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Fruitbody production of *Hericium erinaceus* and its distribution in Slovakia

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The relationships between selected log parameters and occurrence of *Hericium erinaceus* fruitbodies as well as its phenological aspects and distribution in Slovakia were studied for the first time. The research was conducted with two datasets. The first dataset is based on 15-year monitoring of 20 oak logs with the aim to relate *H. erinaceus* preference to selected log variables. The other one comprises records obtained from 63 different localities in Slovakia.

The monitoring data confirmed continual fruitbody production on the same dead log and at the same position for three consecutive years. Furthermore, the fruitbodies were observed for five continual years in the same section of a living oak tree trunk. Of the studied log characteristics, *H. erinaceus* showed preference for smaller log sizes.

Based on the second dataset, the main fructification period is dated from August to November, but fruitbodies can be found until February. Logs with fruitbodies were predominantly classified into the initial wood decay stage (Stage 2). The majority (92%) of the localities were situated in areas with a mean annual temperature above 6 °C.

Key words: fructification, phenology, *Quercus petraea*, wood decay stage.

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Cieľom práce bolo zistiť vzťah medzi vybranými charakteristikami ležiacich kmeňov stromov a výskytom koralovca ježovitého (*Hericium erinaceus*), jeho fenologické prejavy a rozšírenie na Slovensku. Výskum bol uskutočnený použitím dvoch rôznych súborov s údajmi. Prvý súbor pochádza z 15-ročného monitoringu 20 dubových kmeňov realizovaného za účelom skúmania vzťahu medzi výskytom koralovca ježovitého a vybranými charakteristikami kmeňov. Druhý súbor predstavuje záznamy, ktoré boli získané zo 63 lokalít výskytu huby na Slovensku.

Monitoring preukázal kontinuálnu tvorbu plodníc na rovnakom mŕtvom kmeni a v tej istej pozícii na ňom počas troch po sebe idúcich rokov. Okrem toho bol pozorovaný neprerušený výskyt plodníc počas piatich rokov na rovnakej časti kmeňa žijúceho duba. Spomedzi hodnotených charakteristík kmeňov výskyt plodníc najviac súvisel s ich rozmermi. Plodnice boli zaznamenané skôr na kratších kmeňoch s menším objemom.

Z druhého súboru údajov bolo zistené, že tvorba plodníc prebieha od augusta do novembra, avšak plodnice je možné nájsť až do februára. Ležiace kmene s výskytom plodníc boli prevažne klasifikované do počiatočného štádia rozkladu dreva (stupeň rozkladu 2). Väčšina (92 %) lokalít s výskytom huby sa nachádza v oblastiach s priemernou ročnou teplotou nad 6 °C.

Introduction

Fungi of the genus *Hericium* (*Russulales*) are characterised by large, fleshy, pileate or branched fruitbodies with a hydnoid hymenophore, preferably occurring on dead wood (Bernicchia & Gorjón 2010) but also colonising dead heartwood of living trees. Three species of *Hericium* were known to occur in Europe (Holec et al. 2012) and Slovakia (Lizoň & Bacigálová 1998): *Hericium erinaceus*, *H. coralloides* and *H. flagellum*. Recently, *Hericium cirrhatum* was added to the *Hericium* genus after phylogenetic analyses (Larsson & Larsson 2003); previously, this species was known as *Creolophus cirrhatus*. *Hericium* species delimitations are still far from being solved (Hallenberg et al. 2012) and new species are still described (Das et al. 2011). The rarest one throughout Europe is *Hericium erinaceus*, although it is the most widely distributed species of the genus (Koski-Kotiranta & Niemelä 1988). The species occurs in the entire temperate zone of the northern hemisphere – North America, Europe, Russia, China and Japan (Stamets 2000) and although it is widespread in Europe (Piątek 2005), it is rare in central Europe (Pegler 2003). In Europe, according to Hallenberg (1983), *H. erinaceus* is distributed in its central and southern part, in the north reaching southern Sweden. Although it is easily recognisable by its large globular fruitbodies with long whitish spines, its distribution and ecological data are often lacking, similarly to other hericioid fungi (Boddy et al. 2011). Habitat preferences of the species in Slovakia were discussed earlier (Kunca & Čiliak 2017a).

In Slovakia, *H. erinaceus* is red-listed (Lizoň 2001) and legally protected (Anonymus 1 2014). It is also legally protected in several other European countries, e.g. Great Britain (HMSO 1981), Hungary (Siller et al. 2006), Poland (Siwulski et al. 2009), Slovenia (Anonymus 2 2011), Serbia (Ivančević et al. 2012), and red-listed in Denmark (Wind & Pihl 2004), the Czech Republic (Holec & Beran 2006), Romania (Tanase & Pop 2005), Croatia (Tkalčec et al. 2005), Bulgaria (Gyosheva et al. 2006), Switzerland (Senn-Irlet et al. 2007), Norway (Brandrud et al. 2010) and Sweden (ArtDatabanken 2015). *Hericium erinaceus* is included in the candidate species list for the European red-list (European Council for the Conservation of Fungi 1998–2010) and listed in the proposal for inclusion of fungi in Appendix I of the Bern Convention (Dahlberg & Croneborg 2003).

Fruitbody production of wood-inhabiting fungi depends on many environmental factors, including climatic ones. Especially temperature drives fruiting of autumnal saprotrophic fungi (Andrew et al. 2018). However, over a longer time scale (10 years and more) other parameters such as vegetation and forest history rather than climatic ones can play a major role in fructification (Laganà et al. 2002). Besides environmental factors, the variety of woody debris (Abrego & Salcedo 2013), stage of wood decay (Heilmann-Clausen 2001), decomposer characteristics (Pouska et al. 2010), contact with the ground (Pouska et al. 2011) and

canopy gaps (Brazee et al. 2014) can play an important role in fruitbody production as well. However, the relations between deadwood parameters or environmental factors and *H. erinaceus* occurrence have been studied very rarely (Boddy et al. 2011).

Wood-inhabiting fungi have a unique position in forest ecosystems, often forming an easily recognisable component of specific habitats. But many wood-inhabiting fungi are likely to depend on a rich supply of microhabitats rather than the presence of long local forest continuity (Christensen et al. 2005). *Hericium erinaceus* fruitbodies are easy to recognize in the field without the need for special equipment, typically growing in natural biotopes in a spatially and temporarily predictable pattern, which are attributes of a good indicator (Halme et al. 2017). The species was used in evaluations of the status of beech forests in Europe by Holec (2003), Adamčík et al. (2007), Holec et al. (2015) and Langer et al. (2015) and is likely to have a potential to serve as an indicator in old-growth oak forests (Blaschke et al. 2009).

Based on our long-term monitoring of a set of 20 logs we aim to evaluate the effect of selected logs parameters on the occurrence of *H. erinaceus* fruitbodies and continuity of its fruiting. We also summarise data on phenology and geographical distribution of the species in Slovakia and compare them with records in neighbouring Central European countries.

Material and methods

M o n i t o r i n g d a t a s e t. The monitoring plot Skalie, where 20 logs were selected, was established in 2003 in the Štiavnické vrchy Mts., close to Banská Štiavnica, central Slovakia. The plot is situated on the south-eastern slope with 70% inclination, and altitudes range from 640 to 690 m. It is a fragment of an old-growth oak forest with a soil protection function. Sessile oak (*Quercus petraea*) with the oldest individuals reaching ages of 200 years dominates at the plot. The soil at the plot is rocky, formed on biotic-amphibolite andesite. In 1991 many old oak trees fell due to a windstorm in the area (M. Diviak, pers. comm.).

Twenty logs of sessile oak were selected randomly at monitoring plot Skalie (Tab. 1, Log ID 1–20), although due to the steep slope logs were preferably selected close to the forest path (nature trail). These logs were monitored for fruitbody production once in two months from the middle of August to November, every year from 2003 to 2017. There was an equal number of visits to each log. All these logs were lying and dead.

For each log, length, diameter, volume, bark cover and decay stage were measured or assessed (Tab. 1). The diameter was measured in the middle of the log. Wood decay stage was assessed using the classification of Heilmann-Clausen (2001).

Tab. 1. Fruitbody production of *Hericium erinaceus* on 20 logs (1–20) and two living trees (1L, 2L) along with their selected characteristics at monitoring plot Skalie. Numbers in the years of monitoring represent numbers of fruitbodies. Numbers in brackets denote continual occurrence of fruitbodies at the same position. "x" indicates a year when a tree was not monitored.

Log ID	Length (m)	Diameter* (cm)	Volume (m^3)	Bark cover (%)	Decay stage**	Year of monitoring														
						2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
1	6.9	41	0.91	50	2						1	1	(1)	(1)						
2	11.5	24	0.52	0	2															
3	7.2	25	0.35	50	1–2															
4	5.4	15	0.10	100	1			1												
5	14.3	41	1.89	0	2															
6	16.1	42	2.23	0	2–3															
7	17.5	30	1.24	0	2–3															
8	4.8	34	0.44	0	1–2							1								
9	5.5	38	0.62	0	2	1	(1)	(1)												
10	10.5	41	1.39	0	2															
11	18.5	35	1.78	0	2															
12	15.8	26	0.84	0	2															
13	16.4	45	2.61	0	2															
14	16.8	29	1.11	0	2															
15	18.4	59	5.03	100	2															
16	17.4	30	1.23	0	2	1	(1)	(1)	(1)	1										
17	23.0	41	3.04	0	2															
18	10.4	51	2.12	100	2															
19	18.5	51	3.78	30	1–2															
20	16.9	54	3.87	0	2															
1L	–	22×25	–	95	–	x	x	1	(2)	(1)	(1)	(1)		(1)			(1)			
2L	–	32×21	–	90	–	x	x	x	x	x	x	x	1	(4)	(1)					

* Diameter at breast height of living trees was measured in two opposite directions around the tree trunk.

** Two numbers are related to different stages of decay of log parts.

Two standing and living oak trees (*Quercus petraea*), where fruitbodies had been recorded and were occasionally found during the research, were also included in the supplementary monitoring at plot Skalie (Tab. 1, Log ID 1L and 2L). Of these, the first one has been monitored for 13 years since 2005, the other one for 8 years since 2010.

Geographical dataset. To assess the geographical distribution and fructification of *H. erinaceus* we used an existing database of records (Kunca & Čiliak 2017b), supplemented by another 16 recent records. Records of *H. erinaceus* from Slovakia not published in Kunca & Čiliak (2017b) are listed below.

Wood decay stage (Heilmann-Clausen 2001) was altogether assessed for 15 logs from 9 localities all over Slovakia, including five logs with fruitbodies at monitoring plot Skalie (Tab. 1) and three logs from recent collections (see below). The remaining seven records that previously missed data on decay stages (in Kunca & Čiliak 2017b) were added and are published here (Tab. 2).

Tab. 2. Decay stage values of logs at selected localities presented in Kunca & Čiliak (2017b).

No.	Date	Locality	Host tree	Decay stage
29	16 Oct 2010	Dúbravica	*Quercus* sp.	2
32	16 Nov 2010	Snina	*Fagus sylvatica*	2
39	04 Aug 2012	Snina	*Fagus sylvatica*	2
45	25 Nov 2012	NNR Boky	*Quercus cerris*	3
49	01 Oct 2013	NNR Boky	*Ulmus carpinifolia*	3
51	15 Oct 2013	Pustý hrad	*Quercus petraea*	2
53	17 Oct 2013	Kostoľany	*Quercus* sp.	2

The distribution map of the species in Slovakia is based on all available records. The position of the localities in the map is presented in the form of quadrants (Q) of the Central European grid mapping system (UTM). To depict zones with different mean annual air temperature, climatic map layers of the Slovak Republic for 1960–1990 were used (Štastný et al. 2002). More recent layers are not available, but even if they were, data not influenced by climate change should be preferred.

Voucher specimens of recent collections are deposited in the first author's private herbarium (PVKU).

Recent collections documented by vouchers (first published here, arranged geographically from west to east); for each record orographic unit, nearest municipality, name of locality, UTM quadrant, altitude, substrate (in some cases with decay stage), date, finder and identifier are given.

Slovakia. Malé Karpaty Mts., Bratislava, Kamzík hill, Q7868b, 425 m a.s.l., trunk of living *Fagus sylvatica*, 6 November 2015, leg. & det. P. Reťkovský. – Malé Karpaty Mts., Lošonec, hamlet of Majdan, Q7570a, 260 m a.s.l., trunk of living *Quercus cerris*, 23 October 2015, leg. & det. D. Solár. –

Malé Karpaty Mts., Lošonec, Q7570a, 260 m a.s.l., trunk of living *Quercus cerris*, 22 September 2016, leg. & det. D. Solár. – Pohronský Inovec Mts., Obyce, Q7576d, 590 m a.s.l., trunk of living *Quercus* sp., 9 September 2016, leg. & det. R. Borčin. – Vtáčnik Mts., Horná Ves, Lubenská skala hill, Q7477a, 625 m a.s.l., part of dead *Quercus* sp. trunk, 20 November 2016, leg. & det. L. Kalabus. – Štiavnické vrchy Mts., Hronská Breznica, Balov grúň hill, Q7479d, 510 m a.s.l., log of *Quercus petraea* (Decay stage 3), 6 December 2015, leg. & det. V. Kunca. – Kremnické vrchy Mts., Pitelová, Q7479b, 485 m a.s.l., trunk of living *Quercus petraea*, 9 October 2017, leg. & det. V. Kunca. – Kremnické vrchy Mts., Boky National Nature Reserve, Q7480a, 345 m a.s.l., log of *Quercus cerris* (Decay stage 4), 26 December 2015, leg. & det. V. Kunca. – Javorie Mts., Zvolen, hamlet of Neresnica, Q7480b, 350 m a.s.l., log of *Quercus petraea*, 13 November 2016 (Decay stage 2), leg. & det. V. Kunca. – Zvolenská kotlina basin, Príboj National Nature Reserve, Q7281c, 465 m a.s.l., trunk of living *Quercus petraea*, 7 November 2017, leg. & det. V. Kunca. – Zvolenská kotlina basin, Čačínska cerina Nature Reserve, Q7381b, 450 m a.s.l., trunk of living *Quercus cerris*, 16 October 2017, leg. & det. V. Kunca. – Zvolenská kotlina basin, Hrochoť, Chochuľka hill, Q7381b, 720 m a.s.l., trunk of living *Quercus petraea*, 27 October 2017, leg. & det. P. Mathé. – Poľana Mts., Hrochoťská dolina valley, Q7382a, 760 m a.s.l., trunk of dead *Quercus petraea*, 4 December 2015, leg. & det. V. Kunca. – Juhoslovenská kotlina basin, hamlet of Nové Hony, Židova hora hill, Q7684b, 230 m a.s.l., trunk of living *Quercus cerris*, 2 August 2015, leg. & det. J. Hraško. – Východoslovenská nížina lowland, Strážne, Q7697a, 103 m a.s.l., sand dune, stump of *Robinia pseudoacacia*, 24 October 2016, leg. & det. M. Lazor. – Vihorlatské vrchy Mts., Jedlinka Nature Reserve, Q7099c, 790 m a.s.l., trunk of living *Fagus sylvatica*, 5 October 2016, leg. & det. M. Kříž.

RESULTS

Monitoring of fruitbodies occurrence

In total, 14 fruitbodies were recorded from five out of twenty monitored oak logs during 15 years (logs 1, 4, 8, 9 and 16 in Tab. 1). The fruitbodies were located on wounds, at the points of injury or knotholes of the logs. They were observed on the same place for maximum of three consecutive seasons. Although the fruitbodies occurred at the same log for up to four continual years, they were observed at different parts of logs and in different positions of the same log. The occurrence of fruitbodies seemed to be related to the log dimensions. Four out of five logs with fruitbodies were the shortest ones (Tab. 1). Similarly, mean volume of logs with fruitbodies was 0.66 m^3 compared to the mean volume of 2.12 m^3 measured for those without fruitbodies. From 2012 no fruitbody was observed on the logs.

In addition, 14 fruitbodies were recorded on two living trees – eight on the first (1L) and six fruitbodies on the second tree (2L) (Tab. 1). They appeared only at the damaged places caused by lightning or frost and occurred intermittently on the same living tree for 10 years. From 2015 no fruitbody was observed on any of the living trees.

Geographical distribution in Slovakia

According to the compiled database of records from Slovakia, production of fresh fruitbodies of *H. erinaceus* occurred from July to November, not fresh ones

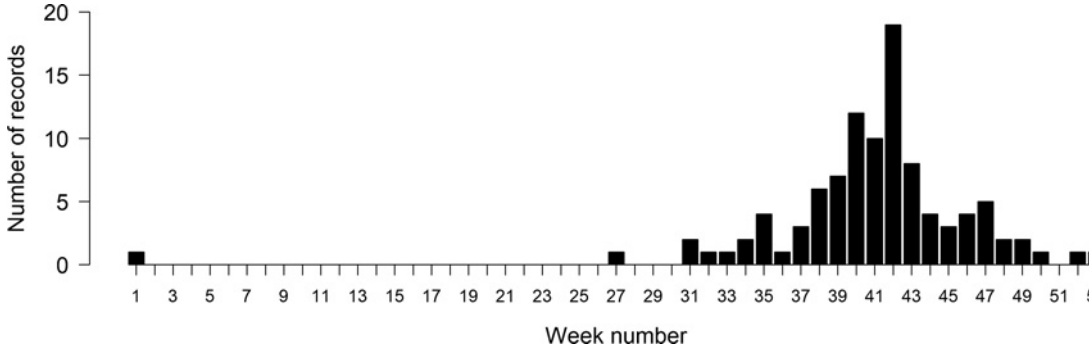

Fig. 1. Time (week 1 = first week of January) when *Hericium erinaceus* was reported fruiting in Slovakia.

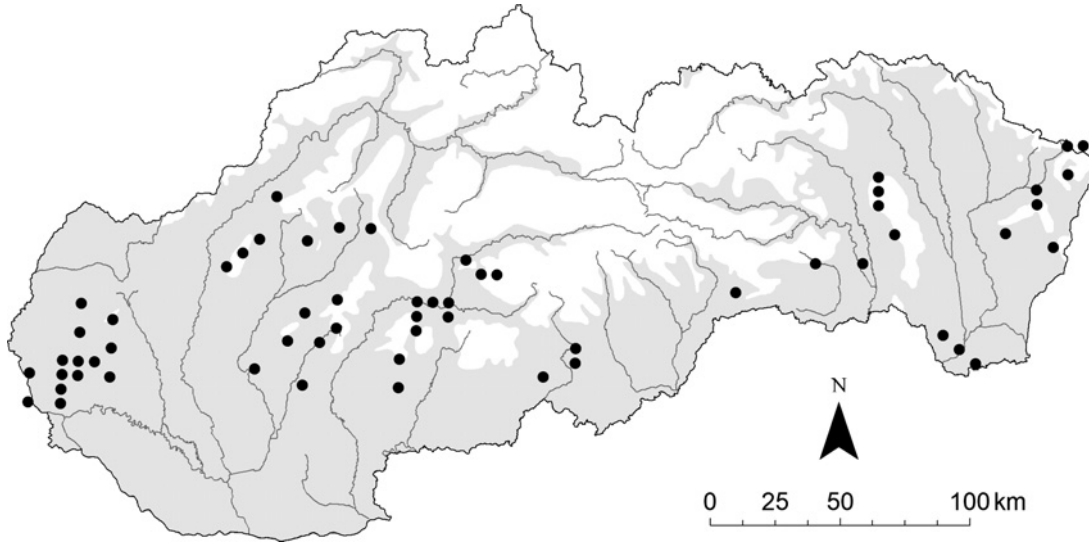

Fig. 2. Distribution of 63 localities of *Hericium erinaceus* in Slovakia. Shaded parts of the map represent areas with mean annual air temperature >6 °C. A single dot may represent two localities.

were rarely found in December and January. Still recognizable, dead and decaying fruitbodies were found until February. More detailed analysis of the data from Slovakia, based on cumulation of data from various years, reveals that the main fructification starts at the end of August and continues in autumn with the peak in 42nd week of the year (Fig. 1). The occurrence of fruitbodies on logs was predominantly linked to the ones in decay stage 2 (Tab. 1, Tab. 2, recent collections above).

Altogether, there are 63 known localities of *H. erinaceus* in Slovakia. More than 92% of the localities lie in area with mean air annual temperature higher than 6 °C (Fig. 2).

DISCUSSION

Substrate preferences

Some wood-inhabiting fungal species can show preference for the type of woody debris (such as diameter, size, stage of decay) on which they grow (Abrego & Salcedo 2013) but vary in their preferences regarding the size of the woody debris they colonise in nature (Juutilainen et al. 2011). Of all studied log characteristics in our study, *H. erinaceus* showed preference for smaller log dimensions as we observed its fruitbodies in most cases on relatively short logs with a small volume. Obviously, short logs are sufficient for fruitbody production of *Hericium* species, including *H. erinaceus* (Grace & Mudge 2015).

Our results thus do not support the general view that occurrence of some rare species is positively correlated with the size of the woody debris size (e.g. Heilmann-Clausen & Christensen 2003, Junninen & Komonen 2011); Heilmann-Clausen & Christensen (2003) also present strong positive correlations between species richness of wood-inhabiting fungi and variables related to log size and complexity. However, the occurrence of fruitbodies in our study could also be affected by log fragmentation. Due to the limits of our dataset caused by the low sample size, we are not able to interpret these relationships more precisely, so our results must be treated with caution.

Boddy et al. (2011) showed fruiting conditions of *H. erinaceus* on living trees may persist for up to 20 years, possibly as long as 40 years. Apparently, this differs depending on the vitality of the tree individual. The species invades the wood of trunks and thick branches through lesions and causes white rot. After the death of the tree, the fungus can continue its growth for many years and produce fruitbodies also on lying trunks and stumps (Fraiture & Otto 2015). In our case, fruiting on two living trees continued for ten and three years respectively. On the latter one, up to four fruitbodies were observed in 2011. Similarly, Marren & Dickson (2000) report to have observed *Hericium coralloides* fruitbodies on the same tree for more than 20 years.

Living or dying trees are more often presented as a suitable substrate for *H. erinaceus* in comparison with logs (e.g. Koski-Kotiranta & Niemelä 1988, Boddy et al. 2011, Fraiture & Otto 2015). It is apparent that fruitbody production is higher on living trees than on logs. The reasons could be specific properties of tree cavities, wounds or knotholes, with rotting wood in various stages of decay, or regular

availability of water absorbed by the living tree from the soil. Boddy et al. (2011) claim that *Hericium* species have been detected as latently present in functional sapwood. Marren & Dickson (2000) observed that *H. erinaceus* is usually found fruiting on living trees which have suffered damage from storms or lightning strikes. This agrees with data from our recent records (see recent collections in Material and methods), where 10 out of 16 records are from living trees, and with a slightly higher prevalence of such records in Slovakia (Kunca & Čiliak 2017a).

Occurrence of fruitbodies of *H. erinaceus* is often associated with old trees or their coarse woody debris (Boddy et al. 2011). However, published data on the wood decay stage preference of *H. erinaceus* is quite rare or missing. Although we observed fruitbodies on logs with a Decay stage ranging from 1 to 4, records from logs of Stage 2 were most numerous. From 2012 onwards, no fruitbodies have been found on the monitored logs. Such a severe decline in the number of fruitbodies could have been caused by a shift in wood decay stage of almost all logs to a higher stage during 15 years of monitoring and the correlating end of *H. erinaceus* fruitbody production in these logs. Similarly, more than 20% of logs inoculated with *H. erinaceus* did not produce any fruitbody over five years during an experiment (Grace & Mudge 2015).

Phenology and occurrence of fruitbodies

In general, *H. erinaceus* fruitbodies are mainly produced from August to November in Europe (Fraiture & Otto 2015). Boddy & Wald (2003) mention that the species starts fructification in early September and continues until late November, with a few records at other times of the year. For the territory of the United Kingdom, Boddy et al. (2011) state the period from August to September to be the usual fruiting season of *H. erinaceus*. Our results correspond with these observations. Although the main fructification season can generally be assigned to autumn, the range of the months differs between countries, even in Central Europe (Fig. 3). One of the reasons could be differences in various climate conditions and different terrain morphology in Europe. Weather conditions in preceding months can influence fruitbody production (Jarvis et al. 2017). However, the fruiting of lignicolous saprotrophs is not influenced by weather factors to the same extent as the fruiting of mycorrhizal species (Laganà et al. 2002).

Based on our data, most fruitbodies were recorded in the 42nd week followed by the 40th week (i.e. the period from early to mid-October). In Austria, likewise, fruitbodies were recorded from the 36th to the 43rd week with most records in the 40th week (Dämon et al. on-line). Dvořák & Hrouda (2005) present maximum incidence in the Czech Republic in October. Especially in the middle of autumn, the fruitbodies are easily visible even from a long distance, due to their relatively large proportions (more than 10 cm) and creamy white coloration.

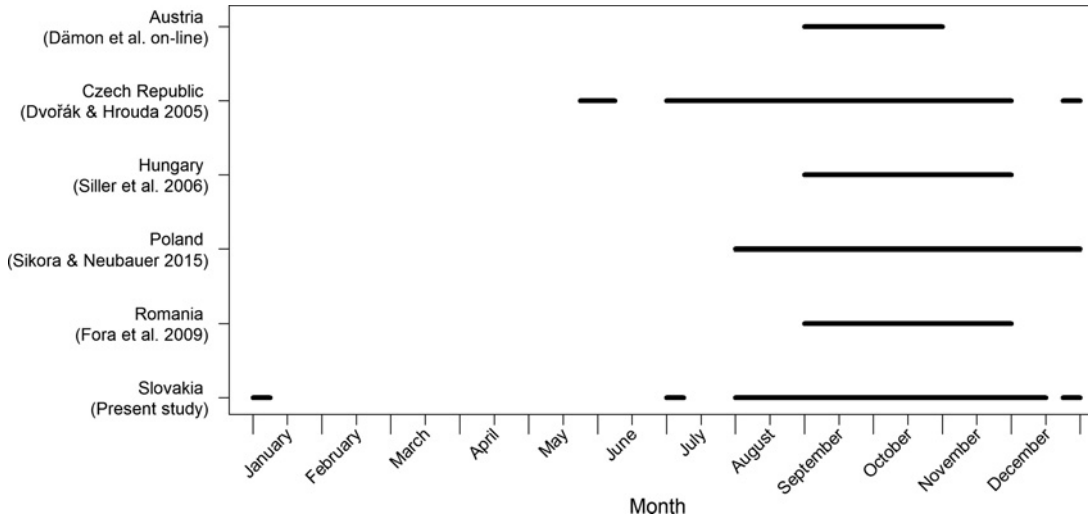

Fig. 3. Fructification period of *Hericium erinaceus* in selected countries in Central Europe.

Distribution range

Broadleaved and mixed forests with suitable conditions for the species, especially those with old or dying trees, occur almost all over Slovakia (Kunca & Čiliak 2017a). Climate mostly limits the occurrence of typical host tree species at higher altitudes. The shaded area in Fig. 2 corresponds fairly well with the distribution or potential territories of oaks and beech, excluding the uppermost areas of beech occurrence. Similarly to Slovakia, four localities in Austria are situated in areas with a mean annual temperature of 6 to 9 °C (Dämon et al. on-line). Temperature maps can thus be used in searching for potential new regions and localities where the species occurs.

Fraiture & Otto (2015) reported occurrence of the species from 29 out of 38 evaluated countries in Europe. *Hericium erinaceus* is not known from countries in the Mediterranean, northern Europe, the Baltic countries and Ireland. Besides Ireland they represent countries with a very warm or cold climate, which limits the presence of or suitable conditions for oaks and beech. Another limit to its occurrence in some of these countries (e.g. Ireland, Cyprus, Iceland and Malta) might be the very low forest coverage and almost missing forests with a natural structure and tree species composition.

Data on habitat preferences from our recent records are in accordance with those evaluated for Slovakia previously (Kunca & Čiliak 2017a), namely its preference for forests with natural tree species composition, in particular old-growth forests. With the new data published here we can refer to 63 localities of the spe-

cies in Slovakia. For comparison, the largest number of localities since 1980 has been reported from France (150 localities) and the United Kingdom (70 localities) (Dahlberg & Croneborg 2003). In the neighbouring Czech Republic, Dvořák (2006) mentioned more than 50 localities. Poland (Sikora & Neubauer 2015) has 23 localities, but in Austria, there are only 7 records from probably four localities (Dämon et al. on-line) while in Hungary, 10 localities are known (Magyar Mikológiai Társaság on-line). Not all finds of the species from Slovakia are reported here. We have not been able to get relevant information on several collections presented by photos on public web pages. In addition, based on our field experience, the fruitbodies are sometimes collected by mushroom hunters in Slovakia.

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