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Patterns of invasion, biology and ecology of *Erechtites hieraciifolia* in the northern expansion range in Europe (C and NE Poland)

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Abstract

The complexity of invasion process of alien species is very high and requires better understanding. Nowadays, the successful range expansion of *Erechtites hieraciifolia* is being observed in Poland. In the study, the distribution of the species in Poland was summarized, based on the available literature and new field data. The fieldworks were conducted in the part of the species expansion zone located in the central and north-eastern Poland. Two case studies on species encroachment into post-fire and transitional bog communities were performed and a case inventory of the species presence on the border of its' main secondary range was conducted. The measurements of height, counting of the number of inflorescences per individual and the number of achenes per flower head, were conducted in selected stands. There was performed a checking of local conditions of growth using ecological indicator values for vascular plants. The analyzed specimens of the species had significantly less inflorescences and achenes than in the other parts of the species expansion zone. They grew also in worse light conditions and in less fertile sites. The species colonized most disturbed patches at first. It spread to the less disturbed ones and omitted natural sites. The massive colonization of the transitional bog could be caused by groundwater level lowering. In the area of the edge of the species main range it was found in many diffuse stands within disturbed patches of the landscape. Based on the obtained results the species is considered to create now still only a moderate threat in the analyzed part of the expansion zone. The possibility of its expansion to wetland sites and sudden appearance in Kampinos National Park needs much more attention.

Keywords: alien invasive species, climate change, American burnweed, expansion, disturbance

Introduction

Invasions of alien species and their impact on colonized ecosystems are difficult to forecast (e.g. Williamson 1996). Only relatively few species that established the populations in new regions can start landscape spread and became invasive (e.g. di Castri 1990). The main factors responsible for successful invasion are in general related with high reproduction and dispersion abilities of the species (Richardson et al. 2000, 2011), its high stress and disturbance tolerance, and availability of resources, for example nutrients, sunlight and water (Davis et al. 2000) and climatic conditions, which should be similar to the original range (Bellon et al. 1977, Richardson et al. 2000). In spite of these, an expansion of ecological range of alien plant species can also be observed (Matesanz et al. 2015). The complexity of invasion process is very high as well as the risk of damage for natural ecosystems and economy. Therefore, there is still a great need for the further research on distribution, biology and ecology of non-indigenous plant species (e.g. Tokarska-Guzik et al. 2014).

American burnweed *Erechtites hieraciifolia* (L.) Raf. ex DC. originates from Northern and Central America (McGregor 1986). Since last decades of 19th century, it has spread within Europe where for the first time it was found in Croatia (the vicinity of Zagreb) in 1876. After that it was noticed in Austria in 1885 and at the beginning of 20th century in Czech Republic, Romania, Germany and Poland (Górski et al. 2003). These records show the ability of extension of the species range in Europe in the rate of circa 600 kilometers per a quarter of century. The species gained more localities in the southern Poland (Zając and Zając 2001) within next three quarters of a century but its expansion to the north did not occur. In the secondary range it occupied mainly oak-pine, acidic oak and wet pine forests, clearcuts, glades, rocky debris and rush communities (Kucowa 1971, Sowa and Warcholińska 1992, Tokarska-Guzik et al. 2009), growing often in the communities belonging to *Epilobion angustifolii* Alliance from *Epilobietea angustifolii* Class (Mucina et al. 2016). The localities of species are found mostly on the oligo- and mesotrophic habitats of mixed forests (with domination of Scots pine and common oak in a tree stand), mostly on fresh or slightly wet soils. Such habitats are predominant in Poland, covering over 50% of forest area (Milewski 2018). The species is also able to colonize the bog forests, which share is less than 5% of forest habitats in the country (Milewski 2018).

Main area of its secondary range in Poland was located in the south part of the Country (Zając and Zając 2001, 2015). Until recently, spread beyond the northern limit of its range established to the end of 20th century was considered to be unlikely (Górski et al. 2003, Tokarska-Guzik 2005). In spite of the fact, further expansion of *E. hieraciifolia* started at the beginning of the 21st century. The species was noted in many new localities in the southern Poland but also in the central and north-eastern regions, which indicates the beginning of its propagation to the north, e.g. (Koczywąs et al. 2012, Zając and Zając 2015, Celka et al. 2017). During regular research carried out in regions of the central and north-eastern Poland as well as occasional inventories in 2015–2017 new stands of *E. hieraciifolia* were found and monitored. This makes the possibility to investigate some patterns of biology of invasion of the species in its expansion zone. The aim of the work was to summarize the present distribution of *E. hieraciifolia* in Poland, investigate the spread of the species based on two case study sites (post-fire pine forest community and transitional bog) in the species expansion zone in Kampinos National Park, describe the distribution pattern on the border of its expansion zone and to bring some new information on height of individuals, production of diaspores and its ecological preferences.

Material and methods

Present distribution of Erechtites hieraciifolia in Poland

The map of the distribution of *E. hieraciifolia* in Poland (Figure 1) was based on ATPOL grid (Zając 1978). It is consisted of data from 20th century (Zając and Zając 2001) and localities recorded in 2001–2017 period basing on the available resources (Górski et al. 2003, Krawczyk 2005, 2010, Bróż et al. 2006, Naks 2006, Nobis 2006, Podgórska 2007, 2013, Trojecka 2007, Bielecki 2008, Oklejewicz et al. 2010, Wolanin and Nykiel 2011, Jaźwa 2012, Koczywąs et al. 2012, Czarna and Górski 2013, Kalinowski 2013, Towpasz 2013, Gdula et al. 2014, Nowak 2014, Wolanin et al. 2014, Dyderski et al. 2015, Puchałka et al. 2015, Zając and Zając 2015, Zarzyka-Ryszka 2015, Dyderski and Jagodziński 2016, Pawlak 2016, Ryś 2016, Celka et al. 2017, Author 1 unpublished, Author 2 unpublished). Ten localities in six new sites surveyed in this study were also included. They were found and monitored while conducting ecological researches in the central and north-eastern Poland by authors.

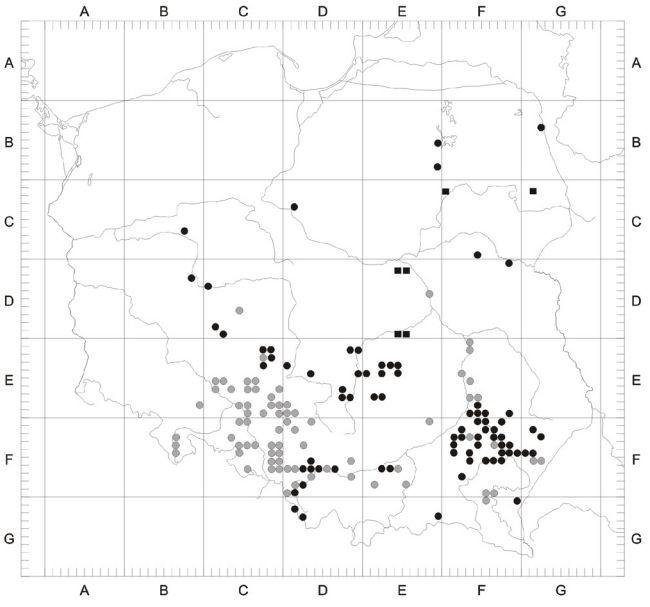

Figure 1. Distribution of *Erechtites hieraciifolia* in Poland
Grey dot – localities known to the end of 20th century (based on ATPOL (Zając and Zając 2001); black dot – other literature and unpublished data from 2001–2017; black square – own data, stands surveyed in 2017.

Colonization and recent distribution of Erechtites hieraciifolia – case study sites

Detailed study including distribution mapping was conducted in three sites. Two of them (Palmiry and Długie Bagno) are located in Kampinos National Park (KNP) in Central Poland (Figures 2a, b and c) in *E. hieraciifolia* present expansion zone. The species occupies the habitat of fire-disturbed oligotrophic semi-dry pine forest and recently dried bog pine forest in these localities (Table 1). The third study site is situated near Kiedrzyn village (South Mazovia, Figure 2d) and represents the population near the limit of range reached to the end of 20th century. In the vicinity of Kiedrzyn, the species is found within secondary oligotrophic Scots pine forest, especially in disturbed habitats. The colonization of *E. hieraciifolia* in surface-fire disturbed pine forest near Palmiry in KNP (Figure 2b) was investigated on the base of 45 permanent plots (100 m^2 each) established in

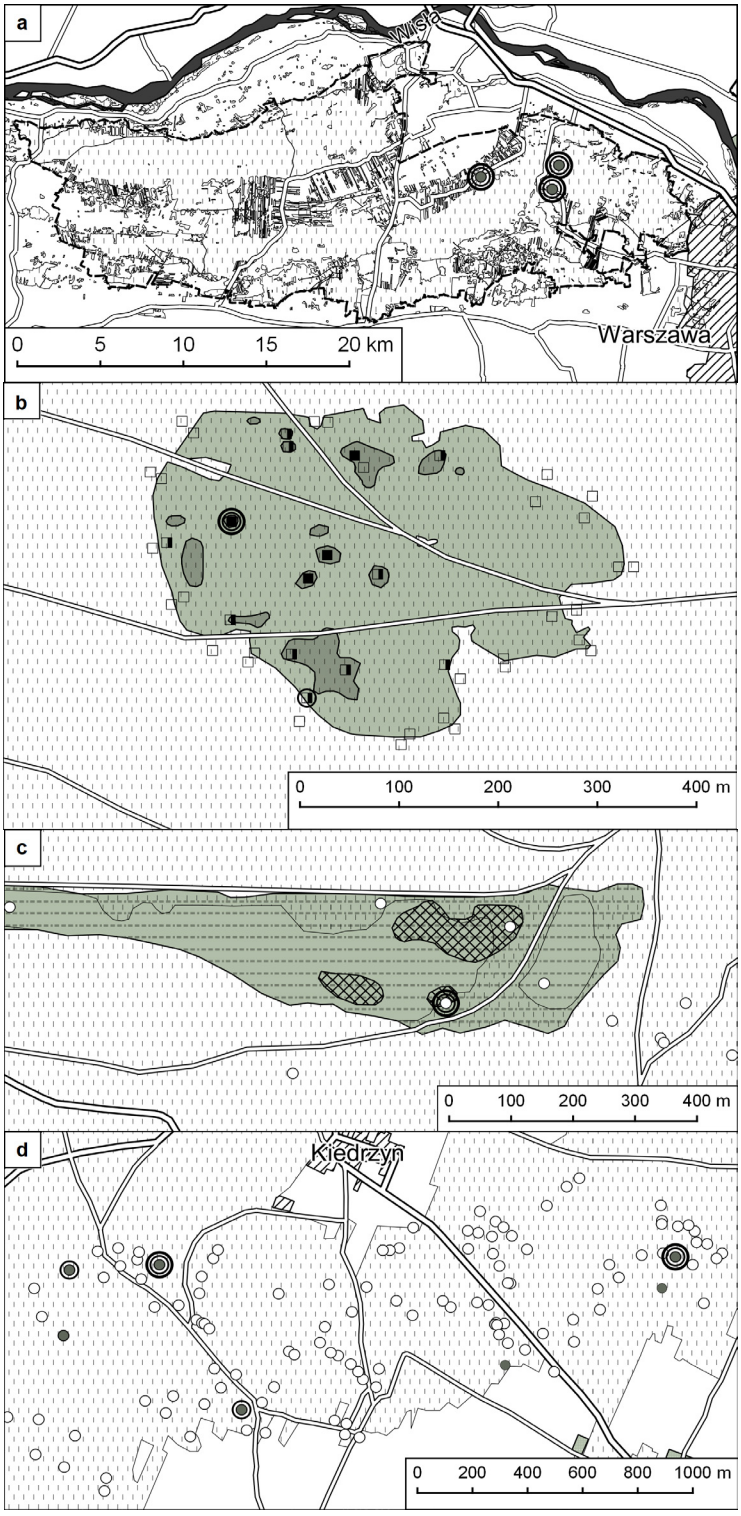

Figure 2. Study sites of *Erechtites hieraciifolia* spread in the expansion zone (a, b, c) and its distribution on the edge of the compact range (d)

a: localities of *E. hieraciifolia* in Kampinos National Park (KNP), b: distribution in post-fire area (Palmiry, KNP), c: distribution within transitional bog (Długie Bagno, KNP), d: distribution on the edge area of compact range (the vicinity of Kiedrzyn): 1 – Vistula river, 2 – main roads, 3 – border of KNP, 4 – main built-up areas, 5 – forests, 6 – week surface fire, 7 – intensive surface fire, 8 – transitional bog, 9 – area of *E. hieraciifolia*, 10 – stands of *E. hieraciifolia*, 11 – permanent plots (a – without *E. hieraciifolia*, b – with the species recorded only in 2017, c – with the species recorded in 2016 and 2017), 12 – localities of stands of the species sampled with relevés, 13 – localities of stands with individual measurements, 14 – relevé plots without *E. hieraciifolia*.

2015 immediately after two spring surface fires covering 10.92 ha. The fire intensity was measured as a percent of the area with total burnout of organic soil horizon. There were three types of permanent plots distinguished within the study area: not burned sites, surfacely burned ones and the sites with domination of total burnout of soil organic horizon (Zaniewski and Otręba 2017). The appearance of individuals and further expansion of *E. hieraciifolia* have been recorded while conducting vegetation sampling with relevé method each year since 2015. The spread of *E. hieraciifolia* within Długie Bagno transitional bog in KNP (Figure 2c) was assessed on the basis of comparison between sampling in 2015 [Author 3, Author 4, unpublished] with relevé method (Figure 2c) and the results of the population mapping in 2017. The third site (circa 300 ha) was located in pine and oak forests with admixture of recently abandoned fields

(Figure 2d). It was carefully mapped using a rout method in 2016 and 2017. All of the found stands of *E. hieraciifolia* were recorded. The other new sites were found in the clearcuts on the habitat of fresh mesic oak-pine forest and in the secondary pine forest plantations (details in Table 1).

Survey of selected features of biology and ecology

Ten from newly discovered stands of *E. hieraciifolia* were sampled using relevé method (area 100 m^2 each) with Barkmann et al. (1964) scale in autumn 2017 (Table 2). In this study the value "rr" was used for the smallest cover (circa 0,01%) of species registered within area of relevé. The number of stems were counted or estimated within each site. Six stands were chosen for more detailed measurement. Fifteen individuals were chosen randomly within each site (Table 1) and the measurements of their height, number of inflorescences on stems were carried out (Table 3). Three flower heads (sampled from top, side and bottom part of the plant) were collected from three randomly selected individuals on each place to test the number of achenes (Table 4) depending on inflorescences position (Celka et al. 2017). Counting the number of achenes in inflorescences from the collected individuals was carried out using stereomicroscope.

Data analysis and map preparation

The significance of differences in height and number of inflorescences between sampled individuals from six stands were verified using Kruskal-Wallis and Mann-Whitney *post hoc* tests with Bonferroni corrected *p*-values. The abundance data from phytosociological relevés (Table 2) was arithmetically transformed (Tüxen and Ellenberg 1937) and a weighted mean was used for further calculation. Ecological indicator values (L – light, T – temperature, K – continentality, W – moisture, Tr – trophy, R – acidity, D – granulometric index, H – organic matter content) for researched vegetation plots were calculated on the basis of Zarzycki et al. (2002). Only the values for non-tree species occurring in the herb layer were used and *E. hieraciifolia* was excluded in order to avoid self-explanation when describing the ecological spectrum of vegetation. Highly eurytopic species with the three-degree ranges of indicator values (in the five-degree scale) were excluded from analysis as not informative. The indicator values obtained for the researched stands were compared with values for *E. hieraciifolia* calculated by Zarzycki et al. (2002) using one-sample Wilcoxon test as well as the number of flower heads per plant and number of seeds within inflorescences in comparison with the literature data (Celka et al. 2017). Statistical analysis was conducted using PAST software (Hammer et al. 2001). The results were presented using a quartile method.

Results

Present distribution pattern of Erechtites hieraciifolia in Poland

To the end of 20th century *E. hieraciifolia* was known from 73 localities in Poland. From the beginning of 21th century the species has gained number of stands (78) mostly in south-eastern part of the Country and has spread to the north and north-east. The present distribution of *E. hieraciifolia* in Poland (Figure 1) can be characterized as more or less compact range in the southern part of the

Table 1. Localities of *Erechtites hieraciifolia* surveyed in autumn 2017

No. of locality	Name of locality and location in ATPOL grid	Geographical coordinates (WGS 84)	Habitat	No. of individuals	Relevé (100 m^2)	Individual measurements
1	Palmiry, KNP (ED15)	20°45'56,7"E; 52°20'26,9"N	Weakly burned fresh Scots-pine forest, inner part of protected big oligotrophic pine forest complex	≈50*	+	
2	Palmiry, KNP (ED15)	20°45'53,0"E; 52°20'32,9"N	Severely burned fresh Scots-pine forest, inner part of protected big oligotrophic pine forest complex	≈200*	+	+
3	Długie Bagno, KNP (ED14)	20°45'29,3"E; 52°19'46,7"N	Edge of transitional bog and Scots-pine bog forest, inner part of protected big oligotrophic pine forest complex	≈300*	+	+
4	Janówek, KNP (ED14)	20°41'43,5"E; 52°20'13,7"N	Gaps in young mesic secondary Scots-pine forest caused by *Heterobasidion annosum* (Fr.) Bref., edge part of protected big oligotrophic pine forest complex	≈500	+	+
5	Płoszyce, Równina Kurpiowska (FC10)	21°36'50,3"E; 53°13'33,7"N	A wild trash dump in the small sand excavation hole in young secondary Scots-pine forest, small forest complex adjacent to big oligotrophic pine forest complex	71	+	+
6	Kiedrzyn, Równina Radomska (ED95)	20°44'10,1"E; 51°35'37,2"N	Small windthrow in young Scots-pine forest within small secondary pine forest complex, adjacent to medium oligotrophic (partially mesic) pine forest complex	38	+	+
7	Kiedrzyn, Równina Radomska (ED94)	20°42'32,7"E; 51°35'37,7"N	Small gaps in young mesic secondary Scots-pine plantation, adjacent to medium oligotrophic (partially mesic) pine forest complex	≈100	+	+
8	Kiedrzyn, Równina Radomska (ED94)	20°42'15,7"E; 51°35'37,3"N	Scots-pine forest clearcut within small secondary pine forest complex, adjacent to medium oligotrophic (partially mesic) pine forest complex	7	+	
9	Kiedrzyn, Równina Radomska (ED94)	20°42'47,5"E; 51°35'20,0"N	Abandoned Scots-pine forest clearcut with spontaneous *Quercus petraea* (Matt.) Liebl. Succession on the edge of oligotrophic secondary pine forest, adjacent to medium oligotrophic (partially mesic) pine forest complex	3	+	
10	Zielona, Puszcza Knyszyńska (GC11)	23°18'46,3"E; 53°09'41,9"N	Clearcut on the habitat of fresh mesic oak-pine forest with admixture of Norway spruce in the tree stand	1	+	

KNP – Kampinos National Park, * – total number of individuals both in Palmiry post-fire area and Długie Bagno transitional bog in KNP were estimated at > 2000 per each site, + – the research carried out.

Table 2. Phytosociological documentation of the researched localities of *Erechtites hieraciifolia*

Number of locality	1	2	3	4	5	6	7	8	9	10
Name of stand	Palmiry	Palmiry	Długie Bagno	Janówek	Płoszyce	Kiedrzyn	Kiedrzyn	Kiedrzyn	Kiedrzyn	Zielona
Year	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017
Area of relevé [m^2]	100	100	100	100	100	100	100	100	100	100
Slope	6°NW	13°S	2°NW	0°	0°	2°N	2°W	1°NW	0°	1°S
Texture of topsoil	sand	sand	decomposed peat on sand	sand	sand	sand	sand on clay	sand	sand	sand on clay
Cover of upper tree layer A1 [%]	30	1	20	30	40	20	50	0	0	0
Cover of lower tree layer A2 [%]	3	0	5	0	5	5	0	0	0	0
Cover of tree layer A [%]	33	1	25	30	45	25	50	0	0	0
Cover of shrub layer B [%]	0.5	1	20	5	0.5	15	3	10	25	0
Cover of herb layer C [%]	18	50	80	25	15	5	30	35	10	15
Cover of moss layer D [%]	7	11	35	80	50	90	75	20	15	0.5
weighted mean ecological indicator values										
Light (L) value	3.65	3.47	3.59	2.79	2.40	3.44	1.95	3.84	3.85	3.16
Temperature (T) value	2.97	3.19	2.90	2.32	2.23	3.05	2.30	3.02	2.89	3.33
Continentality (K) value	3.01	2.79	2.99	2.19	2.29	2.82	1.99	2.98	2.94	2.92
Moisture (W) value	2.91	2.67	4.28	2.23	2.16	2.52	1.97	3.04	2.46	2.97
Trophy (Tr) value	2.39	2.75	1.90	2.31	2.25	2.19	2.18	2.27	2.25	3.18
Acidity (R) value	2.89	2.92	2.03	2.29	2.20	2.90	2.37	2.64	3.05	3.38
Granulometric index (D) value	3.31	3.15	1.75	2.52	2.60	3.09	2.16	3.55	3.05	3.70
Organic matter content (H) value	2.07	1.71	2.70	1.44	1.37	1.50	1.30	2.06	1.82	1.97
tree species										
Betula pendula A2			1			2a				
Betula pendula B				r				+	+	
Betula pendula C	+	1		+		1	rr	1	+	
Betula pubescens B			2a							
Betula pubescens C			+							
Pinus sylvestris A1	3a	+	2b	3a	3b	2b	3b			
Pinus sylvestris A2	+				1	1				
Pinus sylvestris B								1	+	
Pinus sylvestris C	+	+		r	rr	+		2a		
Populus alba C		r								
Populus tremula B		+		r					r	
Populus tremula C	+	2b		r		rr			rr	
Quercus petraea B						1	+	1	2b	
Quercus petraea C						+	r	1		
Quercus robur A2	1									
Quercus robur B					+			1		
Quercus robur C	+	r		r	r					
shrub species										
Frangula alnus B	+		2a	1		r	1			
Frangula alnus C	+		1			rr	r			
Juniperus communis B						+		1		
Juniperus communis C						rr	rr		rr	
Prunus padus C				rr						
Prunus serotina B				+						
Ribes nigrum C					rr					
Salix caprea C	r	r								
Sambucus nigra B				r						
Sambucus nigra C				+						
Sorbus aucuparia B			r							
Sorbus aucuparia C			rr							
Rubus ideaeus C				1			r			1
Rubus nessensis C										1
Rubus plicatus C							2a		r	
dwarf shrubs and semishrubs										
Calluna vulgaris	+	+			+			2a		
Ledum palustre			2a							
Solanum dulcamara	r						r			
Vaccinium myrtillus	2a		2b	rr		r		2a	+	
Vaccinium uliginosum			1							
Vaccinium vitis-idaea	+		1					+		r
forbs										
Atriplex prostrata					+					
Bidens frondosa			r							
Chelidonium majus										1
Convallaria majalis	+	r								
Conyza canadensis	+	2a			r					+
Chamaenerion angustifolium		+					+			
Epilobium hirsutum	r									
Epilobium montanum		+								
Epilobium roseum		+								
Erechtites heraciifolia	+	1	1	2a	1	+	1	r	rr	r
Fragaria vesca										1
Galeobdolon luteum										1
Galeopsis tetrahit									rr	
Geranium robertianum				+			1			+
Gnaphalium sylvaticum			r							
Helichrysum arenarium			r							
Hieracium lachenalii			r							
Hieracium pilosella	+		+	1	+	rr	rr		+	
Hypochoeris radicata				r						r
Leontodon autumnalis	r		+							

Table 2. Phytosociological documentation of the researched localities of *Erechtites hieraciifolia* (continued)

Number of locality	1	2	3	4	5	6	7	8	9	10
Lysimachia vulgaris				r						
Melampyrum pratense	1		r		+			rr		
Moehringia trinervia							1			
Mycelis muralis							2a			
Oxalis acetosella										+
Polygonatum odoratum	r									
Polygonum hydropiper		r								
Polygonum minus	r									
Rumex acetosa				r					rr	
Rumex acetosella	+	+		1	1	+	1	rr	rr	1
Scrophularia nodosa							rr			
Senecio jacobea		r								
Senecio sylvaticus	r	+				rr			rr	+
Solidago gigantea	r	+		r						
Solidago virgaurea				rr	r					+
Sonchus arvensis		r								
Sonchus asper		r								
Sonchus oleraceus		r								
Stellaria media										+
Taraxacum officinale	r	r			rr					
Trifolium pratense					r					
Urtica dioica					1					+
Veronica officinalis										1
Vicia sylvatica										+
Viola reichenbachiana										+
vines										
Humulus lupulus				1						
ferns										
Dryopteris carthusiana			r	1		r	1			r
Pteridium aquilinum							r			
graminoids										
Agrostis capillaris				1	r				rr	+
Agrostis gigantea				+						
Antoxanthum odoratum									rr	
Calamagrostis arundinacea										1
Calamagrostis canescens			1							
Calamagrostis epigejos	r	1	r					r	+	
Carex digitata										1
Carex pilulifera							r	1		
Corynephorus canescens		r								
Deschampsia caespitosa				r						
Deschampsia flexuosa			+	+	+					
Eriophorum vaginatum			3b							
Festuca ovina	1	+		+	r				1	
Holcus lanatus				r						
Holcus mollis									+	
Juncus effusus								rr		+
Juncus tenuis										r
Luzula campestris								rr		
Luzula pilosa										+
Milium effusum										r
Poa compressa				rr			r			
bryophytes										
Brachythecium rutabulum					rr					
Ceratodon purpureus	1	1								
Dicranum polysetum	r	r	+		1	1		2b	2a	
Dicranum scoparium		r	2a		+	rr	rr		+	
Hylocomnium splendens	+				rr					r
Hypnum cupressiforme					r					
Leucobryum glaucum			rr							
Marchantia polymorpha	r	+								
Plagiomnium affine										+
Plagiothecium laetum							+			
Pleurozium schreberi	+	r	2b	1	3b	5b	4b	1	1	
Pohlia nutans	r	r				rr				
Polytrichum juniperinum	+	2a								
Polytrichum piliferum					rr					
Pseudoscleropodium purum	r									
Sciuro-hypnum oedipodium				4a			1			
Sphagnum fallax			1							
lichens										
Cetraria islandica					r					
Cladonia chlorophaea agg.					rr					
Cladonia fimbriata					rr			rr	+	
Cladonia furcata			r		1					
Cladonia gracilis					rr					
Cladonia macilenta agg.					rr			rr	r	
Cladonia mitis					rr					
Cladonia subulata agg.									r	
Placynthiella dasaea								rr		
Placynthiella oligotropha								r		

Table 3. Height and number of flower heads of sampled individuals of *Erechtites hieraciifolia* within researched localities

Number of a locality	2	3	4	5	6	7
No. of an individual	height [cm]					
1	130	140	115	160	65	65
2	115	70	40	50	50	90
3	20	80	65	155	70	85
4	75	90	60	140	55	70
5	50	150	95	60	70	105
6	45	100	55	60	70	45
7	70	90	80	60	40	60
8	120	100	105	135	60	45
9	100	120	50	100	65	50
10	55	40	75	95	35	90
11	50	140	60	80	100	80
12	105	150	105	80	45	120
13	130	100	85	85	60	25
14	115	100	100	140	65	30
15	85	110	100	40	50	60
No. of an individual	number of flower heads per an individual					
1	41	41	17	144	9	3
2	38	25	1	9	16	13
3	1	29	7	38	15	8
4	34	10	8	28	17	8
5	27	64	25	10	21	33
6	11	10	7	27	6	4
7	21	11	15	29	3	6
8	43	16	25	28	9	2
9	34	11	4	22	21	4
10	5	3	8	24	5	19
11	7	42	9	18	45	17
12	32	57	10	17	1	28
13	68	39	10	18	5	2
14	62	16	33	31	22	4
15	38	45	35	6	14	7

Country and expansion zone, which is located north from it. The new stands discovered by us are located in six plots of the ATPOL cartogram grid. Two of them are located on the edge of the compact range of the species in the southern part of Mazovia and the four ones – in the expansion zone.

Colonization and local dispersion

E. hieraciifolia was registered in three sites in KNP (Janówek, Palmiry and Długie Bagno, Figure 2a). Expansion of the species within permanent plots on post-fire area (Palmiry) was presented on Figure 2b. The species did not appear within any of permanent plots in the vegetation season in the year of fire (2015). The colonization has started in 2016, beginning from four severely burned plots. The species spread for next ten plots in 2017, occupying both weakly and severely burned ones.

Distribution of *E. hieraciifolia* in the eastern part of Długie Bagno transitional bog was presented on Figure 2c. The species was not found within relevé plots and their closest surroundings in 2015, but was already present within two of them in 2017. The observed local area of occupancy consisted of three patches and covered 1.82 ha (ca 10%) of the open transitional bog and Scots-pine bog forest.

Pattern of distribution of *E. hieraciifolia* on the site located on the border area of the present compact range (Southern Mazovia, Kiedrzyn vicinity) was shown on the Figure 2d. The species was found on six stands in 2016 (within five relevé plots and one additional observation). In 2017 it was still occupying all of them and was found in new locality on the forest dirt-road edge. The distance between stands varied between (100) 250 and 650 m.

Table 4. Numbers of seeds per investigated flower heads of sampled individuals of *Erechtites hieraciifolia*

Locality no.	No. of an individual	Height [cm]	Number of flower heads	No. of seeds per flower head			Mean number of seeds per flower head	Total number of seeds per an individual
				top	side	bottom		
2	4	75	34	168	138	145	150.3	5111
2	9	100	34	134	166	125	141.7	4817
2	14	115	62	133	140	176	149.7	9279
3	2	70	25	130	140	135	135.0	3375
3	8	100	16	122	71	104	99.0	1584
3	1	140	41	217	145	133	165.0	6765
4	4	60	8	110	116	105	110.3	883
4	5	95	25	138	135	85	119.3	2983
4	1	115	17	147	97	139	127.7	2170
5	2	50	9	131	166	133	143.3	1290
5	3	155	38	101	139	104	114.7	4357
5	1	160	144	134	63	155	117.3	16896
6	10	35	5	98	149	97	114.7	573
6	1	65	9	155	135	236	175.3	1578
6	11	100	45	204	227	145	192.0	8640
7	9	50	4	128	131	129	129.3	517
7	3	85	8	172	164	121	152.3	1219
7	12	120	28	143	164	199	168.7	4723

Selected features of biology and ecology of the species in the expansion zone

Locations and habitats of the surveyed stands of *E. hieraciifolia* are presented in Table 1. The species was found especially in disturbed patches and in wet habitat in one case (Table 2). Height of measured individuals ranged between (20)60–100(160) cm with the median of 80 cm (Figure 3a, Table 3). There was a significant difference between height of the plants in the dataset ($p = 0.003$). The relevant difference was noticed between Długie Bagno (3) and Kiedrzyn (6) stands ($p = 0.002$), and also between Długie Bagno (3) and Kiedrzyn (7) stands ($p = 0.044$). Number of inflorescences per one individual of *E. hieraciifolia* varied between (1)8–30(144) with the median of 16 (Figure 3b). There was a significant difference between the number of inflorescences in the analyzed dataset ($p < 0.001$). The relevant difference was found between Płoszyce (5) and Kiedrzyn (7) localities ($p = 0.036$).

The number of seeds did not differ between distinguished positions of heads on the plants ($p > 0.05$). It varied between (98)126–158(217) with the median of 134 for the heads situated on the top parts of the plants, (63)127–164(227) with the median of 140 for the side heads and (85)105–148(236) with the median of 133 for the bottom ones (Table 4). Total number of seeds per flower head varied between (63)122–155(236) with the median of 135. Calculated total number of seeds per sampled plant varied between (517)1272–5524(16896) with the median of 3179. The differences between analyzed stands in seed numbers per flower head and seed number per individual were generally smaller than between individuals within them.

Ecological preferences of Erechtites hieraciifolia on newly colonized sites

Ecological indicator values calculated on the basis of amplitudes of the species of herbaceous plants accompanying *E. hieraciifolia* are as follows: L (light) – (1.95)2.69–3.70(3.85) with the median of 3.46, T (tem-

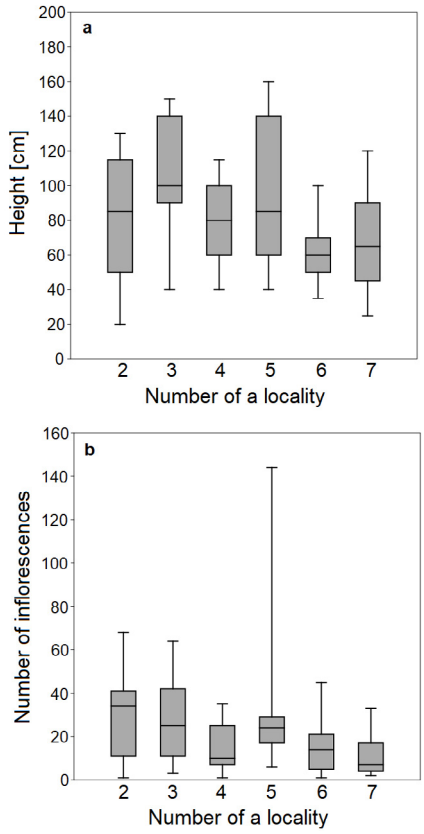

Figure 3. Distribution of selected parameters of *Erechtites hieraciifolia* (quartile method) in the researched localities (2 – Palmiry, 3 – Długie Bagno, 4 – Janówek, 5 – Płoszyce, 6 – Kiedrzyn, 7 – Kiedrzyn): a – height of individuals, b – number of inflorescences per individual

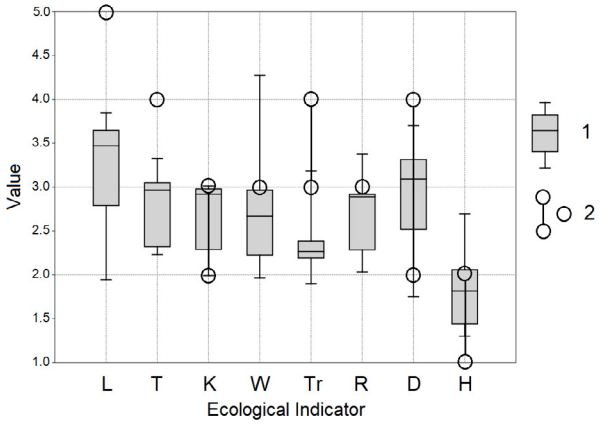

Figure 4. Ranges of indicator values based on the herb layer vascular plant species in researched localities
1 – ranges of the indicator values in the localities (quartile method), 2 – ranges of the indicator values of *Erechtites hieraciifolia* in southern Poland (based on Zarzycki et al. 2002), L – light, T – temperature, K – continentality, W – moisture, Tr – trophy, R – acidity, D – granulometric index, H – organic matter content.

perature) – (2.23)2.31–3.09(3.33) with the median of 2.94, K (continentality) – (1.99)2.26–2.98(3.01) with the median of 2.87, W (moisture) – (1.96)2.21–2.98(4.28) with the median of 2.59, Tr (trophy) – (1.90)2.19–2.48(3.18) with the median of 2.26, R (acidity) – (2.03)2.26–2.95(3.38) with the median of 2.77, D (granulometric index) – (1.75)2.43–3.37(3.70) with the median of 3.07 and H (organic matter content) – (1.30)1.42–2.06(2.70) with the median of 1.77 (Figure 4).

Discussion

Does Erechtites hieraciifolia expansion proceed in two-steps in Poland?

Since the beginning of the 21th century the new localities of *E. hieraciifolia* have been observed, outstanding the range limit reached earlier by the species and crossing Central Poland latitudinally. They are located even 200–300 km north from these ones known at the end of 20th century (Figure 1). This may be a manifestation of the new stage of the expansion of the species.

There are four main steps of biological invasion of alien species distinguished according to di Castri (1990) and other authors (Kornaś 1990, Theoharides and Dukes 2007): first – introduction / transport, second – colonization, third – naturalization / establishment and forth – landscape spread. According to Kornaś (1990), four stages of naturalization of alien species are distinguished: first – introduction of propagules and emergence of first individuals, second – establishment in heavily disturbed sites, third – colonization of less disturbed sites and fourth – invasion into undisturbed sites. Each stage is considered to be more difficult to achieve by alien species. The observed expansion of *E. hieraciifolia* in the 21th century may be fit in both models and compared to second and third stages of the process.

Several main reasons of contemporary spread can be considered. The first one is the climate change, which in Poland is manifested mainly by the annual temperature increase (Kundzewicz and Matczak 2012). The second one may be connected to the extension of ecological amplitude of *E. hieraciifolia*. The species seems to be more shade tolerant at the researched stands than in the main distribution range in Poland (Figure 4). Changes in the light tolerance of the alien plant across only 15-year time interval were recently proved for *Persicaria cespitosa* (Blume) Nakai in North America (Matesanz et al. 2015). Changing in the ecological preferences may have enabled the species to invade also less disturbed habitats. Another reason may be connected with breaking-through the geographical and climatic limits due to new-coming vectors of propagation. In the case of *E. hieraciifolia* the long-distance dispersal by vehicles could play an additional role, as the alien species can spread by this way (von der Lippe and Kowarik 2007). This vector, probably crucial in economic forests, has some limitations, because it cannot explain well encroachment of the species into the core areas of natural mainstays such as KNP. Probably the above-mentioned factors could also work simultaneously.

Propagation of Erechtites hieraciifolia in the species expansion zone

Until recently *E. hieraciifolia* was not known from KNP (Bomanowska et al. 2014). The expansion of *E. hieraciifolia* in post-fire area near Palmiry (Figure 2b) did not start in the year of fire. Due to the fact that the species is perennial, it may be assumed that the colonization started thanks to seed dispersion from outside of the post-fire area. It appeared at four severely burned plots and also in their most damaged surroundings one year after the disturbance. This indicates that the number of achenes being recently available in the landscape scale is relatively high. In the second year it spread to the next plots, including weakly disturbed ones, but still did not appear in control sites. It can be assumed that the chance of successful invasion of the species increases thanks to severe disturbance, resulting here also by many weed and pyrophilous fungi encroachment (Gierczyk et al. 2017, 2019, Zaniewski and Otręba 2017). The colonization could be continued in other available disturbed sites, but it was not possible in intact pine forest surrounding. The strong preference of the species to the disturbed sites in not-wet habitats was also confirmed within other stands from southern Poland (Kucova 1971, Sowa and Warcholińska 1992, Zarzycki et al. 2002, Tokarska-Guzik et al. 2009).

The species was not found during the inventory of Długie Bagno transitional bog (KNP) in 2015 (when five relevés within the site were carried out as well as additional ones in close pine forests). After two years it appeared in two sample sites, where was absent in 2015 and its local area of occupancy was relatively extensive. Due to this fact, it can be assumed that *E. hieraciifolia* became at least much more widespread there between 2015 and 2017. This corresponds to the low precipitation in the area in 2015, which caused desiccation of the bog and the development of young generation of birch in 2016 as a result (Tyburski 2017). It is highly probable, that *E. hieraciifolia* was scarce or maybe even absent in the site and it considerably extended its local area of occupancy after low precipitation season, when the habitat became drier. The ability of the species to invade disturbed wet ecosystems was reported also from its main range (Kucova 1971, Sowa and Warcholińska 1992, Tokarska-Guzik et al. 2009).

The recent distribution of *E. hieraciifolia* in Kiedrzyn study site was elaborated on the basis of intensive fieldworks (including 114 relevés overtaken and more than 100 vegetation observation points within the 300-ha site). For these reasons it can be assumed that it reflects the present state of spread of the species in the landscape within border zone of expansion range. The stands of the species are scattered (Figure 2d) and the tendency to increase the number of localities is not evident (it gained only one new stand between 2016 and 2017). *E. hieraciifolia* occurred mainly in young Scots pine stands, on clearcuts, forest dirt-road edges and small windthrows (Table 1). This corresponds well with the preferences of the species to inhabit the initial clearing vegetation (included to *Epilobietea angustifolii* Class) in the southern Poland (Zarzycki et al. 2002). The local population of the species seems to be more stable than in habitats disturbed by surface-fire (Figure 2b) or water-level drop (Figure 2c).

Height of individuals, number of flower heads and seeds

The height of the researched specimens was not strongly differentiated. In general, the higher individuals were growing in more open and wet habitats of Długie Bagno, while lower ones occupied small gaps within dense pine stands in Kiedrzyn localities. These could indicate the possible positive influence of light and/or water to the increase of the height of the plants. In Wielkopolska (W Poland) and Zhytomyr (Ukraine) regions (Celka et al. 2017) part of the individuals were less than 100 cm and some of them were taller than this. It the researched part of the species expansion zone most of the plants were smaller than 100 cm and the median size was 80 cm. The height range of researched populations (Figure 3b) is probably similar to these from Wielkopolska and Zhytomir regions.

Individuals from the populations of *E. hieraciifolia* expansion zone in Wielkopolska and Zhytomyr regions (Celka et al. 2017) produce up to 50 inflorescences per smaller (up to 1 m) individual and about 120 flower heads per larger individual (above 1 m in height). The populations researched in this part of species expansion zone produce significantly less ($p < 0{,}001$) flower heads (Figure 3b). This may mean the worse species performance.

The variation in number of achenes between flower heads located in the different parts of the plant was not statistically relevant in the analysed part of the population. It is probably much smaller than in the case of specimens collected from Wielkopolska and Zhytomyr regions (Celka et al. 2017). The analysed flower heads contain significantly less achenes ($p < 0.001$) than in the other parts of the species expansion zone (180) reported by Celka et al. (2017). The total number of seeds produced by one individual is also smaller. It starts from only half thousand, the maximum is less than 17 thousand and the median is only a bit more than three thousand. The degree of threat by alien species is often assessed on the basis of seed production. It can be assumed that researched population of *E. hieraciifolia* is less invasive than the other ones.

Differences in preferences to light and fertility conditions between the populations from the main range and the expansion zone

Ecological indicator values for plants in Poland were prepared at the end of 20th century (Zarzycki et al. 2002). Due to this fact, they referred to habitat conditions in former range of *E. hieraciifolia*, which was limited to southern part of the Country. This made the possibility to compare the ecological conditions of the researched stands in

the analyzed part of expansion zone with the main range of the species (Figure 4). The surveyed stands differed significantly ($p < 0,05$) by lower values for light (L), temperature (T), trophy (Tr) and acidity (R). The other ecological values did not differ significantly. The use of ecological indicator values has some limitations in disturbed habitat patches. However, the recorded differences indicated the possibility of population of *E. hieraciifolia* to exhibit at least more wide ecological amplitude in the analyzed part of the species expansion zone. On the other hand, this can also indicate the occurrence of suboptimal conditions for the species at the observed sites. The shortage of light and nutrients could result in lower seed productivity observed by us. Both possible behaviors can be taken in consideration while conducting new research on the expansion of the species.

The threat from Erechtites hieraciifolia

E. hieraciifolia is considered to be invasive in Poland (Koczywąs et al. 2012, Celka et al. 2017). In spite of the extensive fieldworks conducted by authors in many areas of the central and north-eastern Poland in 2015–2017, only a few locations of the species were found. The species was not previously known from KNP (Bomanowska et al. 2014). This indicates that in the last few years the species was not widespread in this part of Poland. The case studies conducted in the analyzed part of the species expansion zone showed that in dry and semi-dry habitats the expansion generally starts from the most disturbed patches and is continued in the less disturbed ones. The species was found in burned sites, clearcuts, gaps in forests caused mainly by windfalls and fungal parasites, forest dirt-road edges and trash dumps. This confirms its preferences to initial, unstable communities, which occurs only at the first stage of regeneration of forest vegetation. The present density of localities on the edge of the species main range (Kiedrzyn) also reflects this distribution pattern. On the other hand, the possibility of expansion of *E. hieraciifolia* inside wetlands needs much more attention. Present distribution of the species observed within Długie Bagno transitional bog (with 10% frequency in relation to whole area in 2017) in KNP raises some concerns. The species can become a serious threat in the nearest future in this site, which preserved some endangered and legally protected plant species including *Chamaedaphne calyculata* (L.) Moench population on the south-western edge of its distribution in Europe (Kobendza 1930, Zając and Zając 2001). The observed situation needs further monitoring. Tokarska-Guzik et al. (2009) described the possibility of massive encroachment of *E. hieraciifolia* into clearcuts on wet habitats. In this study, the highest numbers of individuals were found in seriously disturbed and wet ecosystems. Due to this, it can be assumed that the species may also be a threat on the clearcuts in wet habitats within managed forest stands.

Conclusions

- the rapid expansion of *Erechtites hieraciifolia* observed in Poland started from the beginning of 21th century; it may be the second step of expansion of the species in Central and North Eastern Europe, caused probably by climate change, the expansion of the species ecological preferences or/and breaking-through the geographic barriers due to occasional long-distance transport;
- in the analyzed part of the expansion zone the dispersion of the species can start from the most disturbed sites and be continued in more natural ones; the encroachment to the undisturbed sites was not observed;
- at the edge of the species main range, it can be found in many diffuse stands, mainly within disturbed patches of the landscape;
- the production of flower heads and achenes by the individuals is significantly lower than in the adjacent parts of the former species expansion zone;
- in the analyzed part of the expansion zone the species grows in lower conditions of light, temperature, trophy and acidity than in the main range in the southern Poland; this may indicate the changes in the species ecological amplitude and be the reason of the worse reproduction success;
- on the basis of the obtained results the species is considered to create now only a moderate threat to the (semi)natural vegetation, but the possibility of its expansion to disturbed wetland sites needs much more attention.

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