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Local distribution pattern of *Virga pilosa* (L.) Hill. (Dipsacaceae) as an effect of its life and dispersal strategy

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Abstract. A new locality of regionally alien and rare *Virga pilosa* was recorded outside the compact range of the species in the Wielkopolski National Park, midwestern Poland. It probably appeared as a result of unintentional anthropochory. Local distribution pattern of *V. pilosa* in micro- and mesoscale was described and interpreted in the light of life and dispersal strategy and habitat conditions of the species. Accidental epizoochory and unintentional anthropochory could have been responsible for the mesoscale distribution pattern with population units scattered along human and animal communication routes. Close dense autochory together with the species CR life strategy with a strong competitive component were responsible for microscale distribution pattern alternating in space and time, but always mosaic, including vegetative, generative and mixed patches. The distribution pattern was also influenced by the occurrence of the required combination of the moderately light, moderately moist and nitrogen-rich habitat conditions with favourable human-induced disturbance. Some data on the form of growth, reproductive potential and dispersal mode of the species, as well as on plant-animal interactions were also included.

Key words: *Dipsacus pilosus*, habitat conditions, ecological disturbance, seed dispersal, Wielkopolski National Park, Poland

1. Introduction

Virga pilosa (L.) Hill. (*Dipsacus pilosus* L., according to the World Flora Online 2020) is a widely distributed European species, occurring from western France to central Ukraine with smaller range parts in the Pyrenees, England and the Caucasus region (Meusel & Jäger 1992). Considering floristic zonation, it is classified as a temperate European species (Zając & Zając 2009) or the species related to the submeridionale/mountainous and southern temperate zones (Bräutigam 2017).

Geobotanical studies in the Wielkopolski National Park (called WNP below) started at the beginning of the 19th century and were relatively intensive (Żukowski *et al*. 1995). Flora of this area is, therefore, well-recognised. No information on *Virga pilosa* from the WNP is included in literature, neither in the synthetic study of the WNP flora, including all historical data (Żukowski *et al.* 1995), nor in later publications.

The first documented record of *Virga pilosa* in Wielkopolska (the Greater Poland region, midwestern Poland) originates from 1992 (A. Brzeg, unpublished phytosociological relevés in vegetation patches with this species in the forest near Będlewo). Occurrence of *V. pilosa* was confirmed in that area in 2007 during inventory studies for the future Natura 2000 network. Large populations of this species were discovered at the time in Będlewo forest district, situated close to the WNP (Stachnowicz & Rakowski 2013).

Our study aims to describe a new population of *Virga pilosa*, and especially its local spatial pattern as a consequence of combined species life and dispersal strategy and habitat conditions.

2. Materials and methods

Field research in the main subpopulation (A) was carried out in two vegetation seasons in 2019 and 2020.

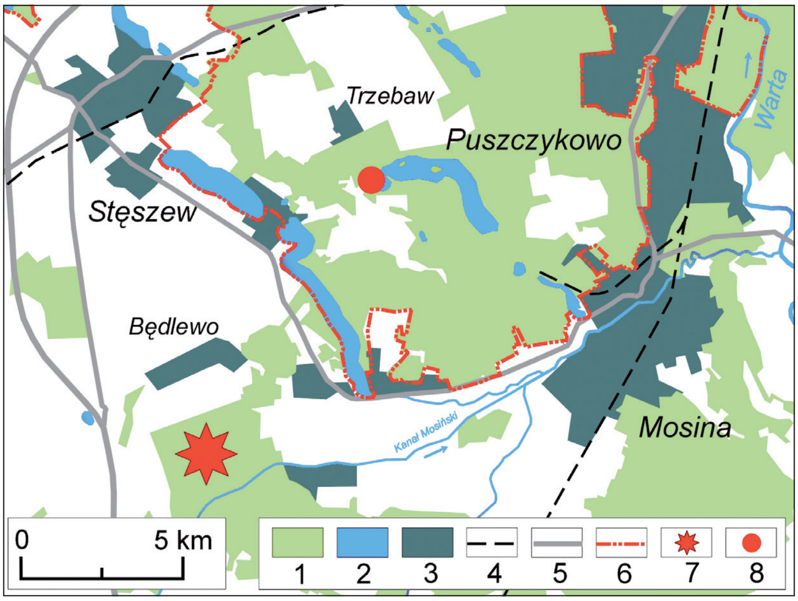

Fig. 1. Distribution of *Virga pilosa* localities in central Wielkopolska (the Greater Poland region)

Explanations: 1 – forest, 2 – waterbodies, 3 – built-up areas, 4 – railway track, 5 – main roads, 6 – boundaries of the Wielkopolski National Park, 7 – location of the nearest population in the forest area near Będlewo (Stachnowicz & Rakowski 2013), 8 – a new locality at Góreckie Lake

Other population units, i.e. subpopulations (B, C) and scattered individuals (d-g) were studied in 2020 (cf. Table 1, Figs 1-2).

During each visit, area covered by a subpopulation was estimated and numbers of generative and vegetative (rosettes in the first year of life) individuals were counted or at least estimated. The local pattern of distribution was also studied, at both the microscale and mesoscale. In the research, microscale is understood as within a subpopulation (generative and vegetative individuals), mesoscale as within a locality (with population units, i.e. subpopulations and individuals, scattered but still spatially related and situated rather close to each other) and macroscale as describing the level of dif-

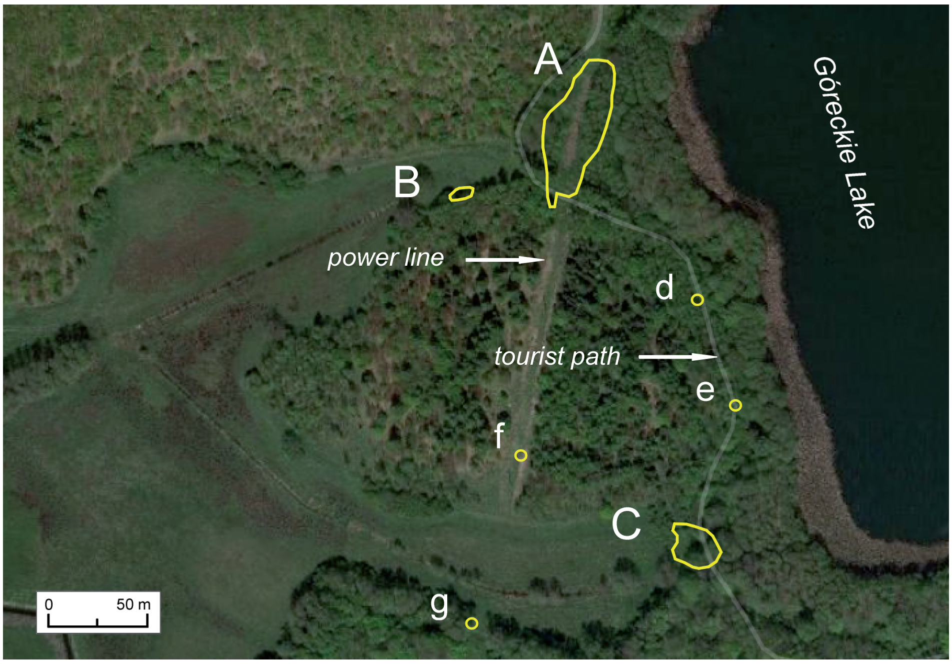

Fig. 2. Detailed presentation of the locality of *Virga pilosa* at Góreckie Lake (against a background of https://www.google.com/maps/)

Explanations: A – main subpopulation; B, C – smaller subpopulations; d, e, f, g – scattered individuals

Table 1. Location parameters of a new locality of *Virga pilosa* in the Wielkopolski National Park

Population unit	Location
	Geographical coordinates
A	52.265517, 16.770956
B	52.265267, 16.770141
C	52.263695, 16.771712
d	52.264808, 16.771826
e	52.264345, 16.772102
f	52.264087, 16.770501
g	52.263422, 16.770250
	Administrative address
A, B, C, d, e, f, g	Stęszew commune
	Forest address (compartment & subcompartment)
A	98-91-1-55-02122A-c-00 (122A-c)
B, f	98-91-1-55-02122A-d-00 (122A-d)
C	98-91-1-55-02122A-f-00 (122A-f,i)
d, e	98-91-1-53-02123-a (123-a)
g	98-91-1-55-02125A-o (125A-o)
	ATPOL code
A, B, C, d, e, f, g	BD1787

Explanations: A main subpopulation, B-C smaller subpopulations, d-f scattered plants; Coordinate system WGS84. Forest address according to BDL (2020). ATPOL square code in the 1x1 km grid (komsta.net/atpol)

ferent distant localities, e.g. situated in different forest complexes. This division was very clear in the study area and species.

The growth form of generative individuals was checked and their height was measured.

Additionally, some data on the species reproductive and dispersal potential were collected. Morphological features of collected fruits were studied with the use of stereomicroscope in the context of their dispersal possibilities.

Structure of vegetation patches with *Virga pilosa* was documented in six phytosociological relevés, made in the main subpopulation (A) according to the Braun-Blanquet's method (1964). Syntaxonomic structure of patches was given according to the scheme proposed by Stachnowicz & Rakowski (2013) to directly compare new data with data collected near Będlewo by those authors.

Scientific names of species are given according to the checklist of vascular plants of Poland (Mirek *et al*. 2002).

The collected specimens are in the herbarium of Nature Collections, Faculty of Biology, Adam Mickiewicz University in Poznań, Poland (POZ). Rich photo documentation of the new population was also taken.

3. Results

3.1. Location

New locality of *Virga pilosa* is situated in the central part of the Wielkopolski National Park, near western end of Góreckie Lake, 1.2 km SSW of Trzebaw (Figs 1-2, Table 1). According to the modified J. Kondracki's geographical regionalisation of Poland (Solon *et al*. 2018), it is situated in Pojezierze Wielkopolskie macroregion (Greater Poland Lakeland) and Wysoczyzna Grodziska mesoregion (Grodzisk Heights).

3.2. Population size and pattern

In 2020, the described population of *Virga pilosa* included seven detected units: three subpopulations (A, B, C) and four scattered plants (d, e, f, g) (Tables 1-2, Fig. 2). Their total area covered ca. 1500 m^2, with more than 80% covered by the main subpopulation (A). The total size of population was estimated at ca. 3600 individuals, with ca. 14% of generative fraction (Table 2).

Straight-line-distances between particular population units ranged between 50 and 220 m, with 50 m between A and B and 130 m between A and C (210 m along a path).

Virga pilosa was exclusively a biennial plant in the study area; no perennial individuals were found. Each subpopulation included both virgin rosettes in the first year of growth (called 'vegetative individuals' in the paper) (Figs. 3c, 3d) and individuals in the second year

Table 2. Numbers of individuals in individual units of the studied population of *Virga pilosa* in the Wielkopolski National Park and areas covered by subpopulations

Parameter	Population unit						
	A	B	C	d	e	f	g
Number of generative individuals	400	6	44		1		1
Number of vegetative individuals (= rosettes in the first year of life)	3000	100	54	1		1	
Area (m^2)	1200	30	250	-	-	-	-

Fig. 3. *Virga pilosa* in the Wielkopolski National Park

Explanations: a – location of the subpopulation A (a clearing under the power line after mulching and forest edge, in August), b – dense patch of generative plants in June, c – vegetative rosettes, d – dense patch of vegetative rosettes in June, e – 17-stemmed individual in November, f – nutlet enclosed in the lignified epicalyx, g – the autumn picture of the dense generative stand (phot. R. Bernard & J. Chmiel)

Table 3. Syntaxonomic position of vegetation patches with *Virga pilosa* in the Wielkopolski National Park (subpopulation A)

No. of relevé		1	2	3	4	5	6
Date		19.08.2019	12.06.2020	12.06.2020	12.06.2020	12.06.2020	12.06.2020
Cover of tree layer	(a) [%]	70	80	70	0	50	20
Cover of shrub layer	(b) [%]	30	30	0	0	20	0
Cover of herb layer	(c) [%]	60	80	100	80	90	100
Cover of moss layer	(d) [%]	0	0	0	0	0	0
Area of relevé	[m²]	45	45	45	9	50	50
Number of species		30	25	16	14	17	17
Ch. *Euonymo-Cornetum sanguinei* Pass. *in* Pass. *et* Hoffmann 1968 and Ch. *Rhamno-Prunetum* Rivas-Goday *et* Borja Carbonell 1961 *ex* R.Tx. 1962							
Sambucus nigra	(b)	3.3	3.3	.	.	2.2	.
Sambucus nigra	(c)		2.2	.	r	1.1	1.1
Crataegus monogyna	(c)	r	r	.	.	r	.
Euonymus europaea	(c)	1.1	r	.	.	.	.
Ch. *Fraxino-Alnetum* W.Mat. 1952, Ch. *Alnion incanae* Pawł. *in* Pawł., M.Sokołowski *et* Wallisch 1928, Ch. *Fagetalia silvaticae* Pawł. *in* Pawł., M.Sokołowski *et* Wallisch 1928 and Ch. *Querco-Fagetea* Br.-Bl. *et* Vlieger 1937							
Alnus glutinosa	(a)	4.4	4.4	2.2	.	2.2	.
Fraxinus excelsior	(a)	3.3	3.3	3.3	.	2.1	1.1
Fraxinus excelsior	(c)	.	r	.	R	.	.
Ulmus laevis	(a)	.	.	.	.	1.1	2.2
Ulmus laevis	(c)	.	.	.	.	R	.
Festuca gigantea		1.1	+	+	.	+	R
Stachys sylvatica		r	r	.	.	+	+
Acer platanoides	(c)	r	r	.	.	.	.
Brachypodium sylvaticum		r	.	.	.	+	.
Ch., D. *Cephalarietum pilosae* and Ch. *Galio-Alliarion* (Oberd. 1962) Lohmeyer *et* Oberd. *in* Oberd. *et al.* 1967							
Virga pilosa	***gen.***	**3.2**	.	**4.4**	**4.2**	**3.3**	**4.3**
Virga pilosa	***veg.***	.	**3.3**	+	**.**	+	**1.1**
Impatiens parviflora		2.2	2.2	2.2	1.1	2.2	2.2
Geum urbanum		2.2	1.1	r	.	1.1	1.1
Arctium nemorosum		1.1	r	.	.	r	r
Chaerophyllum temulum		+	r	r	.	.	.
Torilis japonica		r	.	.	.	.	.
Lapsana communis		.	r	.	.	.	r
Cynoglossum officinale		.	r	.	.	.	.
Alliaria petiolata		.	.	r	.	r	.
Ch. *Agropyro repentis-Aegopodietum podagrariae* R.Tx. 1967 *em.* Neuhäuslová-Novotná *et al. 1969* and Ch. *Petasition officinalis* Silinger 1933 (=*Aegopodion podagrariae* R.Tx. 1967)							
Anthriscus sylvestris		2.2	+	+	r	1.1	r
Ch. *Convolvuletalia sepium* R.Tx. *em.* Oberd. *in* Oberd. *et al.* 1967 and Ch. *Artemisietea vulgaris* Lohmeyer, Preising *et* R.Tx. 1950							
Urtica dioica		2.3	2.2	2.2	3.2	3.3	3.3
Galium aparine		2.3	2.2	3.3	+	.	+
Fallopia dumetorum		1.2	3.3	.	.	1.1	+
Glechoma hederacea		1.1	r	+	.	1.1	.
Myosoton aquaticum		+	+	+	r	.	.
Oxalis fontana		r	.	.	.	.	.
Artemisia vulgaris		r	.	.	.	.	.
Galeopsis pubescens		r	.	.	.	.	.
Cirsium vulgare		r	.	.	.	.	.

Other and sporadic species: *Acer pseudoplatanus* (b) 1 (r), (c) 4 (r), *Atriplex patula* 6 (r), *Betula pendula* 3 (1.1), *Bidens frondosa* 4 (r), *Bromus inermis* (r), *Iris pseudacorus* 1 (r), *Lamium purpureum* 2 (r), 4 (r), *Plantago major* 1 (r), *Poa nemoralis* 1 (r), *Poa trivialis* 2 (r), 3 (r), 4 (r), *Polygonum hydropiper* 4 (+) *Prunus cerasifera* (b) 1 (r), *Rosa canina* (c) 1 (r), c 5 (r), *Sisymbrium officinale* 6 (r), *Stellaria media* 2 (r), *Tussilago farfara* 2 (r)

Explanation: gen. – generative individuals, veg. – vegetative individuals in the first year (rosettes) of life (called 'generative individuals' in the paper). The latter were mostly one-stemmed, but also multi-stemmed plants occurred, possibly as the effect of browsing by large mammals. Multi-stemmed individuals mostly included several stems, up to 17 maximally (Fig. 3e). Multi-stemmed individuals were quite easily distinguishable from densely growing one-stemmed plants. Stems of the former, although emerging singly, were arched near the ground suggesting a clump-like form (Fig. 3e), while one-stemmed plants were always straight even if growing very close to each other. The multi-stemmed form was also followed by a larger number of inflorescences (heads): while typically ranging between 15 and 25 in a plant, it reached 114 in the 17-stemmed individual. Generative stems were unbranched or poorly branched having less heads in more shaded conditions and clearly more branched – regularly with first and second order branches – so richer in heads in more insolated places. Generative individuals mostly reached between 1.3 and 1.8 m, and the largest plants were even 2.2 m high. Such high and dense plants formed a clear high-blooming stratum (Fig. 3g).

Local species pattern of distribution was easily recognisable both in micro- and mesoscale. In the microscale, it included:

- distinctive high and dense stands of generative individuals, without any admixture of vegetative individuals or, at most, with few rosettes at the margin (Fig. 3b, Table 3),
- stands of vegetative individuals, both dense and loose, without any admixture of generative plants (Fig. 3d, Table 3),
- mixed stands including several loosely growing generative plants and dispersed vegetative individuals.

Patches of vegetative individuals frequently occurred exactly at places dominated by generative individuals in the previous year (e.g. relevés No. 1 & 2 in Table 3). This was confirmed not only by repeated observations exactly at the same site, but also by remnants of previous-year stems.

In mesoscale, all subpopulations and single plants were situated on or next to communication routes (Fig. 2). The main subpopulation (A) and two individuals (f, g) occurred in and by a clearing under power line. The subpopulation C and two other individuals (d, e) occurred by a forest tourist path going from power line. The subpopulation B, occurring between forest and meadow, was adjacent to an animal path.

3.3. Habitat conditions

In the study area, *Virga pilosa* grew in a depression forming the westernmost part of Góreckie Lake gully. As in other depressions in the WNP, hydrogenic soils occur there (Borowiec 1973). Due to significant decrease in the ground water level, processes of mineralisation are highly advanced in these soils.

The main subpopulation (A) occurred in a clear depression along NNE-SSW oriented power line. (Figs 2, 3a). A ten-metre-wide belt (a clearing) under the line was treeless due to regular mulching in late summer. The power line crossed about 30-year-old alder-ash forest with elm admixture. *Fraxino-Alnetum* W. Mat. 1952 seems to be a potential natural phytocoenosis there (Matuszkiewicz 2008). This was indicated by species typical of both this plant association and the alliance of *Alnion incanae* Pawł. *in* Pawł., M. Sokołowski *et* Wallisch 1928 (Table 3). A very significant presence of nitrophilous species, typical of tall fringe communities of *Galio-Alliarion* (Oberd. 1962) Lohmeyer *et* Oberd. *in* Oberd. *et al.* 1967 alliance, was worth noticing there.

The main subpopulation (A) covered a forty-metre-long section. The species occurred within the entire width of open clearing under power line, but it was most abundant at forest edge, especially from Góreckie Lake side and, in lesser numbers, at the opposite (western) side of the clearing. In the edge zone of the forest, *V. pilosa* was a dominant species with coverage reaching, locally, even 70% (Table 3, Fig. 3b). However, its numbers rapidly decreased deeper in the forest: it concentrated there within the first two-three metres from the edge and almost all individuals occurred within five-metre-wide zone. Only several individuals grew deeper, up to twelve metres from the edge, but only in small gaps with more light. Also the highest and most branched individuals occurred at the very edge, while the deeper growing plants were lower and less branched.

Subpopulation B occurred between hay meadow and young mixed forest, planted more than twenty years ago on former arable land. Individuals of *V. pilosa* grew along forest margin with *Sambucus nigra*, but entered neither the forest nor the meadow. Subpopulation C was situated in the neighbourhood of a hay meadow, at the margin of eighty-year-old alder forest with peripheral shrubby *Sambucus nigra*, *Salix cinerea* and *S. purpurea*. While ca. 10% of individuals grew there in the forest, up to three metres deep, most of the subpopulation formed a narrow belt narrowly fringing the forest edge.

All three subpopulations occurred in ecotone zones with transitional conditions and some disturbance – such as periodical mowing (B, C), mulching (A) or animal trampling (B) – in the area occupied by *Virga pilosa* and/or directly adjacent to it.

Generally, a clear relationship between the occurrence of *Virga pilosa* and the amount of light, moisture and nutrient richness was recognisable in all three subpopulations. The species occupied typically edge

Fig. 4. Reaction of *Virga pilosa* to strong insolation combined with high temperature, in June: leave blades folded down along midrib or rolled up (phot. R. Bernard)

(including fringing) positions and, mostly, occurred in moderately light to partly (moderately) shaded sites (Figs 3a, 3b). Even the area under power line, though narrowly open, was shadowed during large part of the day and insolated only in a few afternoon hours (Fig. 3a). In hot afternoons, strongly insolated leave blades of individuals growing there were often characteristically folded down along midrib or rolled up (Fig. 4) due to changed turgor in large and relatively delicate leaves.

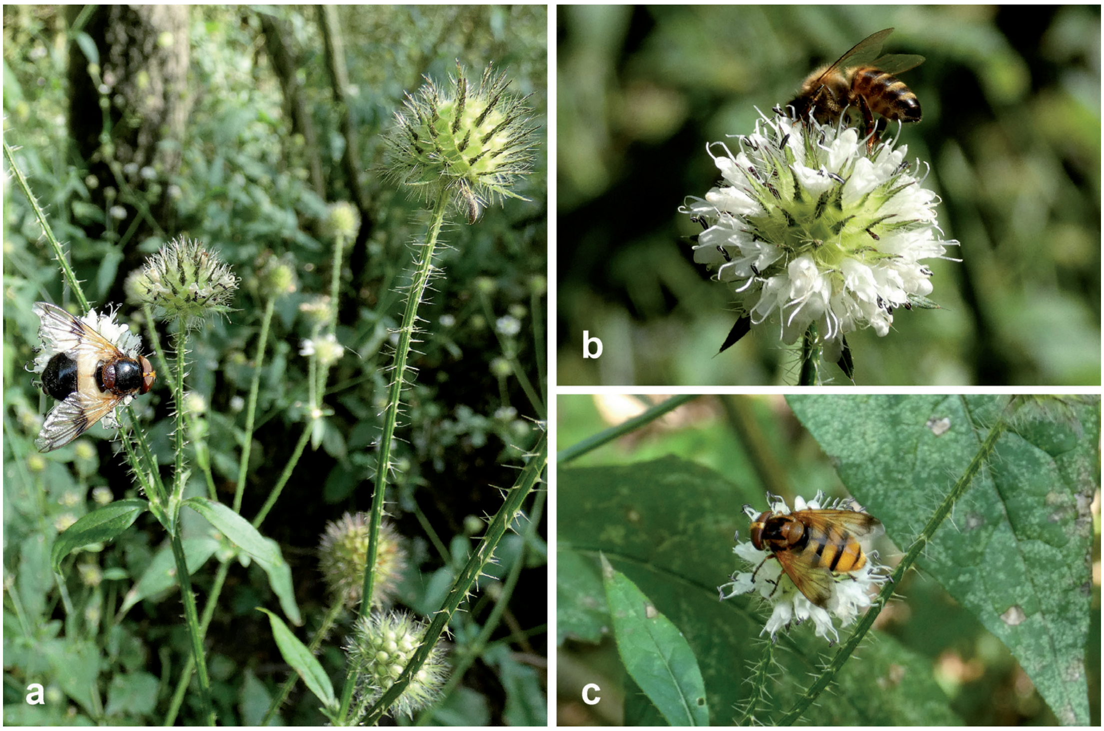

Fig. 5. Pollen vectors on the capitula of *Virga pilosa* in mid-August

Explanations: a – *Volucella pellucens* (L.), b – *Apis mellifera* L., c – *Volucella inanis* (L.) (phot. R. Bernard)

All three subpopulations occupied moderately moist – i.e. intermediate between fresh and wet – habitats. The appropriate moisture was provided due to the situation not only at the edge of forest but, especially, in depressions in the lake gully not far from the lake. This situation was especially favourable in the largest subpopulation located between two hills. In microscale, numerous plants and whole patches grew on low and gentle slopes. It seems that such locations provided some water inflow and reduced water accumulation.

In the study area, *Virga pilosa* occurred in nitrogen-rich habitats. This was recognisable in numerous occurrences of accompanying nitrophilous plant species, especially in the A and C (i.e. the largest) subpopulations.

3.4. Pollen vectors and seed dispersal

Virga pilosa is a nectar plant and its pollen vector are insects. During a short afternoon observation on the 15th of August, representatives of Hymenoptera, Diptera and Lepidoptera were continuously observed on many inflorescences. Numerous bees (*Apis mellifera* L.), originating from a close (200 m) apiary, as well as two species of Syrphidae, *Volucella pellucens* (L.) and *Volucella inanis* (L.), persistently penetrated *Virga* heads for a long time (Fig. 5). On the contrary, butterflies of *Pieris rapae* (L.) and bumblebees of *Bombus lapidarius* (L.) stayed on flowering heads only briefly, the latter 'nervously' moving: it seemed that bumblebees could not find appropriate resources or conditions to collect them.

Other interactions between animals and *Virga pilosa* were rather facultative and could have been concluded only indirectly. In June, the authors found traces of foraging: both leaves and stems were browsed here and there by large mammals, probably by roe deer or deer. Scale of browsing was not large, possibly due to rather prickly nature of this plant. Browsing of young stems might have been responsible for many-stemmed form of some individuals and, consecutively, for their greater reproductive potential.

Reproductive potential of *Virga pilosa* was generally high, but it differed between individuals (Figs 3g, 5a, 5b). Number of heads mostly ranged between 15-25 per individual and in multi-stemmed plants was respectively higher, up to 114 (Fig. 3e). Also heads differed in size. A potential number of fruits per head ranged between 30 and 110 as counting of flowers, developing fruits and compartments in the autumn heads showed (Figs 5a, 5b). However, some fruits/seeds certainly did not develop correctly. In a large head (104 compartments), 19 undeveloped bent or shrunken fruits were found in November. The number of correctly developed fruits was not assessable as large part of compartments was already empty (fruits fell out). Considering these indirect data, the reproductive potential for one plant was carefully estimated at several hundred to a thousand seeds. In a multi-stemmed individual, it might have even reached 2000-3000 seeds.

The *Virga pilosa* fruit is a dry, single-seeded nutlet (*cypsela*) enclosed in a lignified epicalyx (Mayer 2016) (Fig. 3f). This persistent slightly angular epicalyx forms small and very narrow wing-extensions along edges in the subapical part and is partly covered by quite numerous hairs (Fig. 3f). Studying *Virga pilosa* capitula and fruits, the authors found, however, no evident adaptation to a specific dispersal mode. Although the species developed bristly and spiny (but not hooked) bracts in its flowering and fruiting heads (Figs 5a, 5b), they were not 'catching' in strong contrast to well-known hooked bracts in heads of e.g. *Arctium*. An immature fruit remaining in its compartment in the head was additionally covered with a small element (as a cap) with turned up margins bringing miniature bristles. These structures practically also did not hook. Mature fruits collected in November were mostly devoid of these caps. Summing up, armoured capitula in *Virga* (Figs 5a, 5b) seemed mainly to be sharp defences to protect the buds and developing seeds. Despite the evident lack of greater 'catching' possibilities, the easily breakable propagules (distal branchlets with heads or only the heads and their fragments; Fig. 3g) possibly may cling occasionally and thus be transported on/in animal (e.g. boar's) fur or feet. In addition, it cannot be excluded that wet hairy fruits may temporarily stick to (wet) animal fur or dirty feet (including human shoes). The occurrence of scattered plants and subpopulations along animal and human paths suggested such accidental (and incidental?) rather short-distance epizoochory. Finally, unintentional anthropochory may be responsible for dispersal of *Virga pilosa*. It seems that individuals f and g might have sprung from seeds transported by an equipment mulching the clearing under the power line in the late summer.

A small experiment made by the authors in November showed that seeds fall out their bracteate 'cradles' due to rapid movements of stems. It can be imagined, therefore, that a severe wind gust or an animal passing by may sow fruits in the neighbourhood. During the experiment, the *Virga pilosa* fruits distinctly fell on the ground in the range of 1-2 metres showing no larger potential to be caught by wind and travel much further than a few nearest metres. Small and very narrow wing-extensions along edges in the subapical part of the fruit form together a kind of mini-pockets (Fig. 3f). Considering very small surface of these elements in relation to quite large size and weight of fruits, these structures cannot be treated as adaptation to anemochory. Lack of wind-taken structures and the fact that relatively large and heavy fruits behave as gravel rather than as paper coincide with their close-range dispersal. This short-distance and 'dense' dispersal was reflected in frequently occurring quite dense stands of individuals. It should finally be stressed that no elaiosomes were found on mature fruits falling out of the heads in November: all the fruit surface was hard and stiff.

4. Discussion

4.1. Population origin

The origin of some species in Poland cannot be clearly diagnosed at country level and this problem is even greater at regional level. Numerous species, as e.g. *Virga pilosa*, autochthonous or probably autochthonous at country level may be regionally allochthonous. In the past, *V. pilosa* was believed as probably alien (Zając & Zając 2001) or native species (Mirek *et al*. 2002; Zając & Zając 2009; Rutkowski 2011). Vast majority of Polish localities are situated in southern part of the country and they belong to compact distribution range of the species (Fig. 6) (cf. Meusel & Jäger 1992), so the species appears to be native there. The origin of localities situated in lowlands further to the north is, however, uncertain. For example, localities in lower Odra valley spatially correspond with numerous localities in Mecklenburg-Vorpommern, Germany, so their native occurrence cannot be excluded. Stachnowicz & Rakowski (2013) recognised *V. pilosa* as an alien species in Wielkopolska (Greater Poland region) on the basis of:

a) total lack of historical data for such large, physiognomically striking and easily identifiable species in so well-studied region,
b) very local current occurrence, only restricted to part of a forest complex, and
c) very abundant occurrence in disturbed habitats in this small area.

Stachnowicz & Rakowski (2013) convincingly rejected long-distance hydrochory or epizoochory as a causative factor for appearance of *V. pilosa* near Będlewo. Instead, they suggested an accidental anthropochory: originally the species might have accidentally been introduced into agricultural area there and then its propagules (fruits or heads) could have been transported attached to dirty tires of tractors and other vehicles from farmlands to forest roads.

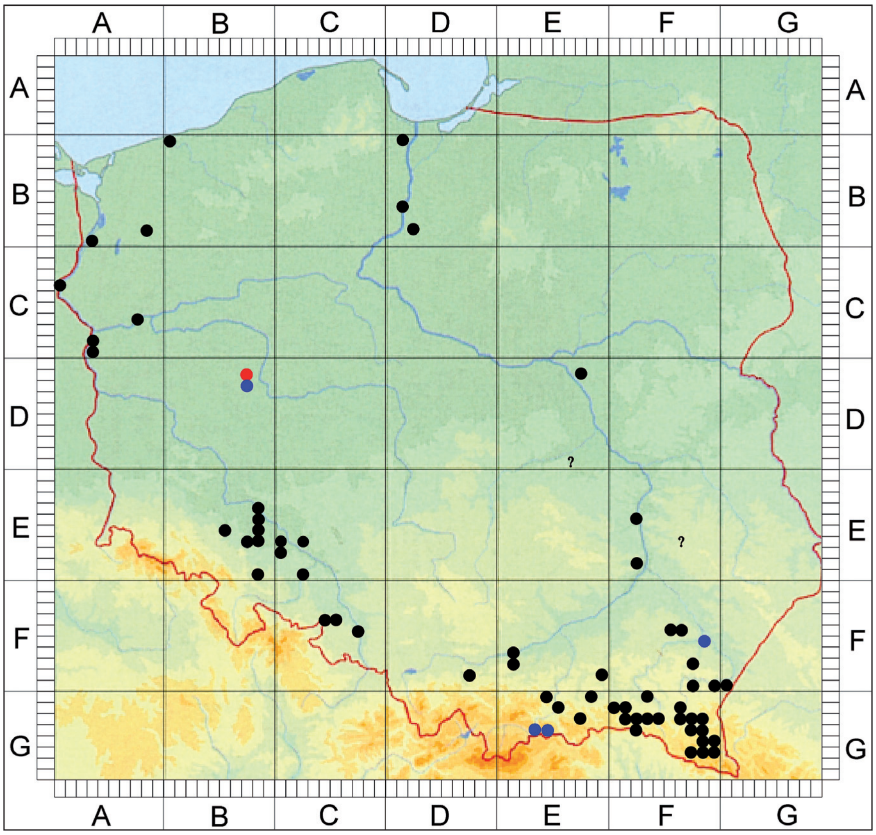

Fig. 6. Distribution of *Virga pilosa* in Poland in the Polish geobotanical ATPOL grid

Explanations: black dots – according to Zając & Zając 2001, blue dots – further localities given by Stachnowicz & Rakowski (2013), Frey & Frey (2014), Jaźwa & Stadnicka-Futoma (2017) and Stawowczyk (2017), red dot – a new locality in the Wielkopolski National Park

Table 4. Local distribution pattern of *Virga pilosa* in the Wielkopolski National Park as a consequence of life and dispersal strategy

<table>
<tr><th colspan="6">Life and dispersal strategy</th></tr>
<tr><td colspan="2">microscale</td><td colspan="2">micro- & mesoscale</td><td colspan="2">mesoscale</td></tr>
<tr><td colspan="2">• close dense autochoric dispersal
• strong competition
• locally oriented strategy of small steps, being focused on consolidation of the species occurrence and dominance</td><td colspan="2">• habitat conditions (moderately light, moderately moist and nitrogen-rich) with favourable disturbance</td><td colspan="2">• accidental epizoochoric dispersal, irregular in time but at least partly regular in space (communication routes)
• ‘by chance’ colonisation strategy</td></tr>
<tr><td colspan="6">Beneficial human influence – human-induced disturbance and unintentional anthropochory</td></tr>
<tr><td colspan="6">Local distribution pattern</td></tr>
<tr><td colspan="3">microscale</td><td colspan="3">mesoscale</td></tr>
<tr><td colspan="3">mosaic of dense vegetative and generative patches assisted with looser mixed patches</td><td colspan="3">primary main subpopulation and secondary smaller subpopulations and individuals scattered along communication routes</td></tr>
</table>

The new locality of *Virga pilosa* in the WNP also probably appeared as a result of unintentional anthropochory. The forest complex near Będlewo and the new locality near Góreckie Lake are only six kilometres distant in straight line, but they are separated by lakes, agricultural areas and a village. The aforementioned power line could have been a key factor in this ‘travel’. It crosses the area of the A subpopulation and, after several kilometres, it reaches the forest complex near Będlewo. The power line requires regular surveys and sometimes repair and maintenance operations. Propagules of *Virga pilosa* could have been accidentally transported on equipment working along the line. This hypothetical event is difficult to date. The new population is at least several years old because it contains a few parts and the A subpopulation is large and well established. However, the population seems to be not older than 15-20 years as forests adjacent to the A and B subpopulations were too young earlier to provide light conditions appropriate for the species.

Summing up, it seems that the long-distance dispersal of *Virga pilosa* is often accidental anthropochory, especially outside compact range of the species. Considering the true rarity of such accidents, absence of the species in great areas of central and northern Poland is quite understandable.

Virga pilosa could be classified as a hemiagriophyte in Wielkopolska as it is a naturalised alien species which can already spread in seminatural or natural but slightly disturbed ecosystems (cf Kornaś 1981). Considering an advancement of naturalisation process and a clear influence on other components of phytocoenosis, *Virga pilosa* ‘behaved’ as a postneophyte in the main subpopulation A (cf Faliński 1968).

4.2. Life and dispersal strategy recognisable in population distribution pattern

Considering data from the new locality, the population distribution pattern of *Virga pilosa* seems to have two evident dimensions: micro- and mesoscale (Table 4, Figs 2, 3b, 3d, 3g). Dispersal mode played a significant role in the creation of both these dimensions. Some literature sources diagnose only one dispersal mode for *Virga pilosa*, e.g. only anemochory is given in the newest Rothmaler-Exkursionsflora von Deutschland (Bräutigam 2017). We found it completely impossible as wind is no more than only some support for autochory. Also epizoochory cannot be treated as either the main or only one dispersal mode as shown above. The most accurate seems to be the diagnosis in the Database of the Czech flora and vegetation (Pladias 2020). With the use of a new classification, based on multiple dispersal modes of individual species (Sádlo *et al*. 2018), the *Allium* type of dispersal has been determined, i.e. prevailing autochory with possible partial or supporting other modes, in this case anemochory and epizoochory. However, probable myrmecochory is also suggested by this source (Pladias 2020). The taxon, probably myrmecochorous, is defined as having a fleshy structure resembling an elaiosome, but the appendage to seed size ratio is very small so that the possible advantage of seed transport for ants would be small. Our study failed to confirm presence of any elaiosome. It seems that the occurrence of elaiosomes and myrmecochory in *Virga pilosa* was only supposed or extrapolated on the basis of true elaiosomes present in *Knautia* species (cf. Mayer *et al*. 2016).

Basing on our studies and literature assessments, the dispersal of *Virga pilosa* can be diagnosed:

a) in the aspect of functional morphology as unspecialised, lacking a clear morphological indication of anemochory or zoochory;
b) technically as based on multiple modes: in microscale – on simple autochory, at most wind-assisted or animal-assisted, and in mesoscale – on accidental epizoochory (and unintentional anthropochory, also playing a significant role in macroscale);
c) functionally as diversified, with aims dependent on the distance and expected effect: microscale dispersal focused on competitive life strategy in local dimension, and mesoscale dispersal directed at 'by chance' colonisation of appropriate not very distant sites.

The accidental epizoochory and anthropochory were responsible for the mesoscale distribution pattern with population units scattered along human and animal communication routes. The pattern included the main (primary) subpopulation which found optimal conditions for growth and smaller (secondary) subpopulations and 'singles', most probably originating from the main subpopulation and constituting a forefront of further colonisation (Table 4).

Close autochory together with the species competitive life strategy were responsible for the microscale distribution pattern alternating in space and time, but always mosaic (Table 4). In this context, the autochoric mechanism of microscale dispersal in *Virga pilosa* was only technically unspecialised, but ecologically it appeared really specialised and purposeful. Close sowing combined with relatively high productivity assured dense occurrence of seeds in the closest range, i.e. under *Virga* 'canopy' and nearby within, at most, several metres. The densely occurring seeds were able to produce dense local stands of next generation. However, a disturbance, understood as change of conditions, was necessary for *Virga pilosa* seed germination (Preston *et al*. 2002). The disturbance was provided by the plant's own life strategy. Dense stand of generative stems of *V. pilosa* exerted strong competitive pressure on coexisting species, highly limiting their occurrence and growth. It could be perceived as some protection for its own next generation, as cleaning of its germination and developmental space from potential competitors. When the whole generative stand died, conditions became disturbed and a possibility for awaiting seeds to germinate in that place and in its direct neighbourhood in the next spring opened. The life strategy of *V. pilosa* was, therefore, highly competitive in microscale. In our opinion, it was a locally oriented strategy of small steps, focused on consolidation of the species occurrence and dominance.

In some places, natural disturbance may have been strengthened by human disturbance. Periodical late-summer mulching of the clearing under power line appeared as very beneficial for the studied main subpopulation (A). Part of first-year rosettes in the clearing, especially those more marginally situated, survived mulching and grew in generative stems next year. At the same time, mulching reduced competitive pressure of coexisting species. Our observations from two consecutive years showed that the generative stage of *Virga pilosa* was continuously present in the open clearing in spite of mulching. Mulching not only influenced individuals in the clearing, but also, and even especially, the basic part of subpopulation within the forest edge zone. Without mulching, the clearing would be totally overgrown with high herbaceous vegetation and then with shrubs in a short period. Light conditions in the adjacent forest edge zone, so important for *V. pilosa*, would be, therefore, significantly changed. Summing up, human disturbance supported the species, both reducing competition and maintaining appropriate habitat conditions. The examples from the British Isles showed how important it may be in some localities. *V. pilosa* was lost there from some Atlas-squares between 1962 and 2002 and agricultural improvement or lack of woodland management might have accounted for the losses (Preston *et al*. 2002).

Virga pilosa was assigned to the competitive (C) life strategy in the BiolFlor database (Klotz & Kühn 2002) with the use of the modified Grime's classification (Grime 1974, 2002). This strategy is advantageous in habitats where resources are abundant, conditions not extreme and disturbance level is low. It is typical of species characterized by great competitive potential, low seed production and frequently occurring storage organs. In this classification, vegetative reproduction is also clearly associated with C-strategy. Considering these criteria, *Virga pilosa* cannot be, however, qualified for pure competitive strategy (C), as it does not reproduce vegetatively, can occur in disturbed (even periodically) systems and does not have storage organs; also the seed production is not so low. In our opinion, a more accurate possibility of assignment is offered by the same Klotz & Kühn's (2002) classification which treats life strategies as a continuum and proposes intermediate types. Their CR life strategy includes large annual overwintering plants or short-living perennials with some features of both competitive (C) and ruderal (R) life strategy. In competitive *V. pilosa*, also such important R-strategy features occur as a) occurrence in disturbed systems – with benefits brought by some disturbance – and b) total investment in generative reproduction. Thus, in our opinion, mixed CR-strategy describes this species most accurately. Qualification for intermediate CR strategy was confirmed by the classification of life strategies based on other criteria, i.e. on three key leaf traits: leaf area (high in competitive taxa), leaf dry matter content (high in stress-tolerant taxa) and specific leaf area (high in ruderal taxa) (Pierce *et al.* 2017). From these data, it calculates scores that express the degree of taxon affiliation to C, S or R strategy, which are measured on percentage scale, and the sum of three scores for individual taxa is 100%. C-score was calculated at 52.6% and R-score at 47.4% for *V. pilosa* with the use of this method (Pladias 2020).

Habitat conditions obviously co-create the species' local distribution pattern. Combination of moderate light exposure and moderately moist and nutrient-rich conditions is commonly described for the species (e.g. Stachnowicz & Rakowski 2013; Bräutigam 2017; Pladias 2020). The Ellenberg's indicators L (light) 7, F (moisture) 6 with some variability stressed, and N (nitrogen availability) 7 (Bräutigam 2017) seem to diagnose this combination the best, also for the locality in the WNP. The indicator value L6 proposed by Pladias (2020), describing occurrence in semi-shaded conditions and only exceptionally in full light, is too low for the habitats at the new locality. However, the spectrum of light conditions can be locally broader: in the forest complex near Będlewo, the species preferred brighter places, but also occurred deep under tree canopy (Stachnowicz & Rakowski 2013). In the WNP, such situation was exceptional (only several individuals) and even in that place, a gap between trees provided more light than under totally closed canopy. It should also be stressed that better light conditions and, at least, some direct insolation promote more intensive activity of insects (pollen vectors), coinciding, therefore, with the total investment of *Virga pilosa* in generative reproduction. On the other hand, as shown by leaf reaction (see: Results chapter), *V. pilosa*, though light-dependent is not a heliophilous species of fully open areas. It is rather a mesophilous species of semi-open to semi-closed areas which can resist sunny and hot conditions only temporarily and with appropriate and rather persistent ground moisture provided.

The question arises whether *Virga pilosa* has potential to colonise many new localities in the WNP and in central Poland. Stachnowicz & Rakowski (2013) suggested that the species can be locally expansive. This suggestion was based on the large and complex population of the species in the forest complex near Będlewo and, especially, on the species occurrence in various plant communities there, showing its potential plasticity. However, this mostly deciduous and rather moist forest complex, additionally rich in disturbed sites, appears to represent the species' habitat optimum, perfectly combining its habitat and life strategy requirements. Such forest complexes are not common in this part of Poland and, what is more, the species' long-distance dispersal possibilities are very limited. It is, therefore, more probable that *Virga pilosa* will remain rather rare species in Wielkopolska and, generally, in central Poland. It may be, however, locally flourishing and spreading due to the combination of its locally oriented life and dispersal strategy.

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