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Original research

Epipactis albensis (*Orchidaceae*) species new to the flora of Lithuania. Data from the northeastern limit of the species distribution area

Mindaugas Ryla[1*], Rimvydas Kinduris[2], Bartłomiej Nurczyński[3], Aušra Žilinskienė[4], Arūnas Pranaitis[5]

[1] Sibirka village, 21101 Trakai distr., Lithuania
[2] Ventos Str. 65–37, 89170 Mažeikiai, Lithuania
[3] Spółdzielcza Str. 11, 28–300 Jędrzejów, Poland
[4] Gėlių Str. 14–16, 68302 Marijamolė, Lithuania
[5] Administration of Žuvintas Biosphere Reserve, Kampelių Str. 10, Aleknonys village, 64351 Simnas municipality, Alytus distr., Lithuania

*Corresponding author. E-mail: mindaugas.ryla@gmail.com

Abstract

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Epipactis albensis Nováková & Rydlo (*Orchidaceae*), a species new to the flora of Lithuania, was found in the southwestern part of the country, in the Bukta Forest (the Žuvintas Biosphere Reserve, Marijampolė district) in 2020, and the nearby Dalginė Forest (the Dalginės Botanical Reserve) in 2021. The closest isolated population is located ca. 340 km southwest, and newly recorded populations form an island outside the main distribution area. Species populations occur primarily in the *Tilio-Carpinetum betuli* plant community showing ecological plasticity. A part of the population occurs in habitats with anthropogenic influence. *Epipactis albensis* is the only obligate autogamous *Epipactis* species known in Lithuania until now. Although its flowering season starts at the end of July or the beginning of August, solitary flowering specimens can be found in September or even later. According to the assessment applying the IUCN criteria, species should be treated as endangered (EN) [B2a,b(ii)c(iv) D] in Lithuania.

Keywords: ecology, morphology, phenology, *Tilio-Carpinetum betuli*.

INTRODUCTION

Eurasia is the main diversity centre of the genus *Epipactis* Zinn. Only two *Epipactis* species grow in Africa, and one native species occurs in America (Fateryga & Fateryga, 2018). Depending on the accepted species concept, the number of European species varies considerably: from 16 species and several infraspecific taxa mentioned by Kühn et al. (2019) to more than 70 species reported by Griebl & Presser (2021) or even 95 included in *Arbeitskreis Heimische Orchideen* database (Baborka, 2022). Describing new, presumably, autogamous taxa and constant debates about the status and synonymy of

particular entities make *Epipactis* genus one of the most taxonomically complex orchid taxa in Europe.

Epipactis albensis has been described in the Czech Republic (Nováková & Rydlo, 1978). The species is considered a Central European endemic (Wünsche, 2013). Two populations of *Epipactis albensis* were found in the southwestern part of Lithuania in Marijampolė district in 2020–2021. *Epipactis albensis* has not been listed in the latest survey on the *Orchidaceae* family in Lithuania (Gudžinskas & Ryla, 2006). Recording the species was a complete surprise for specialists since the population is far outside of the species earlier recorded distribution area.

The paper aims to provide information on the species current distribution in Lithuania, position in its range, estimate population size in the country, describe morphology and diagnostic features, and analyse the ecology, phenology and supposed conservation status of *Epipactis albensis* in Lithuania.

MATERIALS AND METHODS

An evaluation of the population size was performed on 17 August 2020. Most of the plants in the population were in their final flowering phase; many plants had only the last flowers left or were already fruiting. On 2–3 August 2021, the evaluation of population abundance was repeated, investigating additional areas around the known site and a few other forests with visually similar vegetation types in searching for species performed. Again, most of the plants in the population were in the complete flowering phase during the search. Geographical coordinates of plant groups or solitary individuals were recorded to evaluate the spatial distribution of the species.

Thirty flowering specimens (n = 30) were measured for biometrical analysis in 2021. We used the same set of characters after Molnár & Sramkó (2012). Anatomic and morphologic features indicating autogamous fertilisation strategy and size in flower characteristics were evaluated during morphological analysis and photographs taken at a fixed 1 : 1 (macro) scale with a specialised 100 mm macro lens.

Approximate distances between localities were calculated using Google Maps services. Two flowering *Epipactis albensis* specimens were taken (without rhizome) for herbarium documentation. Samples were deposited at the Herbarium of the Institute of Botany of the Nature Research Centre (BILAS) in Vilnius. Hydrometeorological data were taken from the Žuvintas Automatic Meteorological Station (Nr 4371), managed by the Lithuanian Hydrometeorological Service. The station is located 14.8 km away from the study area in an open environment.

Two soil samples were taken for chemical analysis from different habitats of the same population in the Bukta Forest. Each sample was taken from several places adjacent to visible plants. The top of the soil (10 cm) was removed, and three separate subsamples from the root layer (10–20 cm deep) were mixed to form the final sample. One sample was taken in a mature forest area, where plant composition in the community was visually most common in the population area. Another sample was taken from the roadside, artificial gravel slope of a road edge, overgrown by young trees and shrubs. The soil in the mature forest was humus-rich clayish sand, whereas, on the roadside, it was clayish gravel covered with a thin organic layer. Coverage of the tree layer was 80% at both sites; both samples are from the Bukta Forest. Soil tests were performed according to ISO 10390:2005 standard. P, K, Ca, Mg, Cu, Mn, Zn (Mehlich III extraction), pH, N, B, Fe (hand method). The analysis was conducted at the Laboratory of Agriculture Chemistry, Agricultural Research Centre, Saku, Estonia.

Population sites were visited many times during 2020 and 2021 at irregular intervals to register dates of the essential phenological transformations. Observed plants were assigned to several stages according to important phenological features (Table 1).

During multiple visits and surveys on *Epipactis albensis*, possible threats were evaluated. The status of the species was assessed by applying the International Union for Conservation of Nature (IUCN, 2012) criteria.

RESULTS

Distribution of the species and population size in Lithuania

Epipactis albensis was found in the southwestern part of Lithuania in the Žuvintas Biosphere Reserve, the Bukta Forest (Marijampolė district) on 8 August

Table 1. Phenophases of *Epipactis albensis*

Phenophase	Abbreviation	Description
Growing	Gr.	Intense growth. Plant size is not final; flower buds are small and thin
Growing- flowering	Gr.-Fl.	Buds are swelling, and the first flower starts to open
Full flowering	Full Fl.	Two or more flowers in an inflorescence are open, and no wilting of the lowest flowers is visible
Flower fading	Fl. Fading	The lowest flowers are wilting, but the top half of the flowers are still in good shape or buds
End of flowering	End Fl.	The very last one or few flowers are still flowering, but started to wilt. Capsules in the lowest part of the inflorescence swelled and reached their final shape
Seed capsules	Seed ca.	All flowers faded, and capsules and seeds are developing
Start of dissemination	Start. diss.	The lowest capsules (up to a half) are narrowly open; side cracks are very narrow and hard to notice, and seeds are spreading. The leaves and capsules are green
Full dissemination	Full diss.	Most or all capsules are open, with massive dispersion of seeds. Capsules' colouration and leaves become slightly yellowish-green
Yellowing	Yellow	The capsules are fully open; side cracks are easily noticeable; therefore, they are almost empty or empty, and all plant parts are yellowish-green or yellow. Some empty capsules gradually become brown
Brown	Brown	All aboveground parts are dead, brown or black

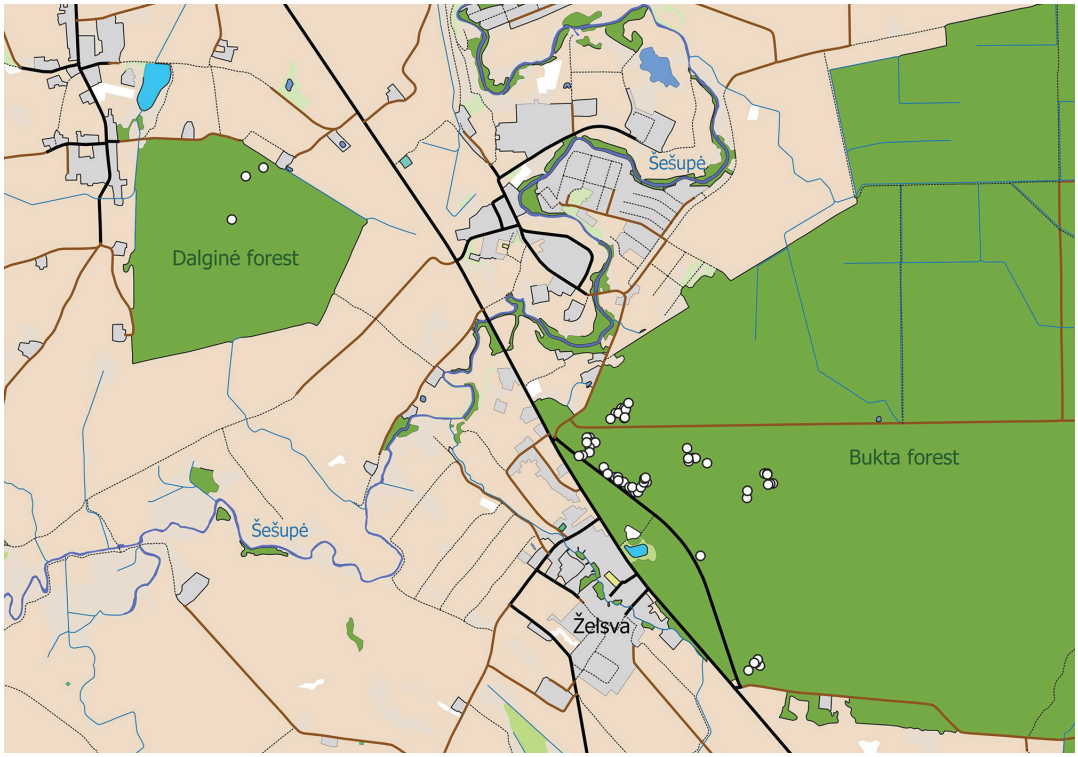

Fig. 1. Distribution of *Epipactis albensis* (○) in Marijampolė district, southwest Lithuania (base map generated from www.geoportal.lt)

2020 by Aušra Žilinskienė. In 2021, a second small population was found in the adjacent Dalginė Forest (Fig. 1).

In the Bukta Forest, 150 flowering individuals were counted in 2020 during regular visits to the area. In 2021, *Epipactis albensis* was found in the adjacent Dalginė Forest (nine individuals), while in the Bukta Forest, 60–80 generative individuals were recorded in 2021. There has been a noticeable decrease in flowering individuals since 2020. Solitary plants or small groups were scattered over large areas (plants were recorded in 110 ha area).

Morphology and diagnostic features

The tallest specimens of *Epipactis albensis* were 44 cm high, whereas the smallest individuals were just 8 cm tall and had 1–2 flowers (Table 2).

Morphological characteristics of *Epipactis albensis* provided are based on observations and measurements of plants in nature (Table 2). Rhizomatous perennial herb. Stem 1, sometimes next to the base, branched into two (at least five such plants were registered in 2020), (8–)14–33(–44) cm in height, with cauline leaves (1–)2–3(–4), the biggest leaves are lanceolate or broadly lanceolate, (15–)33–64(–70) mm length and (8–)12–34(–60) mm wide. Leaves have a soft texture. The veining of the leaves is less pronounced than in *Epipactis helleborine*. Inflorescence (1.2–)3–10(–13) cm length, unilateral, lax, with (1–)3–13(–20) flowers. Flowers are small, 7–9 mm in diameter, usually half-open, and sometimes cleistogamous. Ovaries green. Sepals, petals and lips are light green. Hypochile cup-like, brown, epichile straight, cordate, margins are bent upwards. Viscidium is absent; pollinia are powdery (Fig. 2).

Ecology

In the Bukta Forest, the population's prevailing part was found in *Tilio-Carpinetum betuli* community (EU habitat type 9160). The tree layer was dense, with ca. 80% coverage. The tree layer was composed of *Carpinus betulus*, *Tilia cordata*, *Quercus robur*, *Acer platanoides*, *Betula pendula*, *Picea abies*. The shrub layer usually was sparse; its mean coverage was ca. 20%. The shrub layer was composed of *Carpinus betulus*, *Lonicera xylosteum*, *Acer platanoides*, *Betula pendula*, *Daphne mezereum*, *Fraxinus excelsior*. The herb layer was of various densities; in most places, its coverage was more than 50%, but in some places, *Epipactis albensis* grew in areas with 3% or 90% of the herb coverage. The herb layer was species-rich, composed of *Asarum europaeum*, *Galium odoratum*, *Maianthemum bifolium*, *Hepatica nobilis*, *Viola* spp., *Lathyrus vernus*, *Stellaria holostea*, *Polygonatum multiflorum*, *Lamium galeobdolon*, *Paris quadrifolia*, *Angelica sylvestris*, *Aegopodium podagraria*, *Convallaria majalis*, *Melica nutans*, *Oxalis acetosella*, *Pulmonaria obscura*, *Dryopteris filix-mas*, *Ranunculus lanuginosus*, *Milium effusum*, *Campanula trachelium*, *Equisetum pratense*, *Impatiens noli-tangere*, *Neottia nidus-avis*. The moss layer was scarce; it covered up to 10% of the soil surface. *Plagiomnium undulatum* and *Brachythecium velutinum* were registered. The habitat in the Dalginė Forest was visually very similar to that in the Bukta Forest. *Epipactis albensis* also showed some ecological plasticity: 43 plants were found in *Picea abies* plantation (ca. 40 years old), with a sparse herb or moss layer. Plants grew in bare soil

Table 2. Biometric measurements of *Epipactis albensis* in Lithuania. Values of characters marked by an asterisk (*) were based on three measurements only

Measured features	Mean ± SD	Median	Min	Max
Plant height (cm)	23.5 ± 9.5	23.25	8	44
Length of inflorescence (cm)	6.5 ± 3.5	6	1.2	13
Number of flowers	8.4 ± 4.8	8	2 (1)	20
Number of bract-like leaves	0.7 ± 0.8	1	0	3
Length of lowermost bract (mm)	26.8 ± 9.2	25	15	60
Cauline leaves				
Number of cauline leaves	2.6 ± 0.7	3	1	4
Length of lowest (first) leaf, mm	29.1 ± 8.9	30	15	45
Width of lowest (first) leaf, mm	20.0 ± 9.3	19.5	8	50
Length of 2nd leaf, mm	42.9 ± 11.6	45	14	63
Width of 2nd leaf, mm	23.1 ± 10.9	21	8	60
Length of 3rd leaf, mm	48.8 ± 13.5	50	15	70
Width of 3rd leaf, mm	21.8 ± 12.3	20	5	60
Length of 4th leaf, mm*	60.3 ± 12.7	65	46	70
Width of 4th leaf, mm*	24.7 ± 4.5	25	20	29

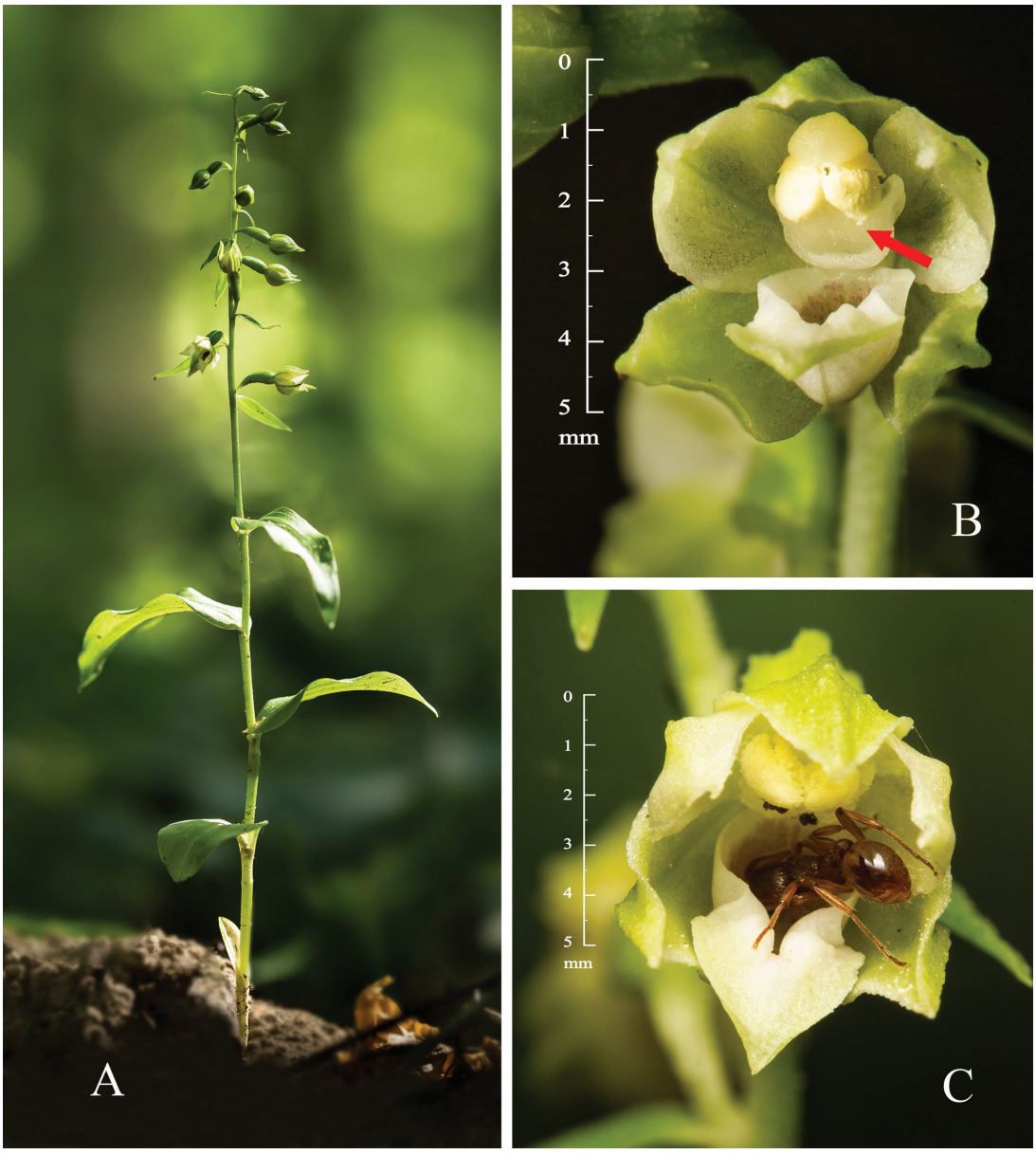

Fig. 2. *Epipactis albensis*: A – habitus; B – pollen grains self-deposited onto the stigmatic surface (red arrow) in freshly opened flower; C – *Myrmica* sp. feeding on *Epipactis albensis* nectar. (Photos by M. Ryla; Bukta Forest, 2020–2021)

covered by a layer of fallen *Picea abies* needles. Furthermore, 30 plants grew on an artificial gravel roadside slope, overgrown by young individuals of *Acer platanoides*, *Fraxinus excelsior* and *Carpinus betulus*. Solitary plants were found in *Tilia cordata*, and *Acer platanoides* stand with scarce herb layer in between decomposing fallen leaves and small twigs or right next to gravel paths of Bukta Nature Trail. Population area in the Dalginė Forest and parts of the Bukta Forest are situated on heavy clayish soil on a flat site with temporary drying water streams or stagnant water bodies during snow melting and heavy rain seasons. Parts of the population area could be classified as alluvial forests (EU habitat type 91E0); however, both sites do not have a connection with any flooding rivers.

Two measured soil samples had slightly acidic to neutral pH – 6.2 and 7.1. Both sites displayed medium nitrogen content (0.24% and 0.26%), other macronutrients varied considerably (Table 3).

Table 3. Results of chemical analysis of soil samples

Habitat	pH	P	K	Ca	Mg	Cu	Mn	B	N	Zn	Fe
		(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(%)	(mg/kg)	(mg/kg)
Mature forest	6.2	27	94	3137	374	2.4	97	1.01	0.26	1.9	444
Roadside	7.1	84	168	4289	273	2.2	76	1.26	0.24	6.5	274

Phenology

When discovered in 2020, plants were already in full bloom (Table 4). It was unclear when plants appeared above ground and how quickly they developed before flowering. In 2021, multiple attempts were made to search and document the initial shoot development stages (Table 5), with the first plants seen in the 28th week of the year. The plants were already well developed, but smaller than their size during the flowering phase. *Epipactis albensis* is a comparatively small plant and not easily noticeable in surrounding vegetation. Therefore, we could not document the exact moment when shoots appeared above ground, despite looking for them multiple times. It seems that initial aboveground shoot development happens very rapidly.

The more exact timing was calculated from the model specimen, which was observed 16 times during the season of 2021. This plant was larger than average, 29.5 cm in height (mean of the population was 23.5 cm), with 15 flowers and two cauline leaves. All flowers developed capsules. On 18 July, the individual was found with tiny buds for the first time. The first flower opened on 23 July, and the last flower in the inflorescence finished flowering on 14 August. It took 22 days from the opening of the first flower to the wilting of the very last flower. It took 49 days from the beginning of the first flower to the first (the same) capsule opening and the start of seed dispersal. It took 78 days of development from a small plant with buds (the exact date of appearance above the ground is unknown, probably a week earlier) to the end of mass dispersal of the seeds. Later the plant stayed yellowish-green until frosts. After a cold spell, its stem and leaves turned brown-black. The whole estimated vegetation cycle continued for about 80–90 days in 2021, but this variable depends on autumn weather conditions. In 2020, the vegetation cycle of *Epipactis albensis* lasted at least one month longer.

Population observations revealed a very irregular emergence of aboveground shoots. Some plants sprout and start to flower much later, while others in the same population already have fruits. Flowering

Table 4. Frequency of phenophase stages in *Epipactis albensis* population in 2020. Phase frequency scale: 1 – one or two solitary individuals; 2 – more than two individuals, but a minority of the population; 3 – a large part of the population, but most plants are in different phenophase; 4 – prevailing phenophase. For phenopase abbreviations, see Table 1

Year		Sprouting–inflorescence emergence			Development of fruit			Dormancy			
2020			Flowering					Maturity			
Week	Date	Gr.	Gr.-Fl.	Full Fl.	Fl. Fading	End Fl.	Seed ca.	Start diss.	Full diss.	Yellow	Brown
32	08 Aug	2	2	4							
32	09 Aug	2	2	4	2	2	2				
34	17 Aug	2	2	2	4	3	3				
37	09 Sept				1	2	4				
38	20 Sept						4				
39	27 Sept						4				
40	03 Oct						4	1			
41	11 Oct						4	3			
43	23 Oct						2	2	4	2	
44	31 Oct						1	2	4	2	
45	05 Nov						1	1	4	3	
47	17 Nov		1					1	3	4	
50	12 Dec		1								4

Table 5. Frequency of phenophase stages in *Epipactis albensis* population in 2021. Phase frequency scale: 0 – searched, but not found; 1 – one or two solitary individuals; 2 – more than two individuals, but a minority of the population; 3 – a large part of the population, but most plants are in different phenophase; 4 – prevailing phenophase. For phenopase abbreviations, see Table 1

Year		Sprouting–inflorescence emergence			Development of fruit			Dormancy			
2021			Flowering					Maturity			
Week	Date	Gr.	Gr.-Fl.	Full Fl.	Fl. Fading	End Fl.	Seed ca.	Start diss.	Full diss.	Yellow	Brown
26	29 June	0									
26	02 July	0									
27	10 July	0									
28	14 July	2									
29	18 July	4	1								
29	23 July	3	4	2							
30	25 July	3	4	3							
31	03 Aug	2	2	4	3	2	2				
32	14 Aug		1	2	3	4	3				
33	19 Aug			1	1	2	4				
33	21 Aug					2	4				
34	24 Aug	1			1		4				
35	01 Sept		1				4				
35	04 Sept		1	1			4				
35	05 Sept			2			4	2			
36	08 Sept			1	1		4	3			
36	12 Sept							3	4		
38	26 Sept								4		
39	03 Oct			1					4	3	
40	07 Oct								3	4	
40	10 Oct					1				4	
41	16 Oct									4	
52	27 Dec										4

Table 6. Comparison of the monthly average of medium day temperature, minimum temperature (°C) and precipitation per month (mm) in 2020 and 2021

Month	2020			2021		
	Monthly average of medium day temp., °C	Registered lowest temp., °C	Precipitation per month (mm)	Monthly average of medium day temp, °C	Registered lowest temp., °C	Precipitation per month, mm
Jul	17.7	7.1	21.4	21.9	10	122.8
Aug	18.6	6.4	12	16.3	4	77.6
Sep	15	4.3	32.8	11.5	1.9	60.6
Oct	10.4	1	0	8.4	-2.3	27.8
Nov	5.2	-3	0	4.3	-5.2	47.6

plants were seen as late as 3 October 2021. In 2020, the latest flowering specimen was registered on 17 November, and this plant continued to flower until winter colds. In mid-December, the plant was found still with flowers frozen into ice.

Comparing temperatures and precipitation in 2020–2021 revealed that it was warmer and dryer in 2020 during *Epipactis albensis* growth period than in 2021 (Table 6).

Threats and proposals for conservation

In 2021, part of the plants showed brown spotting on the leaves. Pathogenic fungi *Absidia orchidis* (Vuill.) Hagem causes similar symptoms; however, specimens were not checked for the presence of pathogens. This pathogen can weaken or cause the death of an infected individual due to rot of roots if the infection reaches the root system. Some plants disap-

peared during the season (presumably were eaten by herbivores). Moth larvae *Arctiidae* Leach were found feeding on capsules of *Epipactis albensis*. There is too little data to tell if such damage can have a long term negative impact on the population, and more extended investigations are needed.

Species status according to International Union for Conservation of Nature (IUCN, 2012) criteria depends on the type of available data collected from taxa under evaluation. Collected data lead us to apply criterion B (a limited distribution with high fragmentation and extreme fluctuations) to a species. Furthermore, both recorded populations meet criterion D (very small or restricted populations). The population of *Epipactis albensis* in Lithuania is outside of the main distribution area of the species. At both known Lithuanian sites, the populations are small, with the total number of specimens less than 200 individuals dispersed in less than 200 ha area. Therefore, we recommend including *Epipactis albensis* into the List of Protected Animals, Plants and Fungi Species of the Republic of Lithuania as endangered (EN) [B2a,b(ii) c(iv) D].

DISCUSSION

General distribution and status of the species in Lithuania

Epipactis albensis has been recorded in several Central European countries, i.e. the Czech Republic (Nováková & Rydlo, 1978), Slovakia (Rydlo, 1982), Hungary (Molnár & Csábi, 2021), southwestern Poland (Zając & Zając, 2001; Czarna et al., 2014, Zając & Zając, 2019) with few outposts in Central Poland, Romania (Molnár & Sramkó, 2012), Ukrainian Transcarpathian Region (Ljubka, 2018), Austria (Breiner et al., 1993) and the Eastern part of Germany (Wucherpfennig, 1993; Hennings, 2019). *Epipactis albensis* also has been reported in Belarus (Lebed'ko, 2017), but its occurrence is based on erroneously identified small specimens of *Epipactis helleborine* (L.) Crantz (personal communication by Valery Tikhomirov). The illustration in the Flora of Belarus (Lebed'ko, 2017) depicts *Epipactis albensis*; however, the picture is based on a slightly changed copy of an earlier published drawing from Romania by Molnár & Sramkó (2012). Still, the general distribution pattern of the species, and recent records of it in Lithuania, show a high probability that this species can also exist in Belarus, especially in the western part of the country (Fig. 3).

The new *Epipactis albensis* population found in the Bukta Forest in 2020 is ca. 340 km away from the population in the environs of Puławy, Lubelskie voivodeship, Poland (Zając & Zając, 2001; 2019). The main distribution area of the species is further to the South, in the foothills of the Tatra and the Carpathian Mountains, and to the South of this mountain range. In the Eastern part of Germany, the species range almost reaches the Baltic Sea in the North (Fig. 3). Thus, the limit of the main distribution area of the species is situated ca. 500 km away from recently documented sites in Lithuania.

The population in Lithuania showed preference or tolerance of the species to partially disturbed habitats. Many plants grew next to the roadside or Bukta Nature Trail of the Žuvintas Biosphere Reserve. The densest part of the population was found next to asphalt crossroads, in very close vicinity of the village. Furthermore, the Bukta Forest is probably one of the best botanically investigated forest areas in the country (Balsevičius, 2001; Katilius, 2001; Brukas et al., 2006); however, no researcher has mentioned this species. This raises a hypothesis about the possible fresh introduction of *Epipactis albensis* seeds in the area by anthropogenic means. Central European nature destinations and Bukta Nature Trail are popular tourist attractions for nature travellers, and orchid seed transportation by boots or clothes is entirely possible. However, during the further investigation of similar habitats in the area, for the occurrence of *Epipactis albensis* in 2021, another small population was found in the Dalginė Forest, with minimal anthropogenic influence and natural vegetation. The Dalginė Forest area is not intended for visitors; it belongs to the area protected on the municipal level (the Dalginė Botanical Reserve). There are no paths or attractions for tourists. The direct distance between the two populations is 2.8 km. They are divided by the River Šešupė, meadows and residential areas. Historically, those two forests probably belonged to one big forest massif, now fragmented due to agriculture and other anthropogenic activity. Such findings indicate a much older presence of species in the country and make the hypothesis about a recent

Fig. 3. Distribution of *Epipactis albensis* in Europe (after Zając & Zając, 2001; Molnár & Sramkó, 2012; Ljubka et al., 2014; Hennings, 2019; Zając & Zając, 2019; Průša, 2019; Baborka, 2022, modified)

anthropogenic introduction of *Epipactis albensis* to Lithuania unlikely. During the investigation of herbarium collections, one specimen similar to *Epipactis albensis* was discovered. It was collected in the Bukta Forest and identified initially as *Epipactis helleborine* (BILAS herbarium sheet Nr 86959) in 2001 by K. Katilius. The specimen is still in buds, with vegetative features like *Epipactis albensis*. The diagnostic flower features easily seen in live plants are very hard to evaluate in dried specimens, especially in buds; therefore, identification of the specimen remains inconclusive.

Diagnostic features and comparison with similar species

Epipactis albensis is an obligate autogamous species. The autogamy is reflected by its floral morphology: its anther is sessile, clinandrium is only slightly developed, viscidium is absent, rostellum is non-functional, and pollinia are powdery (Molnár & Sramkó, 2012).

On the iconographical material, *Epipactis albensis* is quite similar to other *Epipactis* species. In the flora of Lithuania, *Epipactis helleborine* can have whitish-green flowers. *Epipactis helleborine* is one of the most common species of the genus in the country. The most striking difference between the two is size. All *Epipactis albensis* parts are much smaller than those of *Epipactis helleborine*. Even though the stem height of the largest *Epipactis albensis* specimens can be similar to the smallest of *Epipactis helleborine*, the flower size of *Epipactis albensis* is always much smaller, 7–9 mm diameter, while that of *Epipactis helleborine* is 15–21 mm. *Epipactis albensis* is an autogamous species, and such a life strategy can be seen in flower morphology (Figs 2, 4). One of the most accessible characteristics is that the flowers

have a non-functional rostellum and lack viscidium, a prominent feature of heterogamous *Epipactis helleborine* flowers (viscidium is visible only in fresh *Epipactis helleborine* flowers with pollinia). *Epipactis albensis* never opens flat; even in full bloom, flowers are half-opened, sometimes open for a brief, or do not open. 2020 was an arid year, and some specimens had bud shaped, unopened cleistogamous flowers with developing capsules. The lip of *Epipactis albensis* is always straight, pointed to the front of the flower, whereas that of *Epipactis helleborine* is usually bent, with the tip of the lip pointed down or even to the back of the flower (Fig. 4).

Biology and ecology

The anthers of *Epipactis albensis* usually open in the buds and allocate pollen to the upper edge of the stigma (Fig. 2). The overwhelming proportion of flowers produce fruits (Molnár & Sramkó, 2012). Populations of self-pollinated species consist of a mixture of homozygous lines (Singh et al., 2021). Autogamy is helpful in places with few pollinators and harsh conditions (Claessens & Kleynen, 2011) because only a single colonising individual is needed to start a new colony. However, plants have fewer possibilities to adapt to changing conditions (Claes-

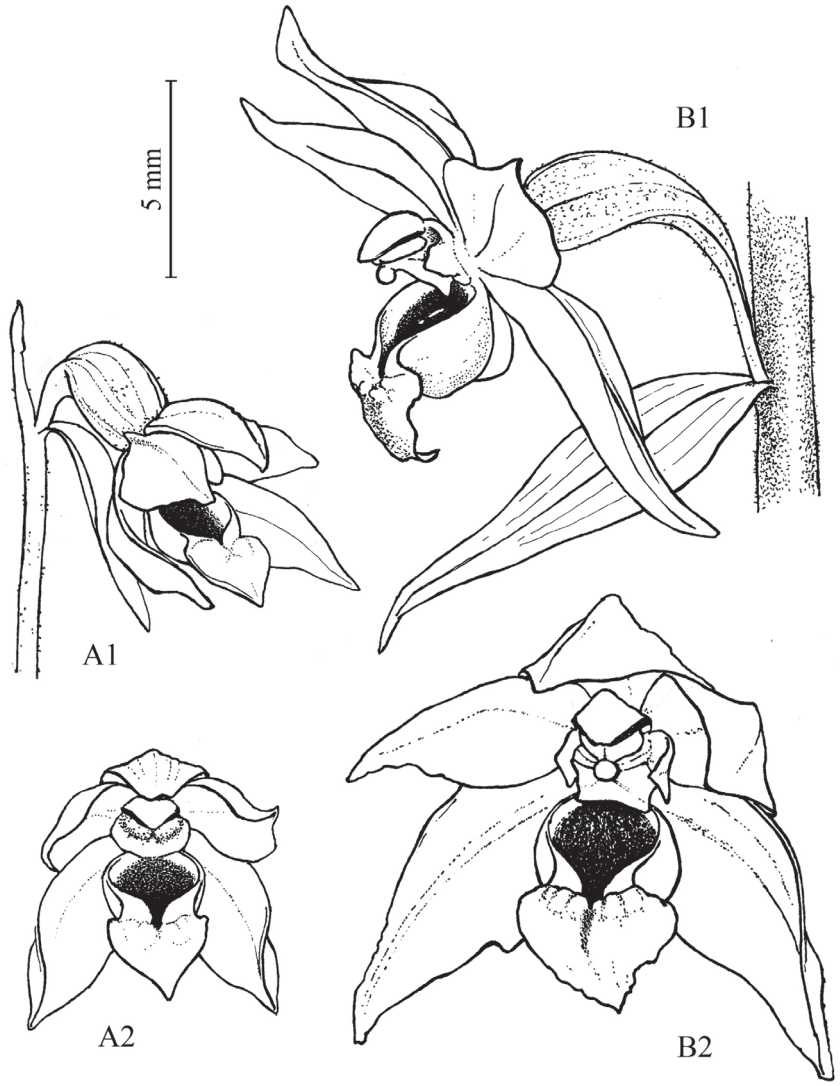

Fig. 4. Comparison of *Epipactis* flower shape and size: A1, A2 – *Epipactis albensis*; B1, B2 – *Epipactis helleborine*. See viscidium in the centre of the heterogamous *Epipactis helleborine* flower, absent in flowers of autogamous *Epipactis albensis* (drawing by M. Ryla)

sens & Kleynen, 2011). Furthermore, *Epipactis albensis* population structure and occupied habitat make cross-pollination difficult. In most cases, plants are few and far apart in a dense dusky forest. In addition, the onset of flowering significantly varies from one individual to another within a population, and this feature further reduces the likelihood of cross-pollination.

In the Bukta Forest, *Epipactis albensis* flowers produced nectar and opened flowers were actively visited by *Myrmica* species (probably *Myrmica rubra* L.) that feed on nectar (Fig. 2). *Myrmica* genus is not listed as a pollinator of any *Epipactis* species since the insects are too small and do not touch stigmatic surfaces during their visit. However, in rare circumstances, cross-pollination of obligate autogamous plants is also possible (Claessens & Kleynen, 2011). Jakubska-Busse et al. (2017) have described a new hybrid between *Epipactis albensis* and *Epipactis purpurata* in Poland. Natural hybrids are a suitable proof of cross-pollination; however, the specimen depicted in the photo material (Jakubska-Busse et al., 2017) looks very similar to *Epipactis purpurata* f. *chlorophylla* (Seeland) P. Delforge and the hybrid origin of the depicted plant is doubtful. Even a very low level of out-crossing would result in the appearance of new gene combinations and lead to the origin of a mixture of different homozygous types. It would be exposed in morphology through homozygosity (Singh et al., 2021). However, generative characters of plants observed in the Bukta and Dalginė Forests were uniform and visually similar to plants from other Central European populations. Uniformity of generative and vegetative characters over a large distribution area of the species means that cross-pollination events are infrequent in *Epipactis albensis* or do not happen at all.

Phenology

Comparing the data collected in 2020 and 2021 (Table 4, Table 5) on *Epipactis albensis* phenology, we revealed specific differences. The beginning of growing season in 2021 started ca. seven days earlier than in 2020. Almost the exact proportion of plants in corresponding phenological stages was registered on 9 August 2020 and 3 August 2021 (Tables 4, 5). However, the end of the vegetating cycle was different by ca. 40 days. Comparable proportions were observed on 23 October 2020 and 12 September 2021 and 17 November 2020 and 7 October 2021. In 2021, the development of plants was quicker even though the year was cooler (Table 6). Only at the beginning of the growing season in July of 2021, it was considerably warmer than in the same period of 2020 (average 24 hours temperatures in July were 17.7°C in 2020 versus 21.9°C in 2021). For the rest of the months during the active development of aboveground shoots, the temperatures were lower (August–October, 2–3.5°C cooler). Such temperature differences should demonstrate opposite results from the data observed since lower temperatures should result in slower plant development. We failed to explain such differences by limiting low temperatures. In both years, the beginning of dormancy (mass seed dispersal and changing plant colour) started well before temperatures dropped below 0 °C. Most likely, plant development in 2020 was delayed because of extreme precipitation deficiency. Thus, sufficient humidity levels probably have a more significant impact on the speed of plant development than higher temperatures in dry conditions.

Population structure

Bukta population in 2020 and 2021 showed considerable variation in aboveground stem numbers. J. Rydlo (1995), in his study on *Epipactis albensis* in the permanent plot, stated that 61% of plants in the population flowered only once over 15 years. Population density has varied by ten in different years (Rydlo, 1995). Investigation of dormant underground plants showed that 50% of found live specimens last time flowered five years ago. One specimen was found that flowered for the last time 15 years ago while still staying alive underground during the duration of the experiment (Rydlo, 1995). Thus, plants can remain in the dormant phase for prolonged periods. Significant variation in density of flowering individuals from year to year is the expected behaviour of the species.

Epipactis albensis ability to tolerate periodical flooding has been mentioned by Süveges et al. (2019). In Central Europe, most *Epipactis albensis* sites are characterised as alluvial softwood and hardwood forests, banks with willows and poplars, and wet margins of forest roads (Molnár & Sramkó, 2012).

The species often grow in secondary habitats in the southern and central parts of its range. For example, this species has been observed in the Czech Republic on *Quercus rubra-Populus ×canadensis* plantation, next to *Populus* trees (Rydlo, 1995). In Ukraine, the species has been found in *Populus nigra–Fraxinus pennsylvanica* stands (Ljubka et al., 2014). This tendency was also observed in Hungary (Süveges et al., 2019). Species have also been found on lignite coal mining heaps overgrown with *Populus ×canadensis*, *Betula pendula*, *Robinia pseudoacacia*, *Padus avium*, *Fraxinus excelsior*, etc. in southeastern Germany (Wünsche, 2013). In the northern part of the species range, Germany and Poland, species grow in broadleaved forests, in most forests with *Fagus sylvatica*, *Acer platanoides*, *Carpinus betulus* (Bernacki 2001; 2008; Pawlak, 2012; Hennings 2019). Gębala (2008) has noticed that the optimal habitats for *Epipactis albensis* in Poland are *Tilio-Carpinetum betuli* communities with a high degree of naturalness. Both populations in Lithuania have also been found in *Tilio-Carpinetum* communities.

Epipactis albensis has a considerably wide soil pH reaction tolerance. The soil pH at different sites in Central Europe ranges from 3.6 to 7.2, but in most localities, the soil is neutral (Ljubka et al., 2014). Therefore, the soil pH value in the studied samples from Lithuania, falls within Central European variation range limits.

We have not documented any individuals in the non-flowering stage during the two years of investigation. Even the most miniature plants (8 cm) had at least 1–2 flowers. Plants without flowers had apparent signs of aborted inflorescence due to some infection or physical damage. Non-flowering individuals could be scarce and hard to see due to their small size in dense surrounding herb vegetation or appear above ground, not every year. Rydlo (1995), in his long-term observation of *Epipactis albensis* population on a permanent plot, has indicated the presence of sterile individuals and individuals that stop growing right under the soil surface and do not appear aboveground. Provided stem height measurements assume that the author under the term ‘sterile’ has included plants with aborted buds (e.g. fertile specimens). Since usually sterile *Epipactis* specimens have a very low stem or leaves are arranged in base rosette without any stem.

Baborka (2022) states that no sterile shoots are known or that sterile shoots are not yet documented for several *Epipactis* species, including *Epipactis albensis*. All species with such population structural features (*Epipactis albensis*, *Epipactis fibri* Scappaticci et Robatsch, *Epipactis moravica* Batou ek, *Epipactis olympica* Robatsch, *Epipactis pontica* Taubenheim) are small, autogamous dark forest floor dwellers. Some species are very closely related to *Epipactis albensis*. Such biological behaviour of the plants could be a strong indication of very tight relationships with mycorrhizal fungi. It enables plants to spend all initial ontogenesis underground until enough resources are saved for the energy-consuming flowering stage. Strong mycorrhizae interactions could also explain heavy variation in numbers of aboveground individuals from year to year. Since non-flowering specimens stay underground. *Epipactis albensis* is known to have achlorophyllous individuals (Jakubska & Schmidt, 2005). Such plant development abnormalities are fatal for many photosynthetic plants, but this phenomenon is well known for the *Epipactis* genus (Lewis, 2015). Chlorophyll-free specimens are fully mycotrophic (Lewis, 2015).

Threats and conservation

Epipactis albensis is a threatened plant species and is included in the lists of protected species in most countries. It is recognised as vulnerable (VU) in Poland (Bernacki, 2008), endangered (EN) in the Czech Republic, Slovakia and Hungary and red-listed in Ukraine (Ljubka et al., 2014).

The most severe predictable threat to populations is related to possible habitat loss. Seedling establishment in the population seems to have a meager success (Těšitelova et al., 2012). The vitality of plants (and population) mostly depends on the root system mycorrhizae since plants spend most of their life cycle underground (Rydlo, 1995). *Ascomycetes* from *Tuberaceae* and *Pyronemataceae* were the most frequently detected ectomycorrhiza fungi in mature *Epipactis albensis* individuals (Těšitelova et al., 2012). *Tuberaceae* fungi also make mycorrhizae with surrounding trees; therefore, strict conservation of forest habitats with populations is required since cutting down trees in habitat would damage feeding mycorrhizae connections (Těšitelova et al., 2012).

Both known sites in Lithuania exist in protected forest areas with very limited forestry. Thus, the conservation status of recently known habitats is sufficient. However, if species are found at other sites in the future, habitat conservation should be organised if necessary.

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MR https://orcid.org/0000-0003-1759-7192