49.03"	*Ulmus minor*	park	*Scolytus multistriatus*
6.1	Kazimierz*	N52°20'40.24" E18°10'50.16"	*Ulmus laevis*	stand	*Scolytus multistriatus*
6.2		N52°20'35.16" E18°10'21.72"	*Ulmus laevis*	stand	*Scolytus multistriatus*
6.3		N52°19'40.44" E18°11'54.59"	*Ulmus laevis*	stand	*Scolytus multistriatus*
6.4		N52°19'51.24" E18°11'53.16"	*Ulmus laevis*	stand	*Scolytus multistriatus*
7	Prusice	N51°23'44.18" E16°59'32.21"	*Ulmus minor*	stand	*Scolytus scolytus*, *Scolytus multistriatus*
8	Ledno	N52°02'19.71" E15°33'01.16"	*Ulmus laevis*	stand	*Scolytus scolytus*, *Scolytus multistriatus*
			Ulmus minor	roadside avenue	*Scolytus ensifer*
9	Żmigród	N51°28'31.73" E16° 55'03.51"	*Ulmus minor*	stand	*Scolytus scolytus*, *Scolytus multistriatus*
10	Starachowice	N51°03'22.32" E21°14'44.88"	*Ulmus laevis*	stand	*Scolytus scolytus*, *Scolytus multistriatus*

* The location (4 stands) was used to determine the hypothetical maximal fecundity of *Scolytus multistriatus*

At the site in Kórnik, the number of outlet holes in cut tree fragments was also recorded in order to determine reproductive success because young beetles exit pupal cells through holes drilled directly above them (Kletečka, 1996).

In order to determine the preferences of *S. multistriatus* to colonize sections with specific diameters, the colonization index was used which specifies the number of feeding galleries per 1 dm^2 of tree surface.

Correlation analysis was applied to assess the dependence between trunk diameter and reproductive success of elm bark beetles expressed in terms of index [*Ri*]. Cluster analysis based on Euclidean distance was used to determine the similarity of the data. The analyses were performed in the Statistica ver.13.1 software (TIBCO, 2017).

Results

Analysis of the species composition of *Scolytus* beetles colonizing elms determined based on the examined feeding galleries and beetles caught in traps showed that two species were most common *S. scolytus* and *S. multistriatus* (Table 1).

Moreover, few incidences of *S. ensifer* and *S. pygmaeus* (Fabr.) were reported – beetles were extracted from the upper parts of trees during juvenile feeding. Both species were found on twigs in the upper parts of young field elms *Ulmus minor* Mill. that were growing along a roadside avenue with some trees that were dead as a result of DED.

Starting at the juvenile feeding site of *S. ensifer* discolorations could be seen indicating infection development. Laboratory tests showed elm infestation by *O. novo-ulmi* in the collected sample (Łakomy, unpublished data).

Colonization preferences. In the Kazimierz Forest Unit (Konin Forest District) the status of elms was evaluated in four stands (experimental sites 6.1-6.4, Table 1) in terms of disease intensity. It was found that in each plot trees showed disease symptoms, however, the percentage of infested trees varied (Fig. 2).

In terms of tree health, the best condition of elms was observed in plot no. 3 in which a vast majority of trees (90%) were healthy with no disease symptoms. The absence of dead and dying trees and a low percentage of weakened trees indicated the initial phase of the disease. Plot no. 4 was classified as the most intensively infested in which the share of healthy trees (stage 0) was

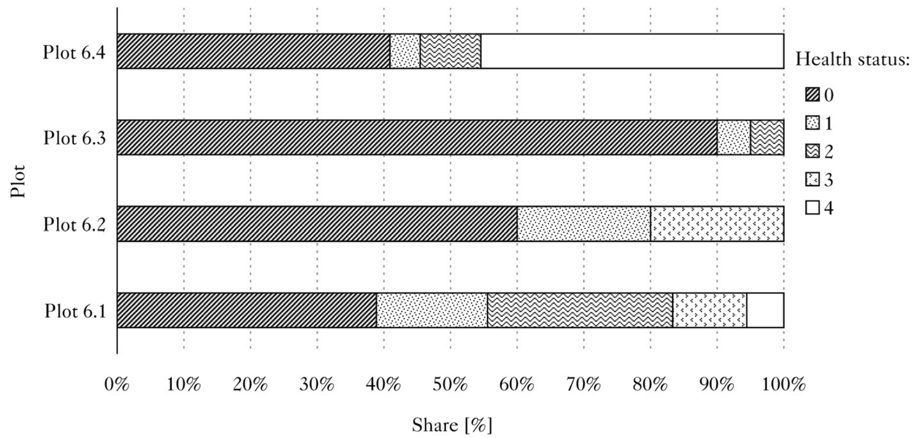

Fig. 2.
Percentage share of trees based on individual degrees of health status in Kazimierz Forest Unit plots (plot no. 6)

greater than in plot no. 1. However, the share of dead trees greater than 45% indicated strong infestation of this plot and an advanced disease process.

Analysis of colonization preferences conducted at the Kazimierz location did not show regularities in log colonization by *Scolytus* beetles. Occasionally the butt-end sections were colonized by the greatest numbers of beetles (trees no. 2 and 3), while in other cases it was the treetop sections (trees no. 1 and 4) (Fig. 3). Considerable variation was observed in the colonization by *S. multistriatus* individual sections of a specific thickness.

The conducted analysis did not confirm a relationship between section diameter and colonization index (r=–0.2680; *p*=0.109). Thus, the diameter of the elm trunk does not affect its colonization by *S. multistriatus*.

Also, the conducted cluster analysis (Fig. 4) showed no regularities in the infestation by *S. multistriatus* of trunk sections with different diameters. For example, one large group with variation below 20% included stem segments 7, 18 and 26 cm in diameter. However, the variation amounts to 100% for sections between of 8 and 9 cm in diameter.

Reproductive potential. Potential maximal fecundity determined based on the number of feeding galleries and the corresponding number of larval galleries in the analyzed trees indicates high variability of the number of beetles which may develop from larvae (Table 2).

It was concluded that the population size of the progeny generation developing in the analyzed trees may range from 784 to over 25 thousand specimens per tree, while there is no marked dependence between the number of feeding galleries and tree trunk length.

The mean number of larval galleries per maternal gallery was within the range of approx. 25-30, and therefore, generally similar. An exception in this case was found in tree no. 4 which was characterized by a stronger colonization rate for which that quotient was on average 65.

Fecundity established based on the number of larval galleries may be treated only as hypothetical. Actual fecundity, due to various factors such as environmental resistance, or depletion of the food resource base, is much lower (Table 3).

The number of maternal and larval galleries were determined for each section of the trunks. The average number of *S. multistriatus* larval galleries per feeding gallery was 33 for tree no. 1 and 52 for tree no. 2 which corresponds to over 11,000 progeny generation specimens obtained from tree no. 1 and approximately 28 thousand larvae developing on tree no. 2.

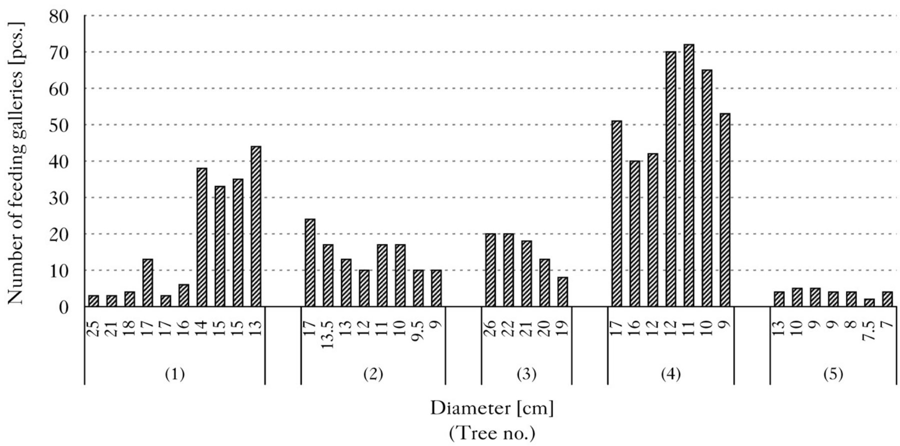

Fig. 3.
Colonization of trees by *Scolytus multistriatus* (Kazimierz; plot no. 6)

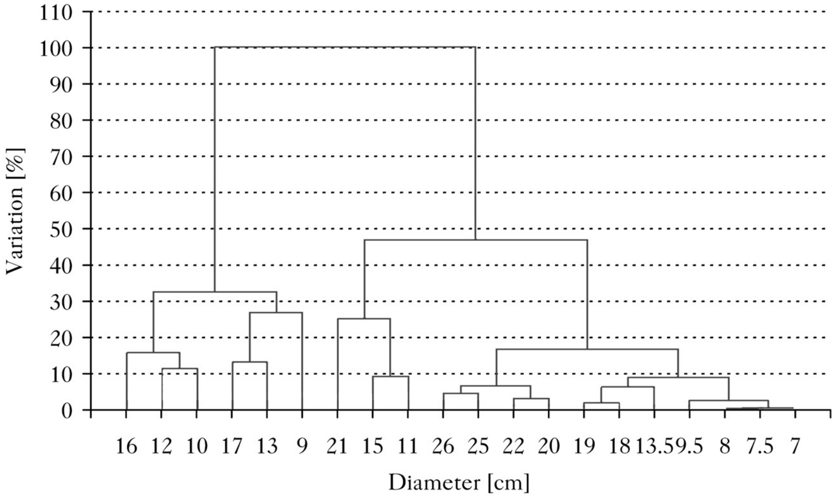

Fig. 4.
Similarity between sections in terms of infestation by *Scolytus multistriatus*

Table 2.
Hypothetical reproductive potential of *Scolytus multistriatus* (Location: Kazimierz)

Tree no.	Trunk length [cm]	Number of feeding galleries	Average diameter of section [cm]	Number of larval galleries	Mean number of larval galleries feeding gallery
1	996	182	17.10	5405	29.70
2	840	118	11.87	3042	25.78
3	465	79	21.60	1952	24.71
4	754	393	12.43	25563	65.05
5	700	28	9.07	784	28.00

Table 3.
Actual reproductive potential of *Scolytus multistriatus* (Location: Kórnik)

Tree no.	Total length (sum of sections) [cm]	Number of feeding galleries	Number of larval galleries per maternal gallery [pcs.]			Number of exit holes	Repro-duction index *Ri*
			mean	minimum	maximum		
1	1501	354	33	17	55	1307	3.69
2	901	549	52	12	82	3970	7.23

The ratio of exit holes to the number of maternal galleries made it possible to establish the reproduction index. The actual recorded reproduction index *Ri* varied greatly and in the case of tree no. 1 amounted to 0.59 up to 17.00 (mean *Ri*=3.69). In the case of tree no. 2, its value ranged from 1.46 up to 27.68 (mean *Ri*=7.23) (Table 3). Thus, the mortality of larvae in trees no. 1 and 2 amounted to 88.8% and 86.1%, respectively.

Overall, a statistically significant negative correlation (r=–0.7809; p=0.0001) was confirmed between the trunk diameter of elm trees and the reproduction index understood as the produced young progeny generation (Fig. 5). This indicates that a decrease in the trunk diameter of elm trees results in the actual reproduction index increasing. In the case of tree no. 1, a marked increase in the reproduction index is evident for six tree-top sections with diameters ranging

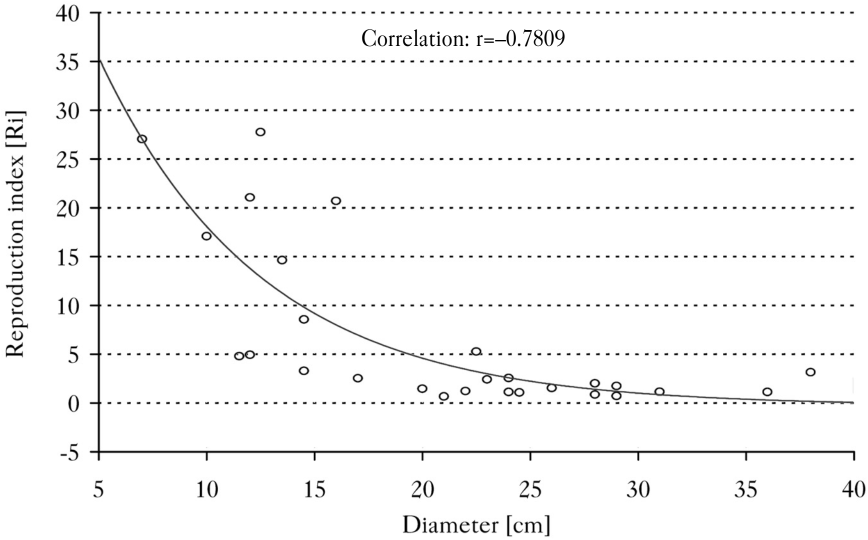

Fig. 5.
The effect of elm trees section diameter on the reproduction index for *Scolytus multistriatus* (Kórnik)

from 10 to 17 cm for which calculated values of *Ri* between 2.45 and 17.00, while for earlier sections (except for the butt-end section) it did not exceed *Ri*<2.00. In the case of tree no. 2, an increase in the values of *Ri* for five tree-top sections (with diameters ∅≤16 cm) was even greater. Apart from the second to last section, *Ri* fell to the range of *Ri* between 20.62 and 27.58, whereas in earlier sections it did not exceed 5.19 and in most cases *Ri* was around 2.

Discussion

Dutch elm disease (DED) is the biggest cause of dieback of trees from the genus *Ulmus* in Europe, Asia and North America. It has grown to the size of a pandemic and sometimes causing considerable losses and mass-scale tree dieback. An example is the dieback of approx. 20 million elms out of approx. 30 million population of these trees in Great Britain (Brasier, 1996; Solheim *et al.*, 2011). It is estimated that, depending on the country, DED has led to the premature dieback of 50-80% trees from the *Ulmus* population (Napierała-Filipiak *et al.*, 2016).

In Poland, this disease was observed for the first time in 1927 in Wrocław (Wollenweber and Stapp, 1928; Mańka *et al.*, 1978). Since then, as in other countries, it has been the primary cause of elm dieback, appearing from time to time with varying intensity. Occasionally, the disease process is very rapid and trees die within one vegetation season. The authors of this study observed such a course of the disease at the Kórnik location. Such a rapid process of tree dieback, lasting as little as one year from the observation of initial disease symptoms, was also observed in Norway (Solheim, 1991; Eriksen, 1993), where it was stated that it is a typical infection caused by *Ophiostoma novo-ulmi* (Solheim *et al.*, 2011).

As we know, the vectors of the disease are insects of the genus *Scolytus* which transfer spores to successive trees. It is assumed that for a successful infection, the required minimum is 1×10^3 spores/1 beetle (Webber and Brasier, 1984; Webber, 1987, 1990; Solheim *et al.*, 2011) and 72 hour contact between infected beetles and wood was sufficient (Basset *et al.*, 1992).

Among *Scolytus* beetles, *S. scolytus* is considered to be the most efficient DED vector due to its large body size and the pupation site, which due to its high moisture content is abundant in large numbers of spores (Webber, 1990). However, the fungus may be effectively transferred to healthy trees also by smaller species from the genus *Scolytus* which carry smaller amounts of spores on their bodies (Faccoli and Battisti, 1997). The island of Gotland (Sweden) may be an example here, as the only known DED vector there is *S. multistriatus* (Menkis *et al*., 2015).

The results of the study analyses stated that the main species from the genus *Scolytus*, which colonized elms, were *S. scolytus* and *S. multistriatus*. This has been confirmed by earlier studies by Michalski (1962) who classified these two species as common *Scolytus* beetles in Western Poland. In relation to the other two *Scolytus* species reported in this study, classified by Michalski (1962), respectively, as the most common in Western Poland *S. pygmaeus* and relatively common *S. ensifer*, it needs to be stressed that these species were reported for tree-top sections of young *Ulmus minor* which were not the main object of the analyses. Thus, they are represented by small numbers of specimens.

However, the presence of *S. pygmaeus* and *S. ensifer* on trees on which no other species from the genus *Scolytus* were found may suggest the potential to transmit disease for these two species as well. This is of great importance in the case of *S. ensifer*. A discovery of this species on thin shoots of trees, on which the disease process was only starting, shows it in a different light. It was assumed, to date, that this species generally attacks significantly weakened trees in which sap circulation is poor and on which young generations of other beetle species from the genus *Scolytus* emerged (Michalski, 1963). Consequently, it was not considered a vector of Dutch elm disease (Michalski, 1963).

In view of the lack of information on the potential transmission of Dutch elm disease by *S. ensifer*, it was assumed that this species, together with *S. pygmaeus*, contributes only to tree-top withering and effectively kill already dying trees (Michalski, 1963). However, this author stressed that the transmission of DED by *S. ensifer* is likely but requires further explanation. The potential confirmation of this fact would mean that the economic importance of this species may be high. Results recorded in this study indicate that *S. ensifer* was most probably a vector of Dutch elm disease which was transmitted to young field elms. Its role in the transfer to large trees is much more difficult to observe, since this species, preferring twigs in tree crowns, is frequently almost impossible to spot. This is in contrast to the relatively large sized and numerous species related to the tree trunk section which are primarily *S. scolytus* and *S. multistriatus*. These two species are considered to be the main vectors of *Ophiostoma novo-ulmi* (Pajares, 1987; Webber, 1990; Martín *et al*., 2004; Santini and Faccoli, 2014, Jankowiak *et al*., 2019). Identification of *S. pygmaeus* in elms infested with DED confirms earlier observations (Faccoli and Battisti, 1997) that this species needs to be classified as a DED vector. In view of its development on twigs, it may be an additional challenge in the control of Dutch elm disease (Faccoli and Battisti, 1997).

Infections via roots are much less frequent than those transmitted by insects from the genus *Scolytus* (Martín *et al*., 2004). It was assumed that damage to tree crowns caused by young beetles during juvenile feeding was the only route of infection in elms growing in isolated locations (Santini and Faccoli, 2014), while the number of beetles, among other things, determines the intensity of spread in the case of *Ophiostoma ulmi* fungi in forests (Marković *et al*., 2011). Thus, actual reproduction of insects from the genus *Scolytus* is directly reflected in the infection potential that determines the spread of the disease. As shown by these analyses, this potential varies greatly and is dependent on many factors. However, even the very high mortality of larvae recorded in the Kórnik location did not prevent rapid tree dieback, and the number of the young-generation beetles posed a real threat to the surrounding elms.

This study showed a lack of correlation between the diameter of round timber and the number of maternal galleries of *S. multistriatus* per 1 dm^2 of circumference area. This may have resulted mainly from the overall tree colonization status and may have been independent of the position of a given section in the trunk. The fact that the top part of tree no. 3 was broken (in the course of tree felling) prevented any definite confirmation of this hypothesis. A similar lack of correlation in the population density (the number of feeding galleries/dm^2 circumference) was previously observed in *S. intricatus* associated with oak (Galko *et al.*, 2012).

The very high mortality of larvae reported in the study for *S. multistriatus* is greater than the level recorded in California (USA), where it amounted to 41-86% (Hajek and Dahlsten, 1985). It even exceeded that listed in Austria (Schroeder, 1974), where it reached 71-85%. The observed mortality (86-89%) most probably resulted from several causes, which at this stage, are very difficult to explain even though factors affecting it have been known for years.

As it was suggested earlier (Beaver, 1967), competition is considered to be a factor that reduces the population density and does not only directly affect mortality of larvae. Further, this leads to qualitative and physiological effects such as the reduction of size in future beetles and probably a decrease in their fecundity (Beaver, 1967, 1974; Lee and Seybold, 2010). However, it is assumed that the dependence between population density and mortality is found in *S. scolytus*, while in *S. multistriatus*, such a direct dependence may not be present (Beaver, 1974). This study confirmed the aforementioned assumption, since a higher reproduction index *Ri* was obtained for tree-top sections of trees with diameters of 10-17 cm, where competition for breeding and feeding resources is greater than in the butt-end sections. Thus, the increasing mortality may not have been associated with the decreasing diameter of the tree sections on which the insects were developing. While such a dependence is known, it concerns branches of diameters below 7 cm (Jones and Lanier, 1977; Hajek and Dahlsten, 1985), while in this study, the control consisted of tree trunks whose sections were a minimum of 7 cm in diameter.

Such a high mortality may not solely be the effect of environmental resistance factors, since their response to the host population density is stable (Truchan, 1970) and does not reach such high values. This may be confirmed by the case of the population from California as parasitoids were responsible for only 2% mortality of *S. multistriatus* larvae (Hajek and Dahlsten, 1985). This indicates that other factors contributed to the recorded high larval mortality while varying within the tree trunk.

Thus, the causes for the varied mortality in the butt-end and tree-top sections may be relatively difficult to explain. The results indicate that sections with diameters of 10-17 cm provided the best conditions for the development of *S. multistriatus*, although competition between larvae in those sections was greater than in the butt-end sections. Nevertheless, other factors may have played an important role as well. It is likely that larvae feeding on such tree assortments were provided with adequate moisture levels (higher than in thinner assortments of less than 7 cm) as well as the favorable temperatures simultaneously which resulted in their more rapid development. In the case of thicker sections (covered with thicker bark), the temperature under the bark may have been lower which resulted in a longer development period and thus, larval stages may have been exposed to the attack of predators and parasitoids for a longer time. However, this assumption still needs to be verified.

Earlier studies concerning the incidence of Dutch elm disease in the area of Poznań indicated greater resistance of Russian elm *Ulmus laevis* Pall. as compared to field elms in the case of DED infestation (Mańka *et al.*, 1978). This was related to an increase in the levels of inherited resistance traits of Russian elm trees remaining in that area which decreased susceptibility to

DED in those trees. However, phytopathological studies (Łakomy *et al*., 2016), as well as the analyses results in this study, did not confirm this assumption. In contrast, dying Russian elms in the Złotniki and Kiekrz locations indicate a recurrent increased intensity of this disease. The repeated activation of DED may have been related to the fact that, at present, the disease is caused by a more infectious fungus *Ophiostoma novo-ulmi* (Łakomy *et al*., 2016). While *Ulmus minor* is the *Ulmus* species most sensitive to DED among all the *Ulmus* species found in Poland (Łakomy *et al*., 2016), the observed dieback process was not dependent on elm species or tree age (Łakomy *et al*., 2016).

Although it is believed that *S. multistriatus* prefers *Ulmus minor* rather than *U. laevis* (Sachetti *et al*., 1990; Piou, 2002), which is least willingly colonized by *Scolytus* species as DED vectors (Pajares *et al*., 2004; Krężel and Filipiak, 2013) probably due to the chemical bark components (Pajares *et al*., 2004), but the recorded results appear not to confirm this. In the course of this study, *S. multistriatus* was more frequently reported on *Ulmus laevis* trees, but this may be due to their more abundant presence in the study area (Napierała-Filipiak *et al*., 2019), rather than the preference of bark beetles. Thus, this may not be an indicator of attractiveness of *Ulmus* species for *S. multistriatus*.

Conclusions

The common occurrence of *S. scolytus* and S. *multistriatus* in Central and Western, as well as Northern Poland, in the locations where elm dieback has been observed, may indicate that these species are the main vectors of disease.

Despite the potentially high reproduction index (the number of larval galleries per feeding gallery), the actual reproduction index amounted to 3.69 and 7.23, which corresponds to 89% and 86% mortality rates of young-generation *S. multistriatus*. Mortality may have been caused by a complex range of factors. Nevertheless, intraspecies competition for breeding and feeding resources among larvae seems to be the least probable explanation. This very high mortality did not protect colonized *Ulmus* trees against dieback within one vegetation season.

No correlation was shown between trunk diameter and the number of maternal galleries, which does not make it possible to indicate tree sections most preferred for colonization by *S. multistriatus*.

A correlation was found between the diameter of the trunk section in elms and the recorded reproduction index. It was highest for the tree sections with diameters of 10-17 cm which indicates that such tree parts are most advantageous for the development of *S. multistriatus*.

Authors' contributions

Idea of research – R.K. P.Ł.; methodology – R.K., M.F., A.N.-F., performed the experiments – R.K., K.N., P.Ł. A.M; data analysis – R.K., A.M., K.N.; performed the statistical analyses, and the visualizations – R.K., T.J., the study of the map – R.K., P.Ł., A.M.; writing-original draft – R.K., T.J., A.N.-F., M.F., P.Ł., A.M.; writing-review – R.K., A.M.; editing – R.K.

Conflicts of interest

The authors declare no conflict of interest regarding the publication of this paper.

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STRESZCZENIE

Ogłodki zasiedlające w Polsce wiązy z objawami holenderskiej choroby wiązów oraz potencjał reprodukcyjny ogłodka wielorzędowego *Scolytus multistriatus* (Marsham, 1802) (Coleoptera, Curculionidae, Scolytinae)

Badania przeprowadzono na stanowiskach zlokalizowanych w północnej, zachodniej i środkowej Polsce (ryc. 1), w miejscach, w których wykazano występowanie grafiozy wiązów. Były to zarówno zwarte kompleksy leśne, jak również drzewa w parkach i przydrożnych alejach (tab. 1). Na każdej z wybranych lokalizacji dokonano identyfikacji korników z rodzaju *Scolytus* zasiedlających drzewa wykazujące objawy holenderskiej choroby wiązów. Skład gatunkowy ogłodków zasiedlających wiązy określono na podstawie występujących żerowisk, znajdowanych chrząszczy oraz odłowów do pułapek barierowych bez stosowania związków wabiących.

Dodatkowo przeprowadzono badania nad potencjałem rozrodczym *S. multistriatus*. W tym celu wybrano 2 stanowiska różniące się nasileniem choroby. Jedno charakteryzowało się występowaniem choroby w bardzo silnym stopniu zaawansowania (co gwarantowało maksymalne obłożenie drzew przez ogłodki), natomiast kolejne wyznaczono w miejscu, gdzie proces chorobowy się rozpoczynał. Wybór powierzchni najsilniej zaatakowanej przez chorobę przeprowadzono w oparciu o ocenę stanu każdego drzewa w drzewostanie według 5-stopniowej skali: „0" (drzewo zdrowe) – brak oznak chorobowych; „1" (drzewo osłabione) – pojawiające się oznaki chorobowe w formie usychających liści; „2" (drzewo zamierające – 1 faza zamierania) – widoczne oznaki chorobowe w postaci zamierających liści i zamarłych gałęzi; „3" (drzewo zamierające – 2 faza) – wyraźne oznaki chorobowe w postaci zamarłych gałęzi oraz łatwo odchodzącej kory; „4" (drzewo martwe) (ryc. 2).

Po ścięciu losowo wybranych martwych drzew określano stan ich zasiedlenia na podstawie występujących żerowisk (ryc. 3). W tym celu ścięte drzewa dzielono na sekcje długości około 1 m, mierzono średnicę w połowie długości sekcji, a następnie na każdej z nich określano liczbę otworów wylotowych i żerowisk, długość chodników macierzystych oraz liczbę chodników larwalnych.

Stwierdzono, że na drzewach z objawami holenderskiej choroby wiązów najczęściej występowały *Scolytus scolytus* i *S. multistriatus* (tab. 1). Na pojedynczych stanowiskach stwierdzono także *S. ensifer* i *S. pygmaeus*, które według literaturowych danych mogą być wektorami choroby.

Wykazano, że w przypadku ogłodka wielorzędowego na 1 chodnik macierzysty przypadało przeciętnie 25-30 chodników larwalnych, co skutkowało możliwością rozwoju na strzale 1 drzewa od około 784 do ponad 25 tys. osobników młodego pokolenia (tab. 2). Mimo potencjalnie wysokiego wskaźnika reprodukcyjnego (liczba chodników larwalnych przypadających na 1 żerowisko) zrealizowana rozrodczość kształtowała się na poziomie 3,69 i 7,26 – co odpowiada 89% i 86% śmiertelności młodego pokolenia *S. multistriatus* (tab. 3).

Nie wykazano zależności między średnicą pnia a liczbą chodników macierzystych (ryc. 4), co nie pozwala wskazać sekcji drzew najbardziej preferowanych do zasiedlenia przez ogłodka wielorzędowego. Stwierdzono natomiast związek między średnicą sekcji pnia wiązu a uzyskanym wskaźnikiem reprodukcji (ryc. 5). Był on najwyższy dla sekcji drzew o średnicy w zakresie 10-17 cm, co wskazuje, że takie części drzewa są najkorzystniejsze dla rozwoju *S. multistriatus*.