

## ORIGINAL PAPER

# The contribution of elms in non-alluvial forest communities depends on the distance from a river

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## ABSTRACT

In this paper, the occurrence of three European elm species was analyzed depending on the location with respect to major or medium-sized watercourses. A river is understood here in a broader sense together with the area of the valley it creates and the riparian communities located in this area. Previous research pointed out that a significant part of the *Ulmus laevis* total numbers occur outside riparian communities in oak-hornbeam forest communities. The aim of the research presented here was to check whether the distribution of oak-hornbeam forest elm localities is shaped only by the distribution of specific habitats or is it perhaps also related to the distance from the river valley.

The study covered 273 randomly selected tree stands in Lower Silesian forests. This is a topographically diverse region with an area of nearly 20,000 km<sup>2</sup> located in the center of Europe and within the geographical ranges of three European elm species. The paper presents patterns of distribution of individual species and the probabilities of their occurrence at various distances from watercourses. *U. laevis*, the prevalent species in the area in question, and *Ulmus minor*, the least frequent one, constitute a statistically homogeneous group of elms that is very closely connected with watercourses. In the case of these two species, more than 1/3 of all localities and over 2/3 of the localities in which elm make up at least 10% of the stand composition are located within 1,000 meters of the watercourse. The connection of *Ulmus glabra* with valleys of major and medium-sized rivers is significantly smaller.

A very significant result of the work presented in this study is the discovery that the contribution of *U. laevis* in the forest site types of 'fresh mixed deciduous forest' (FMDF) and 'fresh deciduous forest' (FDF) which encompass fertile variants of communities of typical oak-hornbeam forests depends on the distance from the nearest medium-sized or big river valley.

## KEY WORDS

ecology, forest composition, plant communities, *Ulmus glabra*, *Ulmus laevis*, *Ulmus minor*

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## Introduction

This paper presents issues related to the distribution of the following three European elm species: the wych (or Scots elm) – *Ulmus glabra* Huds. (UG), the European white elm (also known as the fluttering elm, spreading elm and stately elm) – *Ulmus laevis* Pall. (UL), and the field elm – *Ulmus minor* Mill. (UM). Information on the distribution and abundance of elm species in Polish forests is key for their conservation. Just like Krebs (2014), an analysis of organism distribution (including trees) in relation to various environmental factors may provide new data regarding the ecological properties of the studied plants particularly their habitat requirements. An evaluation was conducted for several years on elm resources in Poland with a view of setting up a base for protecting elms in the country's forest ecosystems. As a result, a significant amount of data was gathered regarding the distribution of elms as well as the size and state of the trees. Nowadays, both in Poland and in Europe, trees of the *Ulmus* genus function as admixture species, and their share in the composition of stands does not exceed one percent and is often even lower. For instance, in Poland it amounts to 0.23% (Napierała-Filipiak *et al.*, 2014).

Recent research suggests that although elms have the highest contribution in alluvial communities, a greater majority of them may grow naturally as admixture in forests other than riparian ones principally occurring in the areas of potential oak-hornbeam forests communities which are dominant in Poland. This applies both to the number of trees and the actual area occupied by the trees in question (Napierała-Filipiak *et al.*, 2014, 2021). As part of this research, the objective was to clarify whether the distribution of elm trees is related to valleys of big rivers (and associated conditions) or does it depend only on the presence of specific habitats.

Elms are 'post-pioneers', which is defined as a species that during succession not only replace pioneer species and clear the way for climax species of stabilised ecosystems but also remain in such final ecosystems as an 'ennobling' admixture by improving the decomposition of forest litter (elms do this very effectively) and the circulation of matter in the ecosystem (Falkengren-Grerup *et al.*, 1998; Falińska, 2004; Polyakova and Billor, 2007; Filipiak *et al.*, 2015).

The absence of elms in local forest environments means not only the loss of 6% of the species composition of Polish forest tree flora, 13% of large tree species (reaching at least 30 m in height) and as much as 43% of large trees from the 'post-pioneer' group but also the loss of a large number of invertebrates, insects and arachnids associated with elms as well as soil-populating fungi, protists and bacteria (Falińska, 2004; Jaworski, 2011; Filipiak *et al.*, 2015). In studies of one of the only three elm species growing in Poland, *U. glabra*, which would be able to cover a small area of the Netherlands, 79 species of insects were found to be closely associated with the tree which suggests its considerable contribution to biological diversity (Heybroek, 2015).

The considerable decrease in the number elms is a result of Dutch elm disease. This is a fungal disease which is spread by beetles. Its creation is likely to have been by humans by crossing two pathogen strains (Brasier, 1991). This disease was one of the factors that led to the premature death of an enormous number of elms in particular old trees as it destroyed over 50% and in some countries over 85% of the tree (Mackenthun, 2013; Łakomy *et al.*, 2016; Martín *et al.*, 2019; Collin *et al.*, 2020). A loss of interest in the cultivation of elms resulted in a noticeable decrease in the number of studies devoted to their ecology as compared to other common trees in Europe climate zone. Present knowledge of tree requirements and the differences between individual species in this respect is also limited (Napierała-Filipiak *et al.*, 2014). Some more important information about the current state of knowledge about elms may be found in our earlier papers (Polyakova and Billor, 2007; Martín *et al.*, 2013; Heybroek, 2015; Santini and Faccoli, 2015; Caudullo and de Rigo, 2016; Napierała-Filipiak *et al.*, 2016, 2019, 2021; Puerto *et al.*, 2017; Chu-

dzińska *et al.*, 2018; Thomas, 2018; Sepúlveda and Johnstone, 2019; Kassahun *et al.*, 2020; Yuan *et al.*, 2020; Camarero *et al.*, 2021). According to the aforementioned sources, the European white elm and the field elm grow on lowlands and not highly elevated highlands, and the wych elm, additionally, in lower mountain locations (Richens, 1983; Diekmann, 1994, 1996; Pirc, 2006; Filipiak and Napierała-Filipiak, 2015; Matuszkiewicz, 2015). Elms in particular prefer peripheral areas of river valleys which are only flooded once every several years as opposed to areas adjacent to the riverbed which are flooded every year. This creates fertile alluvial soil (Diekmann, 1994, 1996; Filipiak and Napierała-Filipiak, 2015; Caudullo, de Rigo, 2016).

Pirc (2006) wrote that 'not a long time ago, elms and linden were among the best known and commonest large trees, with an impact on the entire landscape.' Before the Dutch elm disease pandemic, elms were undoubtedly present in much bigger numbers especially in western Europe (Richens, 1983; Filipiak and Napierała-Filipiak, 2015). Another aspect is that an overwhelming majority of riparian habitats which used to be dominated by elms were taken over by agricultural crops and subsequently partly by cultivated poplars (Jaworski, 2011; Filipiak and Napierała-Filipiak, 2015). The third aspect is that elms are common in forests that have returned to areas previously occupied by glaciers. Palynological studies indicate that over 5,000 years ago *Ulmus* genus constituted no less than 10% of all trees and in many places in Europe the rate exceeded 20% with stands predominated by elms potentially occupying hundreds of hectares. In present day Ireland it is over 25% and sometimes reaching as much as 40% (Caseldine and Fyfe, 2006). The sudden fall in their numbers between 6,000 and 5,000 years ago may have been connected with a possible epidemic similar to the one experienced today along with the development of settlements. Human transformation of riparian forests due to agriculture and burning for pastures increased during that time (Lazarova and Bozilova, 2001; Ralska-Jasiewiczowa *et al.*, 2003; Boratyński, 2006; Caseldine and Fyfe, 2006).

Lower Silesia was chosen as the location for the research as the region encompasses lowland, upland, submontane and mountain areas. The region is characterized by a large number of elms and a similar approach to forest management in the past and at present (Napierała-Filipiak *et al.*, 2014).

The hypotheses that this article will address are the following:

- distribution patterns of individual elm species differ from each other.
- stands with a larger contribution of elm in the forest stand are located, on average, closer to the river valley than localities with a smaller number of elm trees.
- the number of elm localities, regardless of the forest site type in which they grow, depends on the distance from the valley of a large or medium river.

## Materials and methods

**STUDY AREA.** The region covered by the study (Fig. 1) has an area of 19,946.74 km<sup>2</sup> (6.4% of Poland's total area) and is managed by the Regional Directorate of State Forests in Wrocław. Generally, the area corresponds to historical and present-day Lower Silesia (Dolnośląskie province/voivodeship) (FDB, 2020). The area selected for the study covers a section of the North European Plain (macroregions: Silesian-Lusatian Lowlands, South Great Poland Lowlands, Milicko-Głogowski Depression, Trzebnicki Wall and the Silesian Lowlands) as well as the Bohemian Massif (macroregions: Sudeten Foreland, Sudeten Foothills, Western Sudetes, Central Sudetes and Eastern Sudetes) (Kondracki, 2009; Zielony and Kliczkowska, 2010). The mean annual temperature is 7.7 C and the mean annual precipitation is 650 mm. The dominant forest types are fresh mixed coniferous forests (FMCF), mountain fresh mixed deciduous forests (mFMDF) and fresh mixed deciduous forests (FMDF) (Table 1).



**Fig. 1.**  
Location of the study area (hatched area on the map)

Available from: [https://commons.wikimedia.org/wiki/File:Rdlp\\_wroclaw.png](https://commons.wikimedia.org/wiki/File:Rdlp_wroclaw.png) [accessed: 15.07.2023]

**Table 1.**

Characteristics of the study area. The values were calculated on the basis of data from the publications of Kondracki (2009) and Zielony and Kliczkowska (2010)

Area [km <sup>2</sup> ]	Forest area [km <sup>2</sup> ]	Forest area [%]	Average temperature [°C]	Vegetation annual period [days]	Range of average annual rainfall [mm]	Dominant Forest – Site Types percentage of the forest area [%]	Range of elevation m.a.s.l
19,947	5,910	29.6	7.7	170-220	550-1000	FCF – 11 FMCF – 14 FMDF – 12 mFMDF – 14 FDF – 9 uMDF – 7 uFDF – 7 mFDF – 7 MMCF – 5 mFMCF – 3 MMDF – 3 MDF – 2 mFCF – 2 AF – 1 AAF – 1 ASF – 1*	70-1603

\* FC – fresh coniferous forest; FMCF – fresh mixed coniferous forest; FMDF – fresh mixed deciduous forest; FDF – fresh deciduous forest; MDF – moist deciduous forest, MMCF – moist mixed coniferous forest, MMDF – moist mixed deciduous forest, AF – alluvial (reparian) forest, AAF – ash-alder forest, ASF – alder (swamp) forest, m – mountain, u – upland

**DATA SAMPLING.** In this study, the elm locality (EL) is understood as the smallest forest division unit or forest stand where any *Ulmus* is represented (Napierała-Filipiak *et al.*, 2019; Filipiak *et al.*, 2021). A forest stand defined as ‘a contiguous community of trees sufficiently uniform in composition, structure, age, size, class, distribution, spatial arrangement, site quality, condition, or location to distinguish it from adjacent communities’ by Nyland (2007). The examined forest stands and the criteria for selecting ELs are described in more detail in Napierała-Filipiak *et al.* (2016, 2019).

According to official forest documentation the studied area has 9,333 ELs. However, as a general rule the data do not distinguish between individual elm species. In an overwhelming majority of all of the ELs, the elm contribution to the stand was lower than 10% (FDB, 2020). For this reason, a random sample of 200 EL was taken with this share situated in various parts of the studied area and 100 EL where elms account for over 10% of all trees. Not all of these localities were found in the field, and in some cases the real elm percentages differed from that stated in the documents. Ultimately, 201 EL with a contribution of up to 10% and 72 EL with a share of over 10% were examined for a total of 273 ELs. As part of the study, the elm species were determined at each EL. The data was analyzed jointly for all EL and divided into individual species. For *U. laevis*, the ELs were additionally divided into localities with percentage according to forest documentation of elms of up to 10% (UL1) and above 10% (UL2). The last division was not used in the case of *U. minor* and *U. glabra* due to the very small number of localities with a larger percentage of these elm species (one or two sites per species)

**DATA ANALYSIS.** In order to establish the smallest distance of any given EL from the closest major or medium-sized river geometrical layers (State Forests' organisational units, divisions and basic forest management units) of digital maps of the forested areas managed by the State Forests were used from the Forest Data Bank (FDB) made available by the Bureau for Forest Management and Geodesy (FDB, 2020).

The data was processed using the QGIS program version 3.10.4-A Coruña (Open Source Geospatial Foundation (OSGeo) project, Chicago, USA; license: GNU GPL) and MS Excel.

After identifying the ELs for the study, their centroids were established. Next, the smallest distances between the centroids and the rivers with flows of 4 m<sup>3</sup>/s or larger were established. The following rivers in the studied region were taken into account: Barycz, Bóbr, Bystrzyca, Czarna Woda, Czarna Wielka, Kaczawa, Krzycki Rów, Kwisa, Nysa Kłodzka, Nysa Łużycka, Odra, Oława, Orla, Orlica, Polski Rów, Strzegomka, Szprotawa, Ścinawka, Ślęza, and Widawa. The spatial analysis was done by means of QGIS plug-in NNJoin, version 3.1.3 (QGIS plug-in; created by: Håvard Tveite, NMBU, license: GNU GPL). All 273 ELs were subjected to the procedure described above.

The results are presented as maps and graphs with distributions of distances from the watercourse. The data are grouped into 1,000-metre sections with the first range (distance up to 1,000 m) further subdivided into 100-metre sections.

In order to examine whether the observed trend of the occurrence of elms in lowlands was not connected with the general distribution of forest sites types, the presence of *Ulmus laevis* was analysed in more detail which was represented in the biggest number of examined ELs. The data related to the occurrence of this elm species in the fresh deciduous forest (FDF) and fresh mixed deciduous forest (FMDF) site types was compared to the general distribution of this types of site in relation to distance from a big or medium-sized river. The FDF and FMDF forest site types cover the fertile, fresh (non-moist) variants of typical oak-hornbeam forests. Earlier publications indicate that it is this forest site type that has the most (*i.e.* two thirds) oak-hornbeam elm sites. Including other non-riparian habitats (forest site types) in this analysis would not provide a significantly larger amount of data (small number of EL) while significantly increasing habitat variability (Napierała-Filipiak *et al.*, 2014).

In order to examine the general distribution of the FDF and FMDF forest site types, ten areas measuring 10×10 km distributed evenly on the lowland area of Lower Silesia were selected at random (Fig. 2). Each area was overlaid on a 1:10,000 colour map of forest stands and forest sites (habitats). Subsequently, all stands with the FDF and FMDF forest site types that were

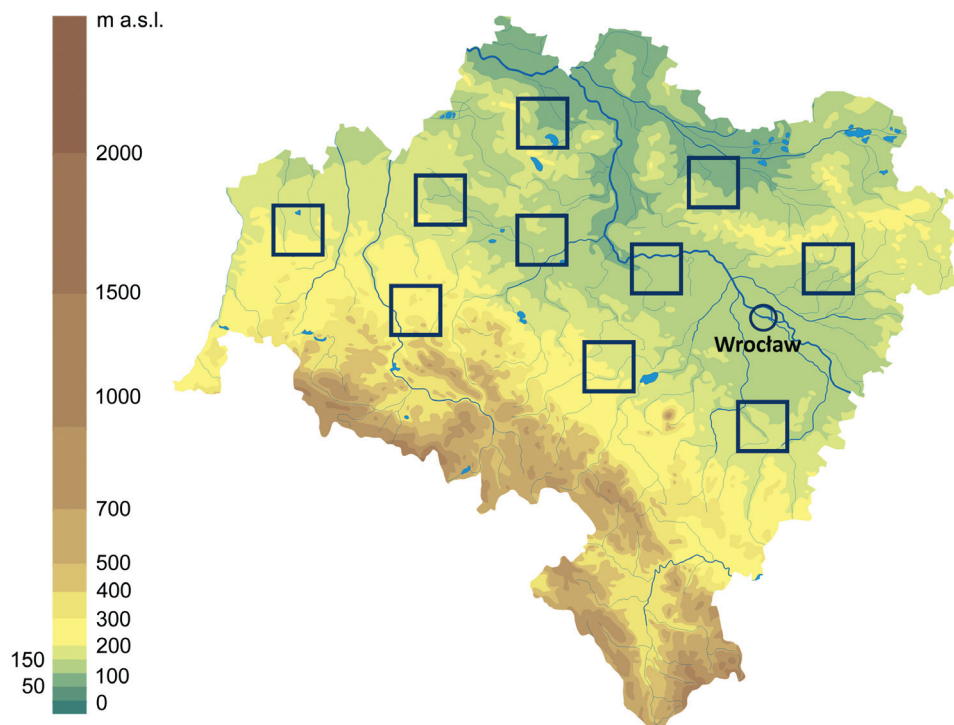


Fig. 2.

Location of the 10 study areas (10×10 km square) used for identification and the general distribution of 'fresh deciduous forest' (FDF) and 'fresh mixed deciduous forest' (FMDf) according distance from a big or medium-sized river

Map available from: Polish Wikipedia, Author: 'Aotearoa', CC BY-SA 3.0, File: Dolnośląskie mapa fizyczna. png, Created: August 29, 2006 (date of first file upload), [https://www.pl.wikipedia.org/wiki/Województwo\\_dolnośląskie#/media/Plik:Dolnośląskie\\_mapa\\_fizyczna.png](https://www.pl.wikipedia.org/wiki/Województwo_dolnośląskie#/media/Plik:Dolnośląskie_mapa_fizyczna.png) [accessed: 18.07.2023]

located within a 13,000 m distance from the bed of a large or medium-sized river were allocated into one of 13 distance ranges with a span of 1km. The analysis covered only stands that were at least partly within the selected map fragment, but their distance was examined from the nearest rivers flowing both within and outside the selected area.

**STATISTICAL ANALYSIS.** For all of the elm species probability distributions of the EL distance from the river were established. The best probability distribution was selected based on the Kolmogorov-Smirnov test. Selected distributions (three-parameter gamma distributions) were used to calculate quantiles and critical values for a given probability (Krishnamoorthy *et al.*, 2008). The use of the gamma probability distribution enabled the tail probability values to be calculated for the adopted distances of 100 m, 1,000 m and 5,000 m from the river and the critical values of 5% and 10% at left and right tails.

The One-Way ANOVA (analysis of variance single classification) was used to verify the hypothesis that the mean distances from the river for individual species were the same. Initially, the data was normalized by a third-order root transformation whereby homogeneous groups were separated (Kutner *et al.*, 2004).

Furthermore, the hypothesis regarding the difference in the distance from the river for two subgroups (UL1 and UL2 for the *U. laevis*) was verified by Student's *t*-test (Kutner *et al.*, 2004).

For a comparison of the empirical distribution of distances from a big or medium-sized river for *U. laevis* localities at the FDF and FMDF forest site types with the general distribution of distances for all stands at those forest site types, a Chi-square test of homogeneity for two samples was used. Additionally, the Kolmogorov-Smirnov test to compare the distributions of the two samples was applied.

Rational functions in the form  $y=w_k(x)/w_l(x)$ , where  $w_k(x)$ ,  $w_l(x)$  which are polynomials of degree  $k, l \leq 2$  were applied to approximate the fractions of the number of sites ( $y$ ) as a function of the distance from a river ( $x$ ) for both cases. In the calculations these functions took a simpler form as the reciprocal of a linear and quadratic function.

### Results

DISTRIBUTION OF INDIVIDUAL SPECIES. The mean distance of ELs from the river for all species was 3,247 m. The smallest distance (2,425 m) was recorded for *U. laevis*, the biggest (5,245 m) for *U. glabra*, and intermediate (3,086 m) for *U. minor* (Table 2, Fig. 3). The distribution of EL distances from the river were skewed for all examined species (Fig. 3). Depending on the species, distances of individual ELs were relatively widely scattered between 24 m *U. laevis* and

Table 2.

Summary statistics of distances from the river for different elm species

Elm tree species	n	Mean	S.D.	Min	Max
UL1	100	2831	3012	24	12.036
UL2	69	1.838	2.649	28	11.163
UL	169	2.425	2.903	24	12.036
UG	72	5.245	3.863	129	14.284
UM	32	3.086	3.219	125	12.442
All	273	3.247	3.429	24	14.284

UL1 – localities of *U. laevis* with a percentage in the stand of less than 10%  
 UL2 – localities of *U. laevis* with a percentage in the stand of more than 10%  
 UL = UL1 + UL2, UM – *U. minor* EL, UG – *U. glabra* EL

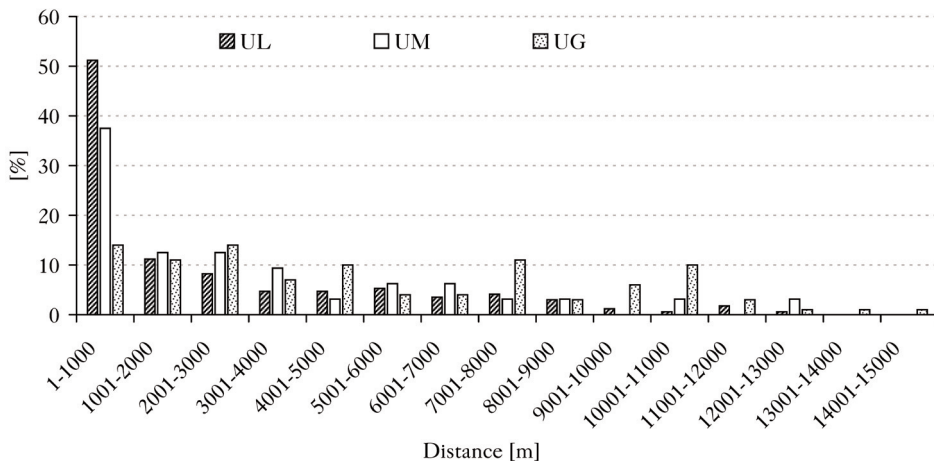


Fig. 3.

Percentage distribution of individual elm localities (EL) depending on the distance from the riverbed of a big or medium river in Lower Silesia

UL – *U. laevis* EL(elm locality), UM – *U. minor* EL, UG – *U. glabra* EL

14,284 m (*U. glabra*; Table 2, Fig. 3). It should also be pointed out that for *U. glabra* and *U. minor* the distance from the river was never smaller than 125 m.

The distribution of distances from the river of ELs revealed that *U. laevis* had the strongest connection with watercourses (Fig. 3). Generally 51% of the localities for this species were up to 1,000 m away from the watercourse, 33% up to 500 m, and the largest number of localities falling within the 100-300 m range (Fig. 3, 4, Table 3, 4). For the UL2 localities with elm percentages over 10%, the data was the following: 64% up to 1,000 m from the watercourse, 48 % up to 500 m, and the largest number of localities within the 100-200 m range (Table 5, 6).

In the comparison of the mean distances from the river between the subgroups of *U. laevis* (UL1 and UL2; Table 5), the null hypothesis about the equal means ( $p=0.028$ ) with the assumption of equality of variance was rejected. The mean distances for the UL1 subgroup were significantly bigger than those for the subgroup UL2 (Table 5).

A slightly weaker connection with the valleys (watercourse) occurred with *U. minor* localities (Fig. 3, 4). Out of 32 localities for this species, 12 (38%) were within 1,000 m from the watercourse and 7 (22%) up to 500 m. The same number of ELs was observed for 101-200 and 201-300 ranges as well as for 401-500 m ranges (Fig. 4, Table 4).

*Ulmus glabra* also showed some connection with valleys of major or medium-sized rivers, but this relationship was significantly weaker than in the two other elm species. Out of the total number of 71 localities, only 14% were within 1,000 m and 8% up to 500 m from the watercourse with the largest number of localities in the 201-300 m range (Fig. 4, Table 4). The map in Fig. 5 indicates that this species grows, mainly, in mountain and submontane areas.

Fitting the probability distribution for the EL distances enabled computation of the probabilities of *Ulmus* occurrence depending on the distance from the river in the form of critical values and distribution quantiles.

From among the twenty considered probability distributions, the best based on the four cases (each elm species and all species jointly), was the three-parameter gamma distribution (Fig. 6).

The probability of any elm species occurrence at a distance from a river of up to 100 m amounts to  $p=0.052$  and varied for the individual elm species from about 10% in *U. laevis* to less than 1%

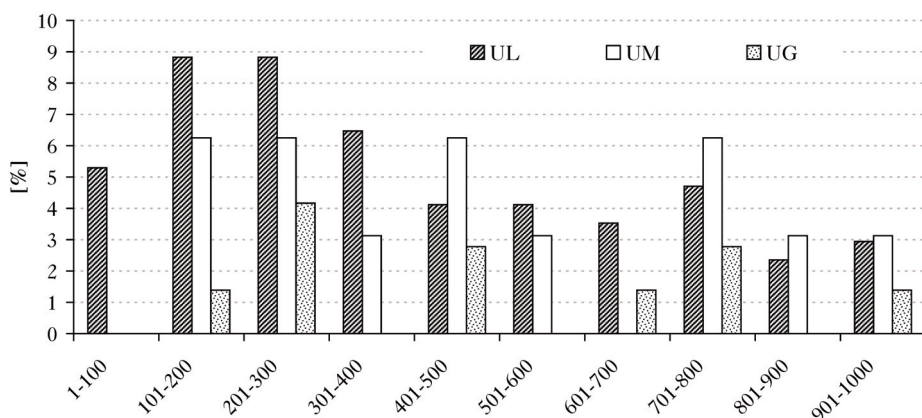


Fig. 4.

Percentage distribution of elm localities (EL) for individual species at a distance of up to 1000 m from the riverbed of a large or medium river in Lower Silesia

UL – *U. laevis* EL (forest plot with elm locality = elm locality), UM – *U. minor* EL, UG – *U. glabra* EL



Table 3.

Distribution of elm localities for individual species depending on the distance from the bed of a large or medium-sized river in Lower Silesia

Distance [m]	UL	UM	UG
	N	N	N
1-1000	87	12	10
1001-2000	19	4	8
2001-3000	14	4	9
3001-4000	8	3	5
4001-5000	8	1	7
5001-6000	9	2	3
6001-7000	6	2	3
7001-8000	7	1	8
8001-9000	4	1	2
9001-10000	2	0	4
10001-11000	2	1	7
11001-12000	3	0	2
12001-13000	1	1	1
13001-14000	0	0	1
14001-15000	0	0	1
1-17000	170	32	71

N – number, UL – *U. laevis* EL (forest plot with elm locality = elm locality), UM – *U. minor* EL, UG – *U. glabra* EL

Table 4.

Distribution of elm localities for individual species at a distance of up to 1000 m from the riverbed of a large or medium river in Lower Silesia

Distance [m]	UL	N	UG
		UM	
1-100	9	0	0
101-200	15	2	1
201-300	15	2	3
301-400	11	1	0
401-500	7	2	2
1-500	57	7	6
501-600	7	1	0
601-700	6	0	1
701-800	8	2	2
801-900	4	1	0
901-1000	5	1	1
1-1000	87	12	10

N – number, UL – *U. laevis* EL (forest plot with elm locality = elm locality), UM – *U. minor* EL, UG – *U. glabra* EL

in *U. glabra* and *U. minor* (Table 7). The probability of occurrence of elm increased for the distances of 1,000 and 5,000 metres from the river (Table 6).

The critical values provided in Table 7 help to determine the distances from the river with a set probability of elm occurrence. For instance, with a probability of 5% *U. laevis* may grow at a distance of 52 m from the river, while the corresponding distances amount to 471 m for *U. glabra* and 162 m for *U. minor*. Similarly, for the upper tail areas for instance, the probability of finding any elm species at a distance of over 10,570 m from a river is equal to 5% (Table 7).

Verification regarding the equality of the mean distances from the river for the three elm species in ANOVA resulted in the rejection of the hypothesis ( $p < 0.0001$ , Table 8). The multiple range tests and Fisher's least significant difference (LSD) procedures proved that the mean distance for *U. glabra* was significantly greater than for the other two species that constituted a homogeneous group at a significance level of 95% (Fig.7).

**Table 5.**

Distribution of localities of *U. laevis* with a percentage in the stand of less than or more than 10% depending on the distance from the bed of a large or medium-sized river in Lower Silesia

Distance [m]	UL1	UL1	UL2	UL2
	N	[%]	N	[%]
1-1000	42	42	44	64
1001-2000	15	15	4	6
2001-3000	9	9	5	7
3001-4000	5	5	3	4
4001-5000	5	5	3	4
5001-6000	6	6	3	4
6001-7000	5	5	1	1
7001-8000	5	5	2	3
8001-9000	3	3	1	1
9001-10000	2	2	0	0
10001-11000	0	0	1	1
11001-12000	2	2	1	1
12001-13000	1	1	0	0
13001-14000	0	0	0	0
14001-15000	0	0	0	0
15001-16000	0	0	0	0
16001-17000	0	0	1	1

UL1 – localities of *U. laevis* with a percentage in the stand of less than 10%

UL2 – localities of *U. laevis* with a percentage in the stand of more than 10%

**Table 6.**

Distribution of localities of *U. laevis* with a percentage in the stand of less than or more than 10% at a distance of up to 1000 m from the riverbed of a large or medium river in Lower Silesia

Distance [m]	UL1	UL1	UL2	UL2
	N	[%]	N	[%]
1-100	3	3	6	9
101-200	6	6	9	13
201-300	7	7	8	11
301-400	5	5	6	9
401-500	3	3	4	6
1-500	24	24	33	48
501-600	4	4	3	4
601-700	2	2	4	6
701-800	5	5	3	4
801-900	4	4	0	0
901-1000	3	3	2	3
1-1000	42	42	45	64

UL1 – localities of *U. laevis* with a percentage in the stand of less than 10%

UL2 – localities of *U. laevis* with a percentage in the stand of more than 10%

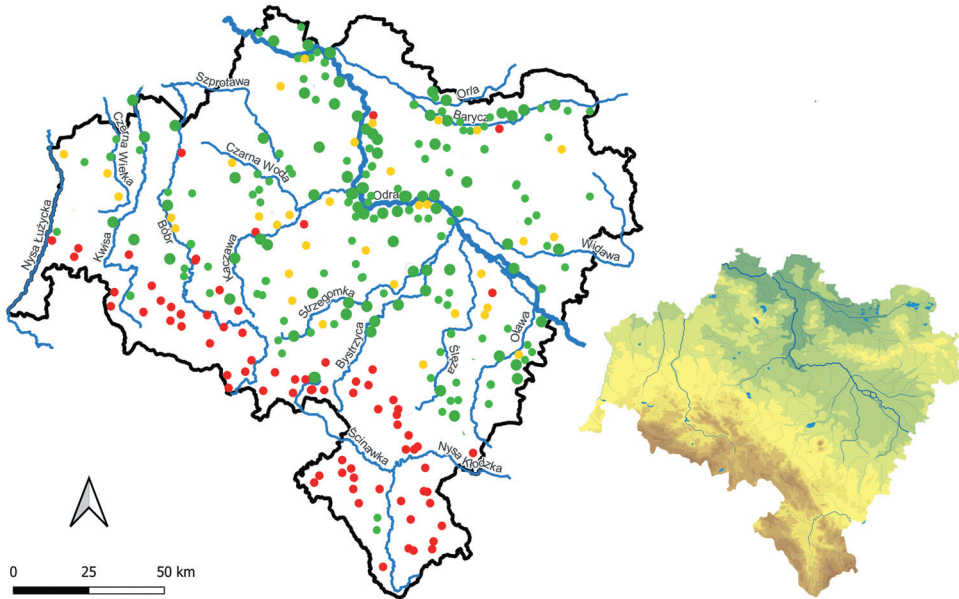


Fig. 5.

The occurrence of localities (EL) of various species of elm in Lower Silesia in comparison with the Map of waters and topography of this region (source and legend of this map – see fig. 2)

Green points – EL of *U. laevis*; yellow points – EL of *U. minor*; red points – EL of *U. glabra*; big points – EL with a contribution of elm in the trees stand of more than 10%

INFLUENCE OF HABITAT DISTRIBUTION ON THE DISTRIBUTION OF ELM. To compare the general distribution of distances from the river for the FDF and FMDF site types with the distribution for *U. laevis* localities in these site types (UL; Fig. 8) the  $\chi^2$  homogeneity test (*chi-square*) was used. The hypothesis about the same probability distributions for the two groups was rejected at  $\alpha=0.01$  ( $\chi^2=615.2 > \chi^2_{\alpha}=26.2$ ). It can be noted that the greatest differences between the frequencies of ELs in the FDF and FMDF habitats and the general distribution of these types of habitats were found in the first two classes of distance from the river (0-1000 and 1001-2000 m; Fig. 8). To further verify the differences between these two groups the Kolmogorov-Smirnov test was used. It was performed by computing the maximum distance between the cumulative distributions of the two samples.

In the case of the distribution of *U. laevis* localities (UL) in the FDF and MFDF site types, the function (reciprocal-y vs. x model) was calculated as follows (Fig. 9):

$$\text{Distr\_freq} = 0,0063 \cdot \text{Distance} + (288,837 / \text{Distance}) \quad y = \frac{0.006266 \cdot x + 288.837}{x} \quad (1)$$

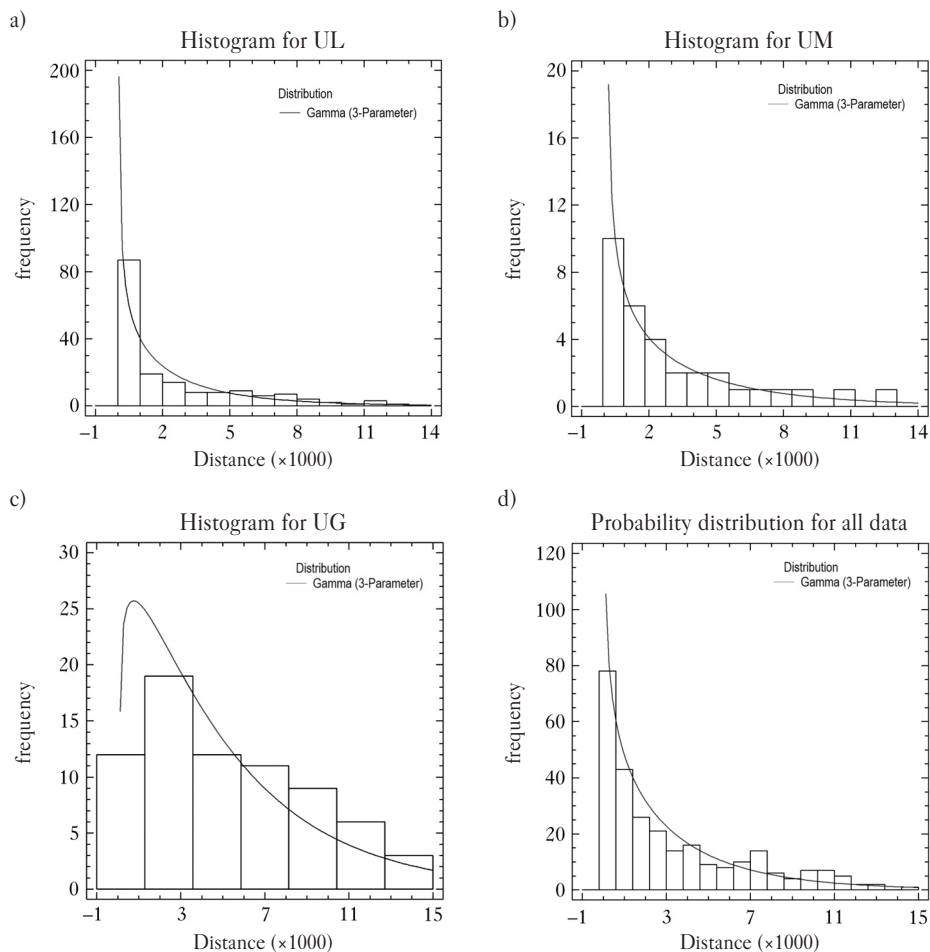
(R-Squared=0.94)

In the case of a general distribution of stands in the FDF and FMDF forest site types the function in the following form (reciprocal-y vs. squared-x model) was calculated as follows (Fig.10):

$$\text{Rel\_freq} = 1 / (9,316 + 8,18897E^{-8} \cdot \text{Distance}^2) \quad y = \frac{1}{9.316 + 0.000000082 \cdot x^2} \quad (2)$$

(R-squared=0.80)

The estimated overall statistic was obtained as DN=0.928571, two-sided sample K-S statistic =2.456 and approximate P-value=0.00001 (in this case the maximum distance is 0.929) indicate a statistically significant difference between these two distributions.



**Fig. 6.**

Frequency histogram and pdf function of distances from the river for different elm tree species  
 UL – *U. laevis* EL (elm locality), UM – *U. minor* EL, UG – *U. glabra* EL, all data = all the studied elm localities (EL), distance [km]

**Table 7.**

Tail area and critical values from the gamma probability distributions describing distances of elm localities (EL) from the river for different elm species

	Tail area [m]			Critical values			
	100	1000	5000	lower tail area		upper tail area	
				5%	10%	10%	5%
UL	0.094	0.431	0.857	52	108	6139	8426
UG	<0.001	0.132	0.604	471	792	11549	14788
UM	<0.001	0.340	0.771	162	238	8662	11871
All	0.052	0.328	0.789	95	206	7872	10570

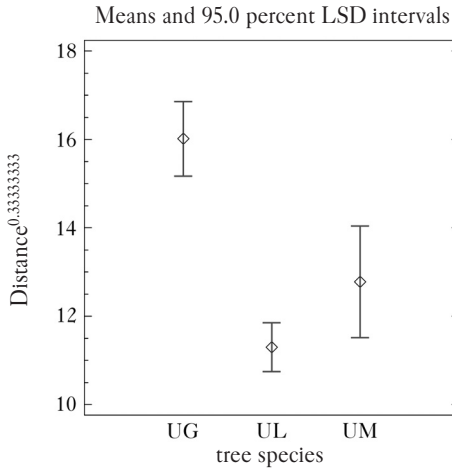
UL – *U. laevis* EL (forest plot with elm locality = elm locality), UM – *U. minor* EL, UG – *U. glabra* EL

**Table 8.**

ANOVA table for the distances of elm localities from the riverbed

Source	Sum of Squares	Df	Mean square	F-ratio	P-value
Between groups	1124.79	2	562.396	21.28	0.0000
Within groups	7134.21	270	26.423		
Total (Corr.)	8259.01	272			

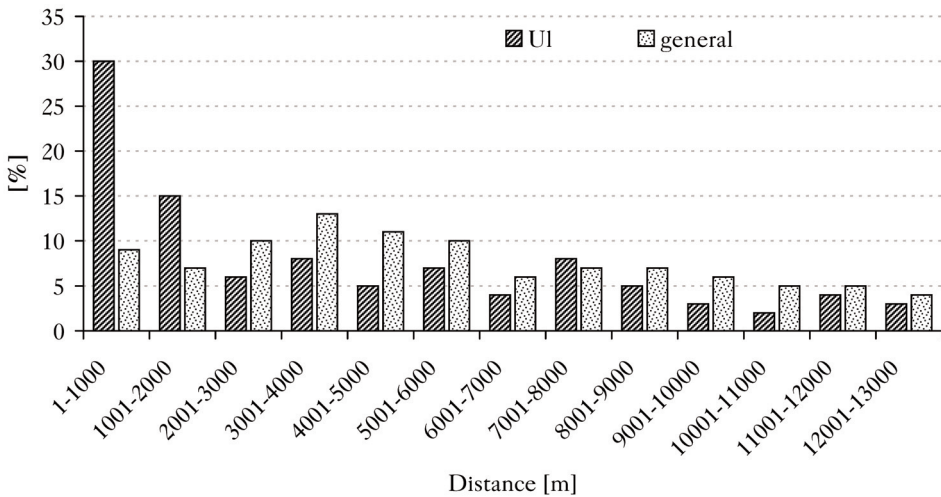
Groups are made up by individual species of elms



**Fig. 7.**

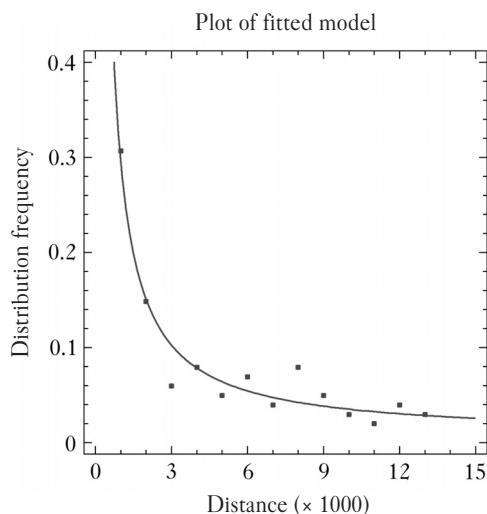
Means and intervals displayed based on Fisher's least significant difference (LSD) procedure for distances from the river and different elm species localities (FPEL) for tree species

UG – *U. glabra*, UL – *U. laevis*, UM – *U. minor*



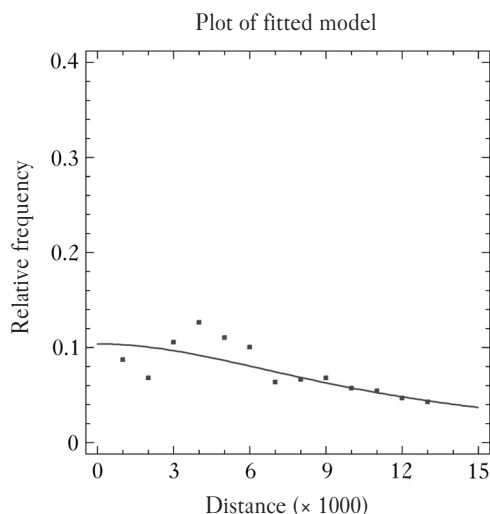
**Fig. 8.**

Percentage distribution of *U. laevis* localities located in the FMDF and FDF forest habitat types against the background of the general percentage distribution of the mentioned forest site types (FMDF and FDF) depending on the distance of a large or medium river on the area of lowland part of Lower Silesia



**Fig. 9.**

Reciprocal-Y squared-X model function matched to the distribution of *U. laevis* localities (UL) in the MFDF and FDF site types depending on the distance from the nearest a medium-sized or big river on the area of lowland part of Lower Silesia



**Fig. 10.**

Function matched to the general distribution of forest plots (FP) in the MFDF and FDF forest site types depending on the distance from the nearest a medium-sized or big river on the area of lowland part of Lower Silesia

## Discussion

The studies conducted so far indicate that the area of research presented in this article is representative of the whole of Poland (Napierała-Filipiak *et al.*, 2014, 2016, 2019, 2021; Łakomy *et al.*, 2016) and probably also of the neighboring regions in Europe (the Czech Republic and Germany).

The data presented here supplement the findings of previous (including our prior) studies (Polyakova and Billor, 2007; Martín *et al.*, 2013; Heybroek, 2015; Santini and Faccoli, 2015; Caudullo and de Rigo, 2016; Napierała-Filipiak *et al.*, 2016, 2019, 2021; Puerto *et al.*, 2017; Chudzińska *et al.*, 2018; Thomas, 2018; Sepúlveda and Johnstone, 2019; Kassahun *et al.*, 2020; Yuan *et al.*, 2020; Camarero *et al.*, 2021). They also draw our attention to the fact that the contribution of elms in oak-hornbeam forest communities differs depending on the distance of the EL from riparian sites which are the optimal places for elms to grow.

This is an important piece of information not only from the perspective of the ecology of elms, particularly *Ulmus laevis*, but also information on plant communities, in the case of which it is generally assumed that in natural conditions they are shaped by ‘climatic, soil or possibly other abiotic conditions’ (Matuszkiewicz, 2015). Less attention is paid to the influence of proximity to other plant communities (Turczański *et al.*, 2021; Oettel *et al.*, 2022), unless it is about the transitional zone. In the case described in this study, the proximity of riparian forests increases the share of elm in the nearby oak-hornbeam forests.

The statement that elms are particularly bound to river valleys and alluvial habitats is not new. However, our data provides a certain pattern for this distribution. It indicates that *U. glabra* differs from the other two species in terms of its preferred location as it is much more loosely connected with major river valleys and grows considerably more frequently in mountain areas than the two other studied elm species.

The aforementioned elm distribution patterns indicate that in the case of the studied area the places from which *U. laevis* and *U. minor* spread to other areas are typical alluvial forests that grow in plain valleys of main or medium-sized rivers. In the case of *U. glabra*, those are various types of fertile forests located on moist slopes at headwaters or surrounding (not always riparian) of small watercourses, or secondly in typical riparian forests. In order to grow properly, the examined species do not necessarily need moist soil as fairly fertile fresh soils are sufficient for them (Orłowski and Nowak, 2007; Napierała-Filipiak *et al.*, 2014, 2021; Caudullo and de Rigo, 2016; Thomas, 2018). Why is it then that as the distance from riparian forests or similar moist areas increases their total percentage falls significantly? It seems that the reasons for this may be found among factors responsible for the ability of the studied trees to regenerate. Their seeds are small and susceptible to drying out, and they germinate at the beginning of the summer which is a season when the top layer of the substrate is likely to dry out (Filipiak and Napierała-Filipiak, 2015). We believe that drying of the top layer of soil is the main factor limiting the number of seedlings and the share of elms in the composition of stands growing on fresh soil. The differences in the distribution of individual species of European elms may also be explained with small differences in production and germination of seeds (Falińska, 1971; Evstigneev, 1988; Emborg, 1998; Modrý *et al.*, 2004; Kramer *et al.*, 2008; Venturas *et al.*, 2014; Filipiak and Napierała-Filipiak, 2015) Some other factors (stochastic disturbance events, flooding, and human use) may also be responsible for differing numbers of individual elm species in various types of communities and in different parts of the natural elms reach. Nuances in the temperature/precipitation system may be here of key importance, rather than average values of these factors over longer periods of time.

According to Dieckman (1994, 1996), in Öland’s forests *U. glabra* has the same ecological properties as the ash *Fraxinus excelsior* L. In contrast, in the light of our studies, the wych elm is less of a ‘riparian forest-like’ species than the ash, but rather is more closely related to the sycamore *Acer pseudoplatanus* L. and partly to the beech *Fagus sylvatica* L. (Jaworski, 2011; Matuszkiewicz, 2015). It would be very unusual if ecologic niches of various species corresponded to one another fully. In this study, *U. laevis* and *U. minor* create a statistically homogeneous group in terms of their relationship to classic riparian forests habitats, and their close connection with flooded river valleys is very clear. However, it can be noted that *U. minor* localities are slightly further away (and probably higher) from the river bed. Some studies suggest that where *U. laevis* and *U. minor* occur jointly near a river, the latter species prefers sites that are situated a little higher up (Venturas *et al.*, 2015). A similar correlation was observed in this study as well (Napierała-Filipiak *et al.*, 2021).

Despite the fact that in terms of taxonomy, *U. minor* is closer to *U. glabra* with which it may create crossbreeds (Collin, 2003), its ecology seems to be closer to that of *U. laevis* in the light of this study.

This study and findings of earlier studies (Napierała-Filipiak *et al.*, 2016, 2021) also show that the greater share of all EL is to be found on fresh soils, generally within fertile variants of oak-hornbeam communities than in the alluvial forests and hydrogenic soils. Similarly, in the case of ash over 50% of its resources grow, in the form of a dispersed diaspora, outside riparian forests, which are the optimum environment for the species (Filipiak *et al.*, 2004). Turczański *et al.* (2021) discovered that a young generation of ash growing outside its optimum environment is significantly less stricken by *Hymenoscyphus fraxineus* Baral, Quelož & Hosoya which is causing mass extinction of the species in Europe. In spite of this, in the case of both elms and ash this dispersed part of the resources (diaspora) often does not attract much attention or is simply ignored in general assessments of resources (Matuszkiewicz, 2015). This diaspora is significant and, as mentioned above, may play a considerable role in the tree's defensive mechanism against fungal diseases with an epidemic nature.

The distribution found in our study for the number of EL within the range of 0-1,000 m (the highest number was in the range of 100-300 m) from the river bed confirms the information in the literature (Filipiak and Napierała-Filipiak, 2015; Matuszkiewicz, 2015; Venturas *et al.*, 2015; Napierała-Filipiak *et al.*, 2019) that within river valleys elms occur peripherally and at slightly higher locations (floodplains). The swollen river waters do not reach those sites every year but rather once every few years as opposed to places closer to the riverbed.

The relatively large numbers of *U. laevis* within 2 km from a big or medium-sized river (Fig. 7) seems to be a result of an additional sowing of seeds from riparian areas. Although it has been shown in studies by Russell and Honkala (1990) and Venturas *et al.* (2014) that a majority of elm seeds fall within 100 m of the tree, some of them must travel further as otherwise it is difficult to explain a much larger number of trees of this species in oak-hornbeam forests located in the vicinity of riparian forests.

In regards to the presence of *U. glabra* in the studied area, it has been shown to be clearly associated (almost unambiguously) with mountain areas. This generally agrees with the description of the species' occurrence and with its name in Polish, *i.e.* mountain elm. However, such a distinct preference for mountainous regions is somewhat surprising as the reach of the species encompasses not only mountains, but larger groupings may be also found outside such areas. Generally, those are areas with lower temperatures, higher precipitation and frequently at least a slightly varied terrain. In all such situations, they are relatively more common amongst microsites where upper soil layer dries out more slowly. These conditions may affect seed germination which is fairly atypical compared to other tree species as in elms it takes place in mid-summer. Such conditions prevail in many lowland areas especially located within the maritime climate in the western or northern parts of Central Europe, *e.g.* in the UK, Denmark, the Netherlands, Norway, Sweden, southern Finland, the Baltic states, northern Germany and Poland. Further south and towards the center of the continent, *U. glabra* grows principally on foothills and in lower elevations of mountains. Richines (1983) points out that in the UK, *U. glabra* is mainly to be found in areas with an average August temperature below 21°C. As mentioned prior, in the area examined in this study the temperatures within the foothills and especially in the mountains are about 1°C lower and precipitation is 100 mm higher than in the lowlands. Further, the lower sections of the slopes are often in shade.

It is worth mentioning that despite significant humidity (where elms grow on moist slopes) soils are usually very well aerated (better than in typical riparian forests) and water contains



large amounts of oxygen (Matuszkiewicz, 2015). It cannot be ruled out that this factor plays a specific role in *U. glabra* preference for such conditions.

The information in this article is important both from the perspective of actions taken in forests excluded from use and subject to various forms of protection as well as for managing multi-functional forests (which are currently predominant in Poland). Due to the projected increase of forested areas excluded from management activities, a scenario is being considered in which the importance and area of typical forests intensely utilized for economic purposes and plantations will grow as well. When managing such forests, attention should be paid to the fact that elms, and probably also other species, may affect the protected areas located even several kilometers away from the source of the seeds due to seed dispersal factors. The aforementioned information is also significant since the currently small role of elms in forests is likely to grow especially for the European white elm (Dyderski *et al.*, 2018; Thurm *et al.*, 2018; Koch *et al.*, 2022). This results from, among other factors, the ability to cultivate this species outside the riparian forests, the highest resilience to Dutch elm disease among native elms (Caudullo and de Rigo, 2016; Łakomy *et al.*, 2016; Napierała-Filipiak *et al.*, 2016, 2021), a larger proportion in forest resources and tree stands in the past (Richens, 1983; Ralska-Jasiewiczowa *et al.*, 2003; Caseldine and Fyfe, 2006; Pirc, 2006), the projected significant resilience to climate change (Thurm *et al.*, 2018; Koch *et al.*, 2022), and the attempts to replace ash which is disappearing from riparian forests with European white elm (Napierała-Filipiak, 2014).

## Conclusions

For the area covered by the study which represents conditions typical of Central Europe, the pattern of distribution of three elm species native to Europe (*U. glabra*, *U. laevis* and *U. minor*) was established in relation to location relative to big or medium-sized rivers (with average flow amounting to at least 4 m<sup>3</sup>/s). Probabilities were computed for the occurrence of elms at a specific distance from the riverbed. Similar to European ash a significant portion of elm, especially *U. laevis*, is dispersed outside riparian forests which are regarded as the optimal type of site for both ash and elms and the location of their mass occurrence. This type of distribution of trees is probably significant for the survival of the species if an epidemic disease occurs.

The distribution of the two studied species (*i.e.* *U. laevis* and *U. minor*) were associated with the valleys of major and medium-sized rivers in a similar way and therefore create a statistically homogeneous group. In regards to this grouping, over 49% of all localities and nearly 65% of localities where elms constitute a minimum of 10% were situated at a distance not exceeding 1,000 m from the river. The respective values for 500 m were 32% and 47%.

The third studied elm species, *U. glabra*, showed a weaker connection with valleys of major and medium-sized rivers. Out of the total number of localities, only 14% were at a distance of up to 1,000 m and 8% up to 500 m away from a watercourse. The species grows on moist slopes at an elevation above the other species of elm where water moves near the soil surface.

In the case of a river valley, most EL occur not within immediate proximity to the riverbed, but rather 100-300 m away from it. Elm localities (EL) with a larger proportion of this tree species in the forest stands were located, on average, closer to the river valley than localities with a smaller proportion of elm.

The proportion of *U. laevis* in the FDF and MFDF forest site types (encompassing fertile variants of communities of typical oak-hornbeam forests) depends on the distance of a given locality from the nearest medium-sized or large river and is not a simple function of the forest habitats distribution.

## Authors' contributions

M.F. – concept development, manuscript planning and writing, literature review, determination of *Ulmus*, data analysis and interpretation, final text editing; L.K. – literature review, data analysis and interpretation, final text editing; J.G. – data collection, main data analysis, literature review, text co-editing; J.J.-J. – data collection, literature review, analysis and interpretation, text co-editing; A.N.-F. – funding acquisition, data collection, final text editing.

## Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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## STRESZCZENIE

### Udział wiązków w zbiorowiskach niełęgowych zależy od odległości od rzeki

W artykule dokonano analizy występowania 3 gatunków wiązków europejskich (*Ulmus glabra* Huds., *Ulmus laevis* Pall. i *Ulmus minor* Mill.) w zależności od położenia względem głównych lub średnich cieków wodnych. Badania prowadzono na terenie lasów Regionalnej Dyrekcji Lasów Państwowych we Wrocławiu (ryc. 1). Jest to region zróżnicowany typograficznie, o powierzchni blisko 20 000 km<sup>2</sup>, położony w centrum Europy oraz naturalnych zasięgów poszczególnych wiązków. Obszar objęty badaniami reprezentuje warunki typowe dla Europy Środkowej (tab. 1). W pracy wykorzystano wyniki własnych prac terenowych (identyfikacja gatunku), mapy cyfrowe obszarów leśnych oraz program QGIS. W pierwszym etapie badaniami objęto 255 losowo wybranych drzewostanów (ryc. 5).

Po zapoznaniu się z pierwszą częścią wyników postanowiono sprawdzić zależność liczby stanowisk wiązków od odległości od rzeki (ryc. 3; tab. 2-4). Chodziło przede wszystkim o ustalenie,

czy nie jest ona funkcją rozmieszczenia określonych siedlisk. Stwierdzono, że będzie to możliwe przy użyciu danych dotyczących licznie reprezentowanych tu typów siedliskowych lasu Lśw i LMśw oraz najliczniejszego z wiązów – *U. laevis* (ryc. 5 i 6; tab. 2-4). W wymienionych typach siedliskowych lasu występuje większość grądowych stanowisk wiązów, a stanowiska te są liczniejsze niż stanowiska wiązów w lasach łęgowych. Aby sprawdzić ogólny rozkład wydzieleni w typach siedliskowych Lśw i LMśw, na barwnej mapie siedlisk leśnych wybrano losowo 10 obszarów o wymiarach 10×10 km rozmieszczonych równomiernie na niżowym terenie Dolnego Śląska (ryc. 2). Na każdym z obszarów wszystkie wydzielenia w typach siedliskowych Lśw i LMśw znajdujące się nie dalej niż 12 000 m od koryta dużej lub średniej rzeki zaliczono do jednego z 12 przedziałów odległości, o rozpiętości 1 km. W wyniku przeprowadzonych prac ustalono schemat rozmieszczenia 3 badanych gatunków wiązów w relacji do położenia dużych lub średnich rzek i obliczono prawdopodobieństwo ich wystąpienia w określonej odległości od koryta rzeki o średnim przepływie wynoszącym co najmniej 4 m<sup>3</sup>/s (ryc. 3-7; tab 2-5). Dwa gatunki – *U. laevis* i *U. minor* – są w podobny sposób powiązane z dolinami głównych i średnich rzek i tworzą pod tym względem grupę jednorodną statystycznie (tab. 5-8). W tej grupie ponad 49% wszystkich stanowisk i blisko 65% stanowisk, w których wiązy stanowią minimum 10%, jest położonych w odległości nie większej niż 1000 m od koryta rzeki. Odpowiednie wartości dla 500 m wynoszą 32% i 47%. Trzeci omawiany gatunek – wiąz górski *U. glabra* – wykazuje słabsze powiązanie z dolinami większych i średnich rzek (ryc. 3; tab. 3 i 4). Z ogólnej liczby miejscowości jedynie 14% leży w odległości do 1000 m, a 8% – do 500 m od cieku wodnego. Wiąz ten na badanym terenie okazał się prawie jednoznacznie związany z terenami górzystymi (ryc. 5), co generalnie zgadza się z opisami występowania tego gatunku oraz polską nazwą, chociaż tak wyraźna preferencja terenów górzystych jest nieco zaskakująca, ponieważ gatunek ten spotyka się także na terenach nizinnych. W przypadku doliny rzecznej większość stanowisk wiązów występuje nie w bezpośrednim sąsiedztwie koryta rzeki, lecz w odległości 100-300 m od niej (tab. 4 i 6).

Podobnie jak w przypadku jesionu wyniosłego, znaczna część zasobów wiązów, zwłaszcza *U. laevis*, rozproszona jest poza lasami łęgowymi (tab. 3), które uważane są za typ stanowiska optymalnego dla obu gatunków i miejsce ich masowego występowania. Ten podział zasobów jest prawdopodobnie istotny dla przetrwania gatunku w przypadku wystąpienia choroby epidemicznej. Udział *U. laevis* w lasach rosnących w typach siedliskowych Lśw i LMśw (obejmujących żywe warianty zbiorowisk grądów typowych) zależy od odległości danego stanowiska od najbliższej średniej lub dużej rzeki oraz zbiorowisk łęgowych znajdujących się w obrębie jej doliny (ryc. 8-10). Naturalne rozmieszczenie stanowisk wiązów na szeroko rozumianym niżu nie jest prostą funkcją rozmieszczenia siedlisk leśnych (ryc. 9 i 10).

Wyniki przedstawione w niniejszej pracy powinny być ważne zarówno dla działań prowadzonych w lasach wyłączonych z użytkowania oraz objętych różnymi formami ochrony, jak i dla gospodarowania w lasach wielofunkcyjnych (skład upraw, wpływ na sąsiednie powierzchnie leśne). Mają one istotne znaczenie także dlatego, że niewielka obecnie rola wiązów w lasach powinna wzrastać, co dotyczy zwłaszcza wiązu szypułkowego. Przemawiają za tym m.in.: możliwość uprawy tego gatunku poza łęgami, największa wśród rodzimych wiązów odporność na grafiozę, większy udział w zasobach leśnych i zadrzewieniach w przeszłości, prognozy dotyczące dobrego wzrostu w warunkach zmian klimatu oraz próby zastępowania wiązem szypułkowym ustępującego z łęgów jesionu.