

The decline and recovery of populations of *Potamogeton coloratus* in Hungary

Ústup a obnova populací *Potamogeton coloratus* v Maďarsku

Balázs A. Lukács¹, Attila Molnár V.², András Mészáros³, Ádám Lovas-Kiss¹, Orsolya Vincze^{1,4}, Kristóf Süveges², Réka Fekete² & Attila Mesterházy⁵

¹Wetland Ecology Research Group, Centre for Ecological Research, DRI, 4026 Debrecen Bem tér 18/C, e-mail: lukacs.balazs@okologia.mta.hu; ²Department of Botany, University of Debrecen, 4032 Debrecen, Egyetem tér 1; ³Balaton-felvidéki National Park Directorate, 8229 Csopak, Kossuth u. 16; ⁴Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Cluj Napoca, Romania; ⁵Hortobágy National Park Directorate, 4026 Debrecen, Sumen u. 2

Lukács B. A., Molnár V. A., Mészáros A., Lovas-Kiss Á., Vincze O., Süveges K., Fekete R. & Mesterházy A. (2020) The decline and recovery of *Potamogeton coloratus* populations in Hungary. – Preslia 92: 73–86.

Fen pondweed (*Potamogeton coloratus*) is a characteristic species of oligotrophic waters, therefore, one of the rarest and most endangered aquatic plants in Europe because of habitat loss and population decline all over the continent. In Hungary, all of its populations disappeared during the 1950s and 1960s and then dramatically recovered in recent years during which many populations that had disappeared recovered and new populations established. In this study, we investigated the role of environmental variables in the recovery of this species and in determining its phenology-environment dependency, as well as the role of dispersal in the establishment of new populations. Our study is the first to assess the dispersal ability of *P. coloratus* by means of endozoochory, evaluated by force-feeding mallards with its seeds. We found that variation in annual precipitation does not affect the presence of *P. coloratus*; however, the variation in the karst water level coincides with the number of populations in the region studied. This indicates that the disappearance-reappearance of *P. coloratus* has been driven by fluctuations in regional karst water levels, which was greatly affected by the development of socialist heavy industry and especially the operation of bauxite and coal mines. Moreover, we show that water temperature determines the phenology of this species. Importantly, we also demonstrate that a relatively high proportion of the seeds of *P. coloratus* force fed to mallards passed through their digestive tract and many of them contained viable embryos. Thus, birds could serve as possible dispersal vectors of *P. coloratus* seeds, hence they might be responsible for the establishment of new populations. Overall, *P. coloratus* appears to be recovering, but regular monitoring is needed to ensure its persistence.

Key words: habitat loss, karstic water, *Potamogetonaceae*, seed dispersal, seed dormancy, phenology, endozoochory

Introduction

Human activities have had a widespread effect on freshwaters, which led to the decline of freshwater ecosystems throughout Europe during the last century. A series of combined threats, including land-use changes, water extraction, exploitation, climate change, pollution and biological invasion are prevalent in these ecosystems (Brondizio et al. 2019).

Among freshwaters, one of the most vulnerable is oligotrophic waters, which have low nutrient concentrations and low primary production, therefore, they are extremely sensitive to human disturbance. They support special plant communities, which have high conservation importance and many of their characteristic species are endangered.

One of the characteristic species of oligotrophic waters is the fen pondweed (*Potamogeton coloratus* Hornem.), which is almost restricted to Europe. It can be found from the Mediterranean to Scotland and southern Scandinavia; additional populations occur in the Asian part of Turkey (Wiegleb 1989), while previous occurrences reported from Algeria (Lechevalier 1952) are currently regarded uncertain and the Arabian populations have recently been identified as *P. nodosus* (Kaplan & Symoens 2005). *Potamogeton coloratus* is known as a plant of shallow, calcareous, slow-moving oligotrophic waters and it occurs in waters with a very low level of phosphate ($10\text{--}30\ \mu\text{g}\cdot\text{l}^{-1}$ annual mean, Robach et al. 1996). It is highly intolerant of physical disturbance and uprooting (Mony et al. 2011); consequently, it prefers undisturbed habitats with stable water levels.

Like many aquatic macrophytes, *P. coloratus* has suffered a considerable population decline because of the eutrophication and hydromorphological alteration of its habitats, which pushed it to the verge of extinction in the last decades and currently it is extremely rare or extinct all over Europe. *Potamogeton coloratus* is listed in national Red Lists or Red Data Books in all countries where it occurs, with status varying from least concerned (LC), critically threatened (CR in Czech Republic) to regionally extinct (RE in Poland) (Kleinsteuber & Wolff 1996, Moser et al. 2002, Kaplan 2010, Danihelka et al. 2012, Grulich 2012, Kaźmierczakowa et al. 2016). Moreover, the specific habitat of *P. coloratus* is considered to be of community interest in the European Union (EUNIS habitat type: C1.131 Oligotrophic pondweed communities, Natura 2000 habitat types: 3260 Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation; 3140 Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp., see Annex I of Habitat Directive).

Historically, special karst springs and their neighbouring wetlands harboured a rich and diverse oligo-mesotrophic aquatic plant flora in the Pannonian Ecoregion (Boros 1937, Felföldy 1990). These freshwaters are unique habitats since they have constant year-round temperatures ($18\text{--}22\ ^\circ\text{C}$) owing to underground post-volcanic activities that create abundant thermal outflows all over the Carpathian Basin. Karst springs and streams are refuges for oligo-mesotrophic aquatic vegetation that are rich in stonewort's and support many rare plant species, such as *Samolus valerandi* L., *Utricularia bremsii* Heer, *Carex davalliana* Sm., *Primula farinosa* L., *Pinguicula alpina* L. and *Calamagrostis stricta* (Timm.) Koeler. One of the most iconic species of plant in these habitats is *P. coloratus*, which is considered to be a “faithful attendant” of thermal-streams by Boros (1937). In Hungary, there were once 16 geographically distinct populations of *P. coloratus*, but all of them disappeared by the 1970s, due to the desiccation of its habitats. In most cases, habitat loss was a direct result of groundwater abstraction for open-cast mining of bauxite, which resulted in a decrease in groundwater levels on a regional scale.

In order to develop an effective conservation plan for *P. coloratus*, we need to understand what lead to its drastic population decline in the 1950s and its successful recovery in recent decades. For instance, we know little about the dispersal potential of this species, which is key to understanding its distribution and potential for colonizing novel habitats. Therefore, the central aims of our study were (i) to summarise the data on the distribution

of *P. coloratus* based on field surveys, literature and herbaria data for the Pannonian Biogeographic Region; (ii) to determine the effect of fluctuations in karst water levels and rainfall on the long term occurrence of this species; (iii) to investigate the effect of environmental variables on the fitness of this species (in terms of the phenological state achieved); (iv) to examine the long-distance dispersal ability of *P. coloratus* by means of endozoochory.

Materials and methods

Historical data

We developed a historical database of the distribution of *P. coloratus* in Hungary, using past and recent records based on critically evaluated herbarium data (from herbaria BP – herbarium acronyms according to Holmgren & Holmgren 1998) and published data (Boros 1937, Mesterházy et al. 2017). All herbarium and literature data were checked and revised to minimize errors due to taxonomic misidentification. The complete list of documented occurrences is given in Table 1. From each herbarium sheet and publication, we obtained information on the date of collection, locality and habitat.

Table 1. – Historical and recent records of *Potamogeton coloratus* in Hungary. Karst water level decreased from 1955 to 1980. References are given for the first record. References are related to herbarium sheet or published article. BP = Herbarium Carpato-Pannonicum, Hungarian Natural History Museum.

Locality	1st record	Disappeared	Reappeared	Habitat type	References
Extinct localities:					
Budapest, Aquincum	1873	1966	-	thermal lake, wet meadow, stream	Simonkai (1876)
Budapest, Stream Rákos	1874	1911	-	stream	Boháts ap. Soó (1934)
Budapest, Lake Lágymányosi	1906	set as 1950	-	lake	Tuzson ap Soó (1934)
Sopronkőhida		1947	-		Kárpáti, BP
Tata	1925	set as 1950	-	thermal spring & stream	Boros, BP
Recovered localities:					
Lesenceistvánd	1923	1958	2006	roadside channel, wet meadow	Boros (1923)
Pétfürdő	1927	set as 1950	2016	thermal spring & stream	Boros (1937)
Pápakovácsi	1938	set as 1950	2014	spring-pool in fen meadow	Boros, BP
Raposka	1938	set as 1950	2004	stream	Bauer (2006)
Tapolcafő	1927	1966	2014	stream and pond	
Tapolca	1926	set as 1950	2006	stream	Gáyer, BP
Újrónafo	1929	set as 1950	2015		Polgár, BP
New localities:					
Vindornyalak	1999	-	-	wet meadow	Lájer (1999)
Vácrátót	1999	-	-	Pools in peat digging	Lájer (1999)
Csabrendek	2007	-	-	artificial lake	Mesterházy et al. (2017)
Káptalanfa	2011	-	-	wet meadow	Mesterházy et al. (2017)

Field surveys

Based on historical data, we conducted field surveys to clarify the present distribution of *P. coloratus* within the main area of its historical distribution, in the foothills of the Bakony Mts, in western Hungary (Fig. 1). In this area there are three karstic groundwater bodies (OVF 2015) and the altitude ranges from 150 to 709 m above sea level. Annual average ambient air temperature is ~10 °C, but seasonal variation in average daily temperatures is high (i.e. 24.5 °C in the central part), partly due to the area being a basin. Annual precipitation varies between 550 to 800 mm, depending on altitude (OMSZ 2018). Many springs in the foothills of the Bakony Mts are special karst springs supplied by karst water circulating within the limestone formations, where hot (40 °C) thermal waters rise to near the surface and are mixed with cool meteoric waters (Lóczy 2015). Water level in the karst dropped dramatically during the period when bauxite and coal mining flourished between the 1950s and 1980s, ultimately leading to a reduction and finally the cessation of the flow water from these springs (Csepregi 2007).

During field surveys, we recorded the presence-absence of *P. coloratus* and its associated species. We recorded the phenological status (none, fresh vegetative shoots, vegetative shoots, flowers, seeds) of this species every month during 2017 at all sites where *P. coloratus* occurs. At every locality, we recorded water temperature, pH and conductivity in every month during 2017 using a HQ40d portable multimeter (Hach Lange Inc). Such information was unavailable for *P. coloratus* habitats from the historical records.

Environmental data

To evaluate the possible effects of environmental factors on the occurrence of *P. coloratus* we collected data on rainfall and karst water levels in the region studied. Data on annual rainfall was obtained from the Hungarian Meteorological Services and was restricted to the nearest locality (Szombathely). This city has the closest meteorological station to the populations studied (~40 km) and also has meteorological records going back over a century. Rainfall data was obtained for the period between 1901 and 2018. Data on annual mean karst water level was obtained for the period between 1950 and 2018 from the karst water level database of the Hungarian General Directorate of Water Management (OVF).

The experiment on dispersal ability

To determine the potential for endozoochorous dispersal of *P. coloratus*, we performed a controlled feeding experiment using eight captive mallards (*Anas platyrhynchos*) each of which were force-fed 100 *P. coloratus* seeds. Prior to the experiment, the seeds were stored dry in paper bags in a refrigerator at 4 °C. The birds were captive-bred and prior the study were housed communally in an outdoor facility and fed with mixed grains (corn, wheat, oat) and green leaves (e.g. *Stellaria media*, *Taraxacum officinale*). Twenty-four hours before force-feeding, the ducks were moved to individual cages (50 × 50 × 50 cm), without any food, to ensure their alimentary canal was empty. The ducks were provided with water ad libitum during the experiment. The floor of the cages was made of wire mesh and clean plastic sheet was placed under the cages to collect the faecal samples. A small plastic cone was used to channel the seeds into the oesophagus during the force-feeding, which ensured that every seed was ingested. The faecal samples were collected

at 1, 2, 3, 4, 5, 6, 7, 21, 31 and 45 h after force-feeding. Each dropping was dried at room temperature and every intact seed was separated and counted under a binocular microscope (see detailed methodology in Lovas-Kiss et al. 2020). We determined seeds to be intact if there were no visible fissure or any damage to their coat. Each mallard was one-year-old and was obtained from a local breeder. After the experiment, they showed no sign of sickness and were returned to the breeder.

Germination ability of the seeds was tested in tissue-plates filled with deionized water. These were kept at room temperature (25 °C) under a Sylvania© Gro-Lux T8 (18W/77) fluorescent lamp set to a 14 h light period. Fifty seeds that were not treated were used as the control. The germination tests lasted 60 days, after which the seeds that did not germinate were subjected to triphenyl-tetrazolium chlorid (TTC) viability tests in which each seed was longitudinally sectioned and then incubated in 2% solution of TTC for 24 hours. Seeds that had healthy embryos and stained a deep red after the TTC treatment were considered viable (Hendry & Grime 1993).

Statistical analyses

Long-term karst water levels and rainfall data available for the regions where *P. coloratus* potentially occurred were used to statistically evaluate the role of these factors in influencing its occurrence. Presence of *P. coloratus* was coded as a binomial variable, taking a value of 1 if the species was recorded at a given site and year and the value 0, when the species was not recorded, or no biotic data was available for a particular site and year. This coding was adopted because there were many years for which there was no biotic data available for potential *P. coloratus* habitats; moreover, data on absence is rarely available. Note, however, that *P. coloratus* is an iconic plant species that was closely monitored by botanists in Hungary, meaning that if no record is available for a given site and year this most likely reflects the absence of this species. In addition, in many cases desiccation of the habitats is well-documented, which further supports the validity of the absence data. We investigated whether annual precipitation and karst water level affect the presence of *P. coloratus*. In addition, we investigated the effect of environmental variables (pH, conductivity and temperature of the water) on the phenology of this species. The data were analysed using Generalized Linear Mixed Models (GLMM). In the first analysis, species presence-absence data was used as response variables in a model with binomial error distribution, with precipitation and karst water level data as covariates and sites and years introduced as random intercept terms. In the second analysis, phenology was used as a response variable in a mixed model with Gaussian distribution, with environmental variables as covariates and sites introduced as random intercept terms. Both models were built using the *glmmTMB* package (Brooks et al. 2017). All continuous variables were log-transformed to improve model residual normality. All analyses were done using the R statistical and programming environment, version 3.6.2 (R Core Team 2019).

Results

We found data on the occurrence of *P. coloratus* at 11 localities from 1873 to 2017 (Fig. 1). This data indicates that the distribution of *P. coloratus* in the region studied is very uneven. There used to be three populations in Budapest, where the species used to inhabit

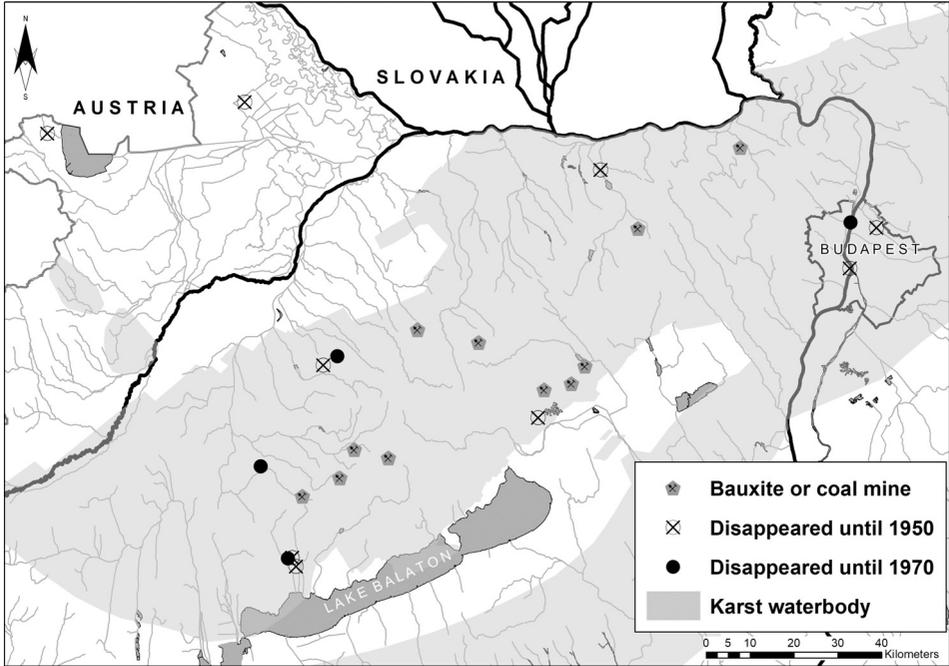


Fig. 1. – Past distribution and time of disappearance of *Potamogeton coloratus* in Hungary between 1940 and 1970.

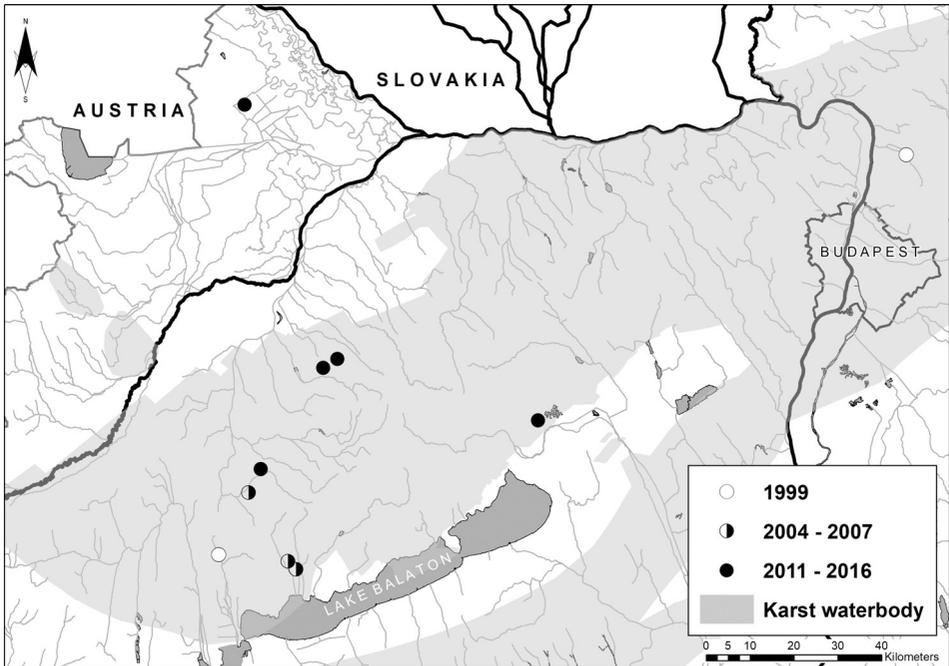


Fig. 2. – The recovery and recent distribution of *Potamogeton coloratus* in Hungary.

Table 2. – Effect of annual rainfall (1901–2010) and karst water level (1955–2010) on the occurrence of *Potamogeton coloratus* in the Bakony Mts (Hungary) using generalized linear mixed model (GLMM) with a binomial error distribution.

	Estimate	S.E.	Z value	P-value
Intercept	-37.875	12.465	-3.038	0.002**
Annual rainfall (mm/year)	0.495	1.708	0.290	0.772
Mean annual karst water level (m a.s.l./year)	6.00	1.49	4.01	< 0.001***
Random effects	Variance	S.D.		
Year	1.930	1.389		
Site	7.479	2.735		

Table 3. – Effect of environmental variables on the phenology of *Potamogeton coloratus* using generalized linear mixed model (GLMM) with Gaussian error distribution.

	Estimate	S.E.	Z value	P-value
Intercept	4.581	2.658	1.723	0.085
Water temperature	0.129	0.031	4.260	< 0.001***
pH	-0.545	0.312	-1.744	0.0811
Conductivity	-0.001	0.001	-0.672	0.501
Random effects	Variance	S.D.		
Site	2.4050	1.5508		

thermal waters, lakes, springs, rivulets and marshes. These populations perished at the end of the 19th century when fast and large scale construction works took place in this part of the city. There used to be five populations in the foothills of Bakony Mts, that were frequently visited by botanists in the past. The extinct population in the vicinity of Sopron was identified based on an herbarium specimen collected in 1947. Finally, a population was found in the city of Tata by Boros (1937).

During the last 20 years, we documented the recovery of *P. coloratus*. It was found at several new localities and in some of its old habitats (Fig. 2). All recent localities are listed and discussed in Mesterházy et al. (2017). Habitats, where the species was recorded included artificial lakes, thermal springs, roadside channels, waterlogged depressions in wet- and fen meadows, spring-pools, pools in peat diggings and fast-flowing streams, all of which were more or less affected by karstic water (Table 1). Statistical analyses indicated that the likelihood of *P. coloratus* being present at a given site and year was significantly higher if the karst water level was high (Table 2, Fig. 3), while annual rainfall was not associated with the presence of this species.

Based on the phenology data collected during our field surveys, we show that at higher water temperatures, *P. coloratus* is more phenologically advanced than at colder temperatures (Table 3). This is indicated by the significant association between water temperature and the number of phenological phases of *P. coloratus* recorded at a given site and year (Fig. 4).

Sixty (7% of force-fed) seeds of *P. coloratus* passed through the digestive systems of the seven ducks. The percentage survival of the seeds in the individual ducks varied widely (26% to 0%). One bird did not pass any seeds. Most of the seeds were passed (57)

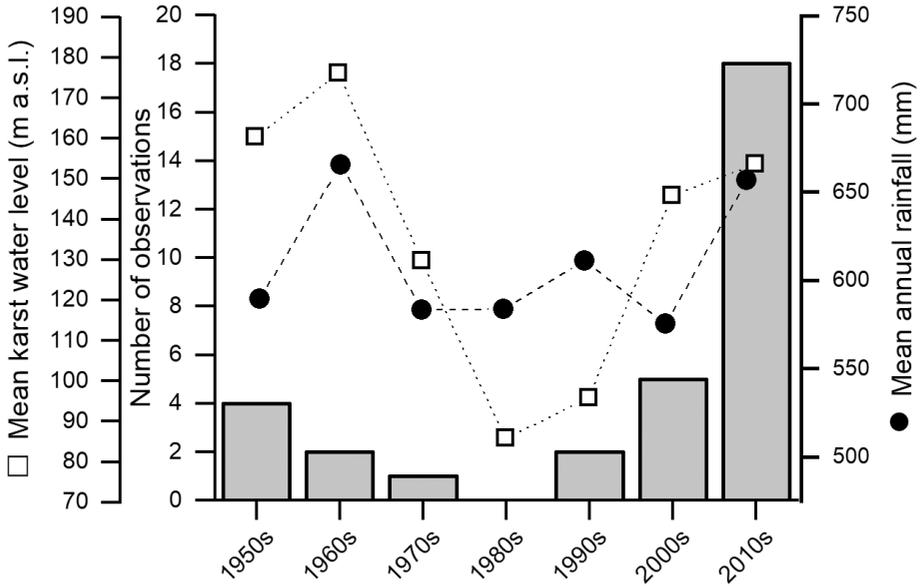


Fig. 3. – The number of records of *Potamogeton coloratus* in Hungary between 1955 and 2018. Mean karst water level and mean annual rainfall in corresponding decades are also illustrated.

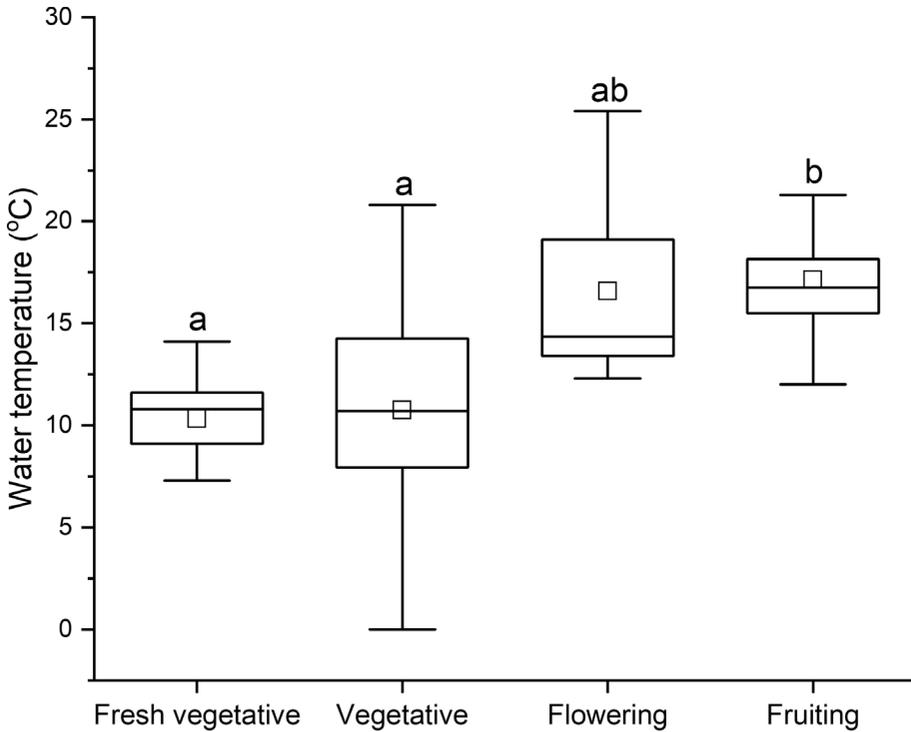


Fig. 4. – Variation in phenology of *Potamogeton coloratus* associated with water temperature in Hungary. Different letters indicate significant differences (Kruskal-Wallis test).

in the first two hours, with one seed passed as late as 7 hours after the force-feeding. Of the control seeds only one germinated and 26 had viable looking embryos, but only four of them were viable after the TTC treatment (i.e. 8.3% control viability). One seed passed in the first hour germinated and the TTC test revealed that three more seeds passed at the same time were viable. In addition, two seeds passed in the second hour stained red, which indicated a 10.0% viability of passed seeds.

Discussion

Sampling effort has an indisputable role in determining the level of knowledge of species distributions (Daníhelka et al. 2009), while difficulties or uncertainties in identification can have an adverse effect. In some cases, for instance, distinctive morphological features of a given taxon can develop under different environmental conditions. In such cases phenotypic plasticity can increase the percentage error of taxonomic identifications, similar to what is reported for several aquatic plant taxa, such as *Elatine* (Molnár et al. 2015), *Batrachium* (Garbey et al. 2004, 2006) and *Potamogeton* (Idestam-Almquist & Kautsky 1995, Kaplan 2002). According to Bruin (1997), *P. coloratus* was collected several times between 1867 and 1978 in The Netherlands, but recently it was declared extinct in that country. He considered these records as taxonomically incorrectly identified and believed that these records of *P. coloratus* were actually of *P. alpinus*, *P. lucens* or *P. polygonifolius*.

We believe that the intensity of floristic research cannot solely explain the conspicuous temporal unevenness in the occurrences of *P. coloratus* that we documented in this study. Although the number of botanists interested in aquatic plants in Hungary was always very low, the intensity of research on this species was relatively constant and reliable over time. This was due to Lajos Felföldy, the most prominent aquatic plant researcher in Hungary, who devoted much of his time to this species. He was scientifically active between 1933 and 2009 and a hard-working plant collector particularly fond of collecting data on rare species of aquatic plants (Molnár V. et al. 2017). Constant sampling was also ensured, given that many of the localities are in the vicinity of rich fen habitats, which are of special interest to conservationists. In this study, we could exclude potential errors in taxonomic identification, because our database has been carefully revised and all herbarium specimens checked and reassessed by several experts (Z. Kaplan, L. Felföldy, R. Soó) during the last decades. There was a single herbarium sheet that was previously erroneously determined as *P. natans* and was later revised by Zdeněk Kaplan in 2004. In addition, botanists tended to erroneously identify other *Potamogeton* taxa (mostly *P. gramineus* and *P. natans*) as *P. coloratus*.

In 1966 *Potamogeton coloratus* disappeared entirely from the flora of Hungary, with the last known occurrence recorded at Tapolcafő. Some of the habitats where the species formerly occurred were destroyed. For example, the populations in Budapest were destroyed by building thermal baths over the habitat. Despite wild populations being wiped out entirely in Hungary, *P. coloratus* has re-established recently mainly from the seed bank and partially by long-distance dispersal. According to our results, this reoccurrence was significantly associated with an increase in the level of the groundwater that started in the 1990s, whereas precipitation did not affect its reoccurrence. The obtained

correlations are intriguing, especially because annual precipitation evidently influences karst water levels. Therefore, we believe that other factors that correlate with karst water levels might be responsible for the disappearance of the species in the 1960s and re-appearance in the 1990s.

Mining and its effect on the karst water level

In Hungary, all mining activities (including coal and bauxite) intensified in the 1950s when the socialist economy flourished. During this era, several new coal mines were established, and underground bauxite extraction started. These mines were located in the Bakony Mts, a karstic region in western Hungary (Fig. 1). As miners had to exploit the deeper layers of coal and bauxite, they also had to decrease groundwater levels. Water extraction by pumping reached its maximum ($700 \text{ m}^3 \cdot \text{min}^{-1}$) in the mid-1960s (when *P. coloratus* disappeared) and remained at the same level for the following 25 years (Csepregi 2007). The amount of water extracted exceeded the natural rate of water supply by 60% ($485 \text{ m}^3 \cdot \text{min}^{-1}$); therefore, groundwater levels decreased at a regional scale, causing a decrease in water runoff into the Hévíz thermal lake and ultimately to the desiccation of several natural springs in the Bakony Mts. This process destroyed rivulets and wetlands, facilitating the invasion of these habitats by terrestrial species such as *Solidago gigantea*. These sites are currently often used as poplar or spruce plantations (Heilmann 1999). The intensity of mining decreased at a considerable rate in 1986, halting karst water exploitation, which was followed by a recovery in the karst water level in the mid-1990s (when *P. coloratus* reappeared).

Possible ways of re-establishment

The re-emergence of *P. coloratus* might have occurred in two ways, either from viable seeds that survived in the sediment or, especially in the case of newly emerged populations, via dispersal (hydrochory, ornithochory or human-mediated). We assume that the sediment at sites where *P. coloratus* used to occur in the past (40–50 or even 60 years ago) must have contained viable seeds of this species. This assumption is based on an experiment conducted in the Czech Republic by Kaplan et al. (2014), who successfully restored a population of *P. coloratus* in a desilted pool in which the species previously occurred. The seed bank in the sediment had an indispensable role in this restoration project, and indicates that seed of *P. coloratus* can survive longer than 30 years in sediment. Moreover, Bruin (1997) concludes that *P. coloratus* quickly colonizes small pools with clean water after turf stripping at many sites in The Netherlands. He assumed that these plants developed from dormant seed buried in the soil for decades.

The nearest localities of recent *P. coloratus* occurrence are: one population in the Czech Republic (Kaplan et al. 2014), three populations in Lower Austria (i.e. Niederösterreich; Karin Pall, pers. comm. 2018), and one in the Vorarlberg (Fischer et al. 2008). It is important to note that these localities are scattered and they are not connected hydrologically, therefore, we can exclude hydrochory as a means of dispersal. The karst springs examined never freeze during winter, consequently serving as a preferred wintering site for several waterfowl (Csörgő et al. 2009).

Our results indicate that viable seeds of *P. coloratus* could have arrived at these habitats most probably with water birds (i.e. ornithochory), and this means of dispersal might

play a significant role in introducing this species to sites where no occurrence was documented before. Unfortunately, no direct field evidence exists to support this hypothesis, i.e. seeds of *P. coloratus* have never been found in avian faecal samples collected in the field. However, our feeding experiment proved that seeds survived the passage through the digestive tract of water birds. In addition, both waterfowl and shorebirds are often observed feeding in these waters (personal observation), therefore, it is possible that birds disperse these seeds. Moreover, seed of its congeners (e.g. *P. pusillus*, *P. pectinatus*) is reported in faeces of wild mallards in Hungary (Lovas-Kiss et al. 2018). The seed of *P. coloratus* is the smallest of the pondweeds, which is known to facilitate rapid, intact and viable passage through the digestive tract of aquatic birds and is thought to facilitate long-distance dispersal (Jakobsson & Eriksson 2000, Soons et al. 2008, Lovas-Kiss et al. 2020). Germination of the seed of some species of plants benefit from the passage through the digestive tract of water birds, which results in both mechanical and chemical scarification, as in *P. pectinatus* (Santamaría et al. 2002), but we were not able to test this in our study on *P. coloratus*.

Since 1999, when the first recent appearance of *P. coloratus* was recorded, several new, previously unrecorded populations of this species were also discovered. Many of the localities are within a radius of 10–12 km of the first recently recorded specimens and are frequently visited by field botanists. As such, we cannot exclude the potential role of humans (soles of boots, vehicles) as short-distance dispersal vectors of *P. coloratus* and promoters of its recent population expansion.

Conservation outlook

The end of the socialist economy was a major socioeconomic driver in almost every central European country in the early 1990s (Liira et al. 2008). This economic crisis was especially pronounced in heavy industry, like mining and metallurgy, and had many positive and negative effects on biodiversity and nature conservation in post-Soviet central and eastern European countries. The collapse of socialist industry left behind numerous devastated and disturbed habitats, leading to an accelerated invasion by non-native species, or in some cases the establishment of habitats of high nature conservation value (Mihók et al. 2017). Our study highlights that a valuable and rare freshwater ecosystem can be restored spontaneously and quickly after industrial disturbance cease.

Overall, our study has a clear message with relevance to nature conservation. Conservation of this species should target the hydrographic restoration of its potential habitats, which is indicated by the strong correlation of its occurrences with the karst water-level. Currently it seems that the future of *P. coloratus* is no longer threatened in Hungary, but regular monitoring of these habitats is strongly recommended. We cannot provide a generally suitable management practice for the protection of this species, because *P. coloratus* lives in various types of habitat. Consequently, various factors (channel dredging, pollution, water drainage, etc.) could threaten its future existence. In the future, it is our responsibility to ensure the well-being of this species and duty (beyond avoiding the mistakes committed in the past) to ensure the undisturbed quality and quantity of water flowing from these valuable karst springs.

Acknowledgement

We appreciate the help of Tünde Zagyva and Jenő Labdy (General Directorate of Water Management) in providing us with the long-term karst water-level dataset. We thank Karin Pall for information on the status of the species studied in Austria. The feeding experiment was approved by the scientific council of the Babeş-Bolyai University of Cluj Napoca (reference number: 14689/31.08.2018). The instrumental and infrastructural support of National Research, Development and Innovation Office – NKFIH, OTKA K104279, OTKA K132573, FK127939 and KH129520 grants were highly appreciated. This research was also supported by the GINOP-2.3.2-15-2016-00019 project. BAL, L-K and OV were supported by the Janos Bolyai Research Scholarship of the Hungarian Academy of Sciences. BAL, L-K, OV and KS were supported by the New National Excellence Programme of the Hungarian Ministry of Innovation and Technology.

Souhrn

Potamogeton coloratus je charakteristicky druh oligotrofnıch vod a jeden z nejnazcnejsıch a nejhrozenejsıch druhu vodnıch rostlin v Evrope v dusledku ztraty stanovist a ubytku populace na celem kontinentu. V Maarsku vsechny jeho populace zmizely behem padesatych a ˇedesatych let, v poslednıch letech se vsak mnoho zaniklych populacı zнову objevilo a vznikla řada novych. Zkoumali jsme, jaky vliv na tuto regeneraci melo prostředı a jak se na vzniku novych populacı podılelo endozoochornı šířenı kachnami. Zjistili jsme, že variabilita v rocnıch uhrnech srazek nesouvisı s vyskytem *P. coloratus*, duležitym faktorem je vsak kolısanı hladiny krasove vody. To ukazuje, že zmizenı a opetovne objevenı se *P. coloratus* souviselo s kolısanım hladiny vody v krasovych oblastech, kterou vyrazne ovlivnoval rozvoj socialistickeho tezkeho prumyslu a zejména provoz bauxitovych a uhelnych dolu. Relativne vysoky podıl semen *P. coloratus*, která prošla travicım traktem kachen, obsahoval žıvotaschopna embrya. Ptacı tak mohli sloužit jako vektor šířenı semen *P. coloratus* a prıspıvat ke vzniku novych populacı. Celkove se zda, že se populace *P. coloratus* obnovujı, k zajistenı jeho prıtrevanı je nicmene nutne pravidelne sledovanı.

References

- Bauer N. (2006) A *Potamogeton coloratus* Hornem. Magyarországon [*Potamogeton coloratus* Hornem. in Hungary]. – Flora Pannonica 4: 111–119.
- Boros . (1923) Florisztikai jegyzetek 9 [Floristical notes Nr. 9]. – Mscr., MTM Novenytar, Budapest.
- Boros . (1937) Magyarországi hevızek felsobbrendu novenyzete [Higher plants of Hungarian thermal waters]. – Botanikai Kozlemenyek 34: 85–115.
- Brondizio E. S., Settele J., Dıaz S. & Ngo H. T. (eds) (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. – IPBES Secretariat, Bonn, Germany.
- Brooks M. E., Kristensen K., van Benthem K. J., Magnusson A., Berg C. W., Nielsen A., Skaug H. J., Maechler M. & Bolker B. M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – The R Journal 9: 378–400.
- Bruin J. W. (1997) Over herkenning, voorkomen en oecologie van Weegbreefonteinkruid (*Potamogeton coloratus* Hornem.) in Nederland [On the identification, occurrence and ecology of fen pondweed (*Potamogeton coloratus* Hornem.) in the Netherlands]. – Gorteria 23: 49–69.
- Csepregi L. (2007) Karsztvızkıvetelek es forrashozamok [Karst water removal and well yields]. – In: Alfoldi L. & Kapolyi L. (ed.), Banyaszati karsztvıkszıntıllyesztes a Dunantulı-kozephegysegben [Lowering the karst water level for mining purposes in the Dunantulı-kozephegyseg (Hungary)], p. 84–89, MTA Foldrajztudomanyi Kutatotıntezet, Budapest.
- Csorgo T., Karcza Z., Halmos G., Magyar G., Gyuracz J., Szep T., Bankovics A., Schmidt A. & Schmidt E. (eds) (2009) Magyar madarvonulasi atlasz [Hungarian bird migration atlas]. – Kossuth Kiado, Budapest.
- Danihelka J., Chrtk Jr. J. & Kaplan Z. (2012) Checklist of vascular plants of the Czech Republic. – Preslia 84: 647–811.
- Danihelka J., Niklfeld H. & Šıpořova H. (2009) *Viola elatior*, *V. pumila* and *V. stagnina* in Austria, Czechia and Slovakia: a story of decline. – Preslia 81: 151–171.
- Felfoldy L. (1990) Hınar hatarozo. Vızugyi Hidrobiologia 18, Kornyeztvedelmi es Teruletfejlesztesi Miniszterium [Aquatic plant identification manual. Hydrobiology and water management Nr.18]. – AQUA Kiado es Nyomda Leanyvallalat, Budapest.

- Fischer M. A., Oswald K. & Adler W. (2008) Exkursionsflora für Österreich, Liechtenstein und Südtirol. Ed. 3. – Biologiezentrum der Oberösterreichischen Landesmuseen, Linz.
- Garbey C., Thiébaud G. & Muller S. (2004) Morphological plasticity of a spreading aquatic macrophyte, *Ranunculus peltatus*, in response to environmental variables. – *Plant Ecology* 173: 125–137.
- Garbey C., Thiébaud G. & Muller S. (2006) An experimental study of the plastic responses of *Ranunculus peltatus* Schrank to four environmental parameters. – *Hydrobiologia* 570: 41–46.
- Grulich V. (2012) Red List of vascular plants of the Czech Republic: 3rd edition. – *Preslia* 84: 631–645.
- Heilmann P. E. (1999) Planted forests: poplars. – *New Forests* 17: 89–93.
- Hendry G. A. F. & Grime J. P. (1993) *Methods in comparative plant ecology: a laboratory manual*. – Chapman & Hall, London, UK.
- Holmgren P. K. & Holmgren N. H. (1998) Index herbariorum: a global directory of public herbaria and associated staff. – New York Botanical Garden's Virtual Herbarium, URL: <http://sweetgum.nybg.org/ih>.
- Idestam-Almquist J. L. & Kautsky L. (1995) Plastic responses in morphology of *Potamogeton pectinatus* L. to sediment and above-sediment conditions at two sites in the northern Baltic proper. – *Aquatic Botany* 52: 205–216.
- Jakobsson A. & Eriksson O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. – *Oikos* 88: 494–502.
- Kaplan Z. (2002) Phenotypic plasticity in *Potamogeton* (*Potamogetonaceae*). – *Folia Geobotanica* 37: 141–170.
- Kaplan Z. (2010) *Potamogetonaceae* Dumort. – rdestovité. – In: Štěpánková J., Chrtek J. & Kaplan Z. (eds), Květena České republiky [The Flora of the Czech Republic] 8: 329–384, Academia, Praha.
- Kaplan Z., Šumberová K., Formanová I. & Ducháček M. (2014) Re-establishment of an extinct population of the endangered aquatic plant *Potamogeton coloratus*. – *Aquatic Botany* 119: 91–99.
- Kaplan Z. & Symoens J. J. (2005) Taxonomy, distribution and nomenclature of three confused broadleaved *Potamogeton* species occurring in Africa and on surrounding islands. – *Botanical Journal of the Linnean Society* 148: 329–357.
- Kaźmierczakowa R., Bloch-Orłowska J., Celka Z., Cwener A., Dajdok Z., Michalska-Hejduk D., Pawlikowski P., Szczęśniak E. & Ziarnik K. (2016) Polska czerwona lista paprotników i roślin kwiatowych. [Polish Red List of pteridophytes and flowering plants]. – Instytut Ochrony Przyrody Polskiej Akademii Nauk, Kraków.
- Kleinsteuber A. & Wolff P. (1996) *Potamogeton polygonifolius* und *Potamogeton coloratus* in Baden-Württemberg. – *Carolina* 54: 180–183.
- Lájer K. (1999) Florisztikai adatok a Dunántúlról, valamint Vácraótó környékéről [Floristic data from Dunántúl and Vácraótó (Hungary)]. – *Kitaibelia* 4: 311–317.
- Lechevalier P. (ed.) (1952) *Flore de l'Afrique du Nord*. Vol. 1. – Rou de Tournon, Paris.
- Liira J., Schmidt T., Aavik T., Arens P., Augenstein I., Bailey D., Billeter R., Bukáček R., Burel F., De Cock R., Miklová P., Roubalova M., Schweiger O., Smulders M. J. M., van Wingerden W. K. R. E., Bugter R. & Zobel M. (2008) Plant functional group composition and large-scale species richness in European agricultural landscapes. – *Journal of Vegetation Science* 19: 3–14.
- Lóczy D. (ed.) (2015) *Landscapes and landforms of Hungary*. Springer, Cham.
- Lovas-Kiss Á., Vincze O., Kleyheeg E., Sramkó G., Laczkó L., Fekete R., Molnár V. A. & Green A. J. (2020) Seed mass, hardness, and phylogeny explain the potential for endozoochory by granivorous waterbirds. – *Ecology and Evolution* 10: 1413–1424.
- Lovas-Kiss Á., Vizi B., Vincze O., Molnár V. A. & Green A. J. (2018) Endozoochory of aquatic ferns and angiosperms by mallards in Central Europe. – *Journal of Ecology* 106: 1714–1723.
- Mesterházy A., Vidéki R., Lukács B. A., Mészáros A. & Molnár V. A. (2017) Adatok a színes békaszdőlő (*Potamogeton coloratus*) hazai előfordulásához [Recent Hungarian distribution of *Potamogeton coloratus*]. – *Kitaibelia* 22: 77–83.
- Mihók B., Bíró M., Molnár Zs., Kovács E., Bölöni J., Erős T., Standovár T., Török P., Csorba G., Margóczy K. & Báldi A. (2017) Biodiversity on the waves of history: conservation in a changing social and institutional environment in Hungary, a post-soviet EU member state. – *Biological Conservation* 211: 67–75.
- Molnár V. A., Csányi B., Vidéki R., Bauer N., Dolánszky F., Papp V. G., Nótári K., Buczkó K. & Virók V. (2017) Lajos Felföldy: a prominent Hungarian botanist and hydrobiologist – *Kitaibelia* 22: 3–25.
- Molnár V. A., Tóth J. P., Sramkó G., Horváth O., Popiela A., Mesterházy A. & Lukács B. A. (2015) Flood induced phenotypic plasticity in amphibious genus *Elatine* (*Elatinaceae*). – *PeerJ* 3: e1473.
- Mony C., Puijalón S. & Bornette G. (2011) Resprouting response of aquatic clonal plants to cutting may explain their resistance to spate flooding. – *Folia Geobotanica* 46: 155–164.
- Moser D., Gyax A., Bäumler B., Wyler N. & Palese R. (2002) Rote Liste der gefährdeten Farn- und Blütenpflanzen der Schweiz [Red List of the threatened ferns and flowering plants of Switzerland]. –

- Bundesamt für Umwelt, Wald und Landschaft, Bern; Zentrum des Datenverbundnetzes der Schweizer Flora, Chambésy; Conservatoire et Jardin botaniques de la Ville de Genève, Chambésy.
- OMSZ (2018) Climate of Hungary. General characteristics. – Hungarian Meteorological Services, URL: <https://bit.ly/2VRGRD4>.
- OVF (2015) Danube river basin management plan. – General Directorate of Water Management, Budapest, URL: <https://bit.ly/31t1Gpp>.
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robach F., Thiébaud G., Trémolières M. & Muller S. (1996) A reference system for continental running waters: plant communities as bioindicators of increasing eutrophication in alkaline and acidic waters in north-east France. – *Hydrobiologia* 340: 67–76.
- Santamaría L., Charalambidou I., Figuerola J. & Green A. J. (2002) Effect of passage through duck gut on germination of fennel pondweed seeds. – *Archiv für Hydrobiologie* 156: 11–22.
- Simonkai L. (1876) Adatok Magyarhon edényes növényeihez [Data to the vascular flora of Hungary]. – *Mathematikai és Természettudományi Közlemények* 11: 157–211.
- Soó R. (1934) A Magyar vizek virágos vegetációjának rendszertani és szociológiai áttekintése II. Magyarország Potamogetonjai I. [The taxonomical and phytosociological summary of Hungarian waters II. Potamogetons of Hungary I]. – *A Magyar Biológiai Kutató Intézet Munkái* 7: 135–153.
- Soons M. B., van der Vlugt C., van Lith B., Heil G. W. & Klaassen M. (2008) Small seed size increases the potential for dispersal of wetland plants by ducks. – *Journal of Ecology* 96: 619–627.
- Wiegand G. (1989) On *Potamogeton coloratus* (*Potamogetonaceae*) in Turkey. – *Willdenowia* 19: 121–125.

Received 28 October 2019

Revision received 10 February 2020

Accepted 13 February 2020