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Clonal structure, habitat age, and conservation value of the moss *Philonotis marchica* in Kotouč quarry (Czech Republic)

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Abstract – *Philonotis marchica* was rediscovered in the Czech Republic after almost 50 years. The plants were collected from a limestone quarry; associated bryophytes and vascular plants are described. The site has been available for less than 20 years. The genetic structure of populations of sympatric *P. marchica* and *P. calcarea* was studied using allozyme markers. Low levels of genetic diversity within both populations contrast with results obtained from a previous study of *P. fontana* and *P. caespitosa*. Founder effects, habitat fragmentation, and predominant asexual reproduction are possible reasons. It is unclear why *P. marchica* is so rare in Central Europe as the species is often locally abundant and produces prolific bulbils.

***Philonotis* / isozymes / population structure / genetic diversity / bryophyte**

INTRODUCTION

Philonotis marchica (Hedw.) Brid., first recognized by Willdenow 1787, occurs in calcareous wetlands of Europe, North and Central America, northern Africa, Macaronesia, Caucasus, China, and Korea (Wijk *et al.*, 1967) from lowlands to lower montane areas. Specimens of *P. marchica* in European herbaria (e.g., BP, PRC, Z) indicate that the species was once rather widespread on the continent. Nevertheless, the species was never as common as, for example, *P. fontana* (Hedw.) Brid., and it has more recently become threatened in Central Europe because of drainage and cultivation of many wetland habitats (Grims *et al.*, 1999; Urmi pers. com.). It was collected in the Czech Republic from only nine sites (Buryová 1996). The last known collection from the country was from East Bohemia in 1958 (Hradec Králové: In terra humida prope pag. Libišany, *ca* 350 m, V.1958 *leg. Z. Pilous* herb. BRNM). At least six of the sites where *P. marchica* had been collected previously have been destroyed by drainage,

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agricultural activities, or other forms of development (Buryová, 1996, and unpubl.). In 2003, however, the second author discovered a new locality in the limestone quarry, Kotouč, near the town of Štramberk (North Moravia). A large population of *P. marchica*, together with *P. calcarea* (Bruch & Schimp.) Schimp., was found during a botanical survey of the abandoned seventh quarry floor prior to its destruction.

Philonotis calcarea is present at the Kotouč site in approximately equal abundance to *P. marchica*. The former species is known from Europe, northern Africa, Asia Minor, Caucasus, Himalaya, Tibet, and Greenland (Wijk *et al.*, 1967; Griffin, 2003). In the Czech Republic, it occurs in calcareous fens and around springs mainly in southeastern Moravia (Hostýnské vrchy, Javorníky a Bílé Karpaty hills), with *ca* 15 recently documented sites (Buryová, 1996; Hájek, 1998; Hájková & Hájek, 2000). Sporophytes have been observed in 19% of the specimens collected from the Czech Republic (Buryová, 1996). Specialized propagules for vegetative reproduction have not been observed in this species in the Czech Republic, but regeneration from stem fragments or deciduous branches commonly occurs, as in other species of *Philonotis* (Field, 1988).

Outside of the Czech Republic, approximately 30% of the specimens of *Philonotis marchica* examined from European herbaria (BP, FD, PRC, Z) included sporophytes (Buryová, personal observation). Sporophytes were observed only once among the Czech specimens. Reproduction in *P. marchica* is primarily by bulbils that are produced in leaf axils (Petit, 1976; Buryová, 1996).

Philonotis marchica has been included in the "data deficient" IUCN threat category for the recent red list of bryophytes in the Czech Republic (Kučera & Váňa, 2003) due to a lack of information on population decline, present distribution, total population size, number of sites, and estimated loss of relevant habitats over the last 10 years or three moss generations (Hallingbäck *et al.*, 1998). The population dynamics and genetic structure of *P. marchica* populations have not been studied.

The purpose of this study was to document habitat characteristics of *Philonotis marchica* and levels of genetic variation at isozyme loci in populations of *P. marchica* and *P. calcarea* growing at the Kotouč site. While "species" are the most common currency for measuring biodiversity, it is important to know something about levels of genetic diversity in species that are targets for preservation. Before steps are taken to preserve the one known population of *P. marchica*, we need to know if we are attempting to preserve a single clone, a highly diverse population, or something in between.

MATERIAL AND METHODS

Population sampling — A total of 19 samples of *P. calcarea* and 29 samples of *P. marchica* were collected in a haphazard manner with 3-40 m between samples. All samples were kept in closed plastic containers by a north-facing window for 2-3 weeks before extraction. Enzymes were extracted from rapidly growing apices.

Protein extractions and electrophoresis — Extractions and electrophoresis were conducted at the Institute of Botany, Academy of Sciences, in Průhonice, Czech Republic, during July 2003-January 2004. Apices from 6-30 stems (*ca* 0,03 g) from each sample were extracted in 700 µl of iced extraction buffer according to Boisselier-Dubayle & Bischler (1994), modified as follows: 0,1 M Tris-HCl, pH 7,5;

10 mM KCl; 10 mM $MgCl_2$; 1 mM EDTA – 3Na; 5 mg PVP-40 for 0.2 ml of buffer; 30 mM mercaptoethanol. Extracts were centrifuged at 7 °C for 10 minutes at 13,000 rpm, and the supernatant was divided into 170 µl aliquots and stored at – 75 °C until use. Electrophoresis was performed on 1 mm vertical polyacrylamide gels at 4 °C, using 35 µl of extract (for details, see Buryová, 2004). Gels were stained for the following enzyme systems: alcohol dehydrogenase (ADH), esterase (EST), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (=malic enzyme, ME), NADH-dehydrogenase (NADH DH), phosphogluconate dehydrogenase (6-PGDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimate (=shikimic acid) dehydrogenase (SHDH), and superoxide dismutase (SOD). The staining procedures followed Vallejos (1983) and Wendel & Weeden (1989) with modifications described by Buryová (2004). Concentrations of substrates were increased over the levels given in Buryová (2004) for several enzyme systems in order to enhance staining when activity was low (AAT: 300 mg aspartic acid, 50 mg a-ketoglutaric acid, 33 mg pyridoxal-5-phosphate; ADH: 20 mg NAD, 15 mg MTT, 2 × 10 ml cooled ethanol; EST: 35 mg a-naphthyl acetate, 35 mg b-naphthyl phosphate; IDH: 63 mg isocitric acid; LAP: 45 mg Fast Black K Salt; NADH-DH: 21 mg menadion, 20 mg NADH; 6-PGHD: 15 mg 6-Phosphogluconic acid; PGI and PGM: 100 mg Glucose-1-P, 25 mg $MgCl_2$, 20 mg Fructose-6-P, 10 µl Glucose-6-P DH; SHDH: 35 mg shikimic acid). SOD patterns were read as regions of negative staining on 6-PGHD and NADH-DH stained gels.

Data analysis — Alleles were numbered sequentially from zero, beginning with those having the shortest migration distances. Samples were clustered based on Nei's genetic distance using the program GDA (Genetic Data Analysis; Lewis & Zaykin, 2002). The phenograms were further explored using PAUP (Swofford, 2001), and the 'show reconstructions' option of the Trees command was utilized to map genetic changes and identify alleles diagnostic for each species. GDA was also used to estimate descriptive genetic statistics for the two species. The following statistics were estimated: 1. allele frequencies by locus; 2. percentage polymorphic loci (P); 3. mean number of alleles per locus (A); 4. mean number of alleles per polymorphic locus (AP); and 5. expected heterozygosity (H_e); GDA was used to calculate Nei's (1978) genetic identities and distances between *P. calcarea* and *P. marchica*.

HABITAT DESCRIPTION

The limestone quarry Kotouč is formed by Jurassic limestone. It is situated on an exposed slope with southern exposure, at ca. 300-520 m a.s.l. The slope is the remnant of the largely destroyed Mt. Kotouč (539 m a.s.l.). Open south-facing walls and floors were subjected to continuous high quality lime mining from 1881 until recently (Kvita *et al.*, 2001). Part of the seventh level has been left untouched for almost 20 years and has undergone secondary succession. The substrate is wet lime gravel with spring water seeping from a nearby rock wall. There is a moderate level of dust deposition from adjacent mining activities. The successional plant community that has developed includes *Chara* sp., *Phragmites australis*, *Potamogeton berchtoldii*, *Typha latifolia* in pools, and *Carex distans*, *C. flava*, *Epipactis palustris*, *Equisetum variegatum*, *E. ramosissimum, Juncus articulatus*, *J. bufonius* on moist to wet muddy soils. There is a rich

Table 1. Relevés of *Philonotis marchica* sites, 19.6.2003 in Kotouč limestone quarry, 360 m a. s. l. Abundance is given in %. Description of sites: #1: driest site in locality, flat ground [system S42, M33 E3725,67-N5499,25]; #2: S-facing wet margin of a pool [E3725,70-N5499,24]; #3: margin of a ditch [E3725,73–N5499,26].

Site #	*1*	*2*	*3*
Area (m)	4	0,49	1,05
Inclination	0	10	0
E2 total			20 %
E1 total	35 %	50 %	14 %
E0 total	40 %	80 %	75 %
E1			
Agrostis stolonifera	10	1	0,5
Achilea millefolium	0,5		0,5
Betula pendula juv.	0,1		0,1
Calamagrostis epigejos	12		3
Carex flava		10	5
Euphrasia stricta	0,5	0,1	0,1
Hieracium pilosella	0,1		1
Hypericum maculatum		0,5	0,1
Juncus articulatus	0,5		0,5
Linum catharcticum		2	0,1
Lotus corniculatus	0,5	1	0,1
Lycopus europaeus		0,5	0,1
Daucus carota	0,5	0,5	
Salix purpurea	8	4	0,5
E0			
Dicranella varia	15		1
Pellia endiviifolia		0,5	10
Philonotis calcarea		2	50
Philonotis marchica	0,1	75	10

Species present in only one relevé: E2: *Betula pendula* 3: 20; *Salix purpurea* 3: 0,5. E1: *Acer pseudoplatanus* juv. 3: 0,5; *Bidens frondosa* 1: 0,5; *Epipactis palustris* 3: 1; *Equisetum arvense* 2: 25; *Eupatorium cannabinum* 3:1; *Juncus inflexus* 2: 5; *Leontodon autumnalis* 1: 0,5; *Odontites vulgaris* 1: 0,5; *Plantago* juv. 1: 0,1; *Populus alba* juv. 1: 0,5; *Salix alba* 1: 2; *Salix caprea* 2: 1; *Tussilago farfara* 1: 0,1; *Typha latifolia* 3: 1. E0: *Aneura pinguis* 1: 10; *Brachythecium* sp. 2: 3; *Bryum bimum* 3: 5; *Cratoneuron filicinum* 3: 0,1; *Didymodon tophaceus* 1: 15; *Nostoc* sp. 1: 1.

bryophyte ground cover dominated by *Bryum bimum*, *Dicranella varia*, *Didymodon tophaceus*, and *D. fallax* in drier parts of the site, with *Cratoneuron filicinum*, *Pellia endiviifolia* and both species of *Philonotis* in wetter parts (Tab. 1; nomenclature of vascular plants follows Kubát (2002), nomenclature of mosses follows Kučera & Váňa (2003)).

RESULTS

Among nine enzyme systems examined, 12 putative gene loci were scored: ADH, EST-1, EST-2, ME, NADH-DH-1, NADH-DH2, PGI, PGM, SHDH, SOD-1, SOD-2, 6-PGDH. ADH, 6-PGDH, SOD-1 and SOD-2, were monomorphic with a single band expressed in all samples. For ADH, three loci

Table 2. Genetic diversity within *P. calcarea* and *P. marchica*, summarized across the 12 isozyme loci. N = mean sample size; P = percentage polymorphic loci; A = mean number of alleles per locus; A_p = mean number of alleles per polymorphic locus; H_e = expected heterozygosity (assuming Hardy-Weinberg equilibrium).

Population	*N*	*P*	*A*	*Ap*	*He*
P. calcarea	19,0	0,17	1,17	2,0	0,025
P. marchica	28,7	0,17	1,17	2,0	0,011

were detected but only the fastest, monomorphic locus could be stained for all samples. A complex pattern of EST bands was obtained. The slowest band was scored as EST-1. The fastest region of activity (EST-2) consisted of one band or four co-migrating bands, depending on the species and quality of staining. It was scored as one phenotype. The intermediate bands of EST were not evenly stained, and therefore were not scored. A complex system of bands was also obtained for NADH-DH. The fastest and slowest bands were scored, but the intermediate bands were not evenly stained, and therefore were not scored. For ME, two co-migrating bands were stained for *P. calcarea*, but only one faster band appeared for *P. marchica*. The two patterns were scored as phenotypes. Two co-migrating bands were stained for SHDH in all samples. They were scored as one phenotype. Only one band was stained for PGM in both species. Two PGM loci exist in most plant species (Weeden & Wendel (1989) and two bands, almost certainly representing the two loci, were resolved in *P. fontana* and *P. caespitosa* (Buryová, 2004). In contrast, a single-band pattern was observed in *P. marchica* and in *P. calcarea*. The single band in *P. calcarea* and *P. marchica* was more intensely stained than were either of the two bands in *P. fontana* and *P. caespitosa*. For this reason we interpret the pattern as two loci with alleles that have the same migration rate (and which therefore completely overlap), rather than the occurrence of a null allele at one of the loci. Polyploidy appears to be rare in the Bartramiaceae. Fritsch (1991) reported n = 6 for all species of *Philonotis* except *P. rigida* and *P. thwaitesii*. In the latter, both n = 6 and n = 12 populations have been observed. Multiple isozyme bands observed in some species of *Philonotis* could also involve gene duplication or some form of post-transcriptional modification (Weeden & Wendel, 1989). The final genetic interpretation of banding patterns requires a formal genetic analysis involving crosses, so our scoring represents a conservative approach.

Genetic diversity in both species was very low (Tab. 2). For 12 scored loci, 7 exhibited species-specific alleles (NADH-DH-1, NADH-DH-2, ME, EST-1, EST-2, PGI, SHDH). Four loci were monomorphic across all samples (ADH, SOD-1, SOD-2, 6-PGDH). Four variable loci were found: EST-1 and EST-2 in *P. marchica*, NADH-DH-2 and PGM in *P. calcarea*. Within each species, all but two plants shared an identical multilocus haplotype, with the two deviant individuals differing at just one locus each. Thus, a total of only three haplotypes were detected within each species.

DISCUSSION

Genetic diversity within the only Czech populations of *Philonotis marchica* and the sympatrically co-occurring *P. calcarea* appears to be extremely low. Only three haplotypes were distinguished among a sample of 19 plants of

P. calcarea, and the same number of haplotypes was found in a sample of 29 plants of *P. marchica*. These results suggest that vegetative reproduction is the predominant, if not exclusive, mode of propagation for both species at this site. There are no data from populations in other parts of the geographical range of either species, but comparable population-level data are available for two other species of *Philonotis*: *P. fontana* and *P. caespitosa* (Buryová, 2004).

Buryová (2004) studied genetic patterns within and between *Philonotis fontana* and *P. caespitosa*, two relatively widespread and common species in the Czech Republic. European plants of both species were relatively diverse: the proportion of polymorphic alleles was 0,46 in both, and levels of expected heterozygosity were 0,19 and 0,16 in *P. fontana* and *P. caespitosa*, respectively. Moreover, the proportions of polymorphic loci were 0,27 and 0,33 within a Czech population of the same two species, respectively. There appears to be a substantial difference in levels of within-population genetic diversity in *P. fontana* and *P. caespitosa* vs. *P. calcarea* and *P. marchica*. Only 10 plants were sampled from the populations of *P. fontana* and *P. caespitosa*, whereas 19 and 29 were sampled for *P. calcarea* and *P. marchica*, respectively, so the difference in genetic diversity is not a sampling artefact. Additional population sampling is obviously needed, but these data do not support the view that low levels of within-population genetic diversity is the norm in *Philonotis*.

Low levels of genetic diversity in *P. marchica* and *P. calcarea* could reflect a founder effect associated with relatively recent colonization of the site. Loss of genetic diversity from within this site because of habitat fragmentation and genetic drift could be exacerbated by decreased levels of inter-population migration, a general reliance on asexual reproduction and consequent clonal population structure, or some combination of these factors (Wilson & Provan, 2003). The Kotouč site was not available for plant occupation more than 20 years ago, placing a maximum date on the age of the *P. calcarea* and *P. marchica* populations. The higher levels of within-population genetic diversity detected in *P. fontana* and *P. caespitosa* probably reflect repeated colonization of sites by new genetic variants, and longer periods of habitat availability during which variation can accumulate.

The closest known recent occurrence of *P. marchica* is near the Tatra Mountains in Slovakia (R. Šoltés, dupl. in DUKE!). The occurrence of *P. marchica* in some other site(s) that could serve as a source for the Czech population cannot be eliminated because of insufficient recent collecting in lower elevations of this country (Pospíšil, 1987). The closest known recent occurrence of *P. calcarea* is ca. 30 km SE and SW of the Kotouč site in the Hostýnské vrchy hills and Javorníky hills (Buryová, 1996).

Both *P. marchica* and *P. calcarea* are dioecious. Only female (archegonial) stems of *P. marchica* were observed at the site. This observation is consistent with the possibility that the site was colonized once, by a single genotype. If that is the case, the two rare alleles must have arisen in situ by mutation. *P. calcarea* produces sporophytes at the site. The presence of both males and females means that a minimum of two colonization events occurred. Nevertheless, both species have low levels of genetic diversity at the site. Unless new alleles arrive in the population by mutation, or by immigration from elsewhere, sexual recombination associated with meiosis and spore formation in *P. calcarea* cannot be expected to increase the number of genotypes, at least judging from the allelic diversity at the isozyme loci sampled in this study.

Why is *P. marchica* so rare when the potential for vegetative reproduction seems to be high in this species? Populations are infrequent, but where it

occurs, *P. marchica* is often abundant. Fragmentation may affect the relative rates of extinction and colonization at different spatial scales; small populations have an increased risk of extinction because of stochastic factors (Söderström & Herben, 1997). Population parameters most important for the survival of a species in fragmented habitats are within-population growth rate, diaspore production, dispersal distance, diaspore survival, and establishment rate (Söderström & Herben, 1997). Habitat parameters that influence species survival most strongly are duration, size, and favourability of a patch, distance between patches, and spatial pattern of habitat patches (Söderström & Herben, 1997). There are no demographic data available to help answer the question of how *P. marchica* spreads on any spatial scale. Extensive cover area of *P. marchica* in the newly discovered site, and the ability of plants to spread vegetatively on a local scale were observed not only in the Kotouč locality, but also at other sites. In the Munich Botanical Garden, for example, *P. marchica* appears to be actively spreading with soil among wetland plants (Buryová, personal observation). On the Isle of Wight, Shanklin, *P. marchica* is abundant around calcareous sandstone cliffs with dripping water (Buryová, personal observation). A common characteristic of all these sites seems to be a high level of habitat disturbance. Persistence at each site requires effective dispersal and colonization. Yet at the regional scale, in Europe, the species is rare. At small scales, dispersal in the species appears to be effective, but at a broader scale, dispersal distance, diaspore survival, establishment ability and/or habitat availability appears to be highly limiting.

Knowledge about the distribution of genetic diversity and factors that maintain such diversity is important for the effective conservation of rare mosses. Mapping genetic variation within species is essential to ensure that populations selected for preservation represent an appropriate sample of the existing genetic diversity (Wyatt, 1992). It is generally assumed that the long-term stability and fitness of such populations increase with higher genetic diversity. The IUCN (2001) threat categories do not take into account differences in genetic diversity and/or genetic structure within species. Perhaps in the future, assessments of threat will formally incorporate information about genetic structure to the extent that such information is available for target species. An interesting philosophical issue raised by our genetic results on *P. marchica* and *P. calcarea* is how to weigh the conservation significance of very low genetic diversity. Should the conservation priority of the Kotouč locality be decreased because of information that each rare species is represented mainly by a single clone, based on the argument that the long-term prospects for survival are so poor? Perhaps limited conservation resources should be focused on cases where there is a higher probability of success. Or, to the contrary, do our results argue for an even higher conservation priority for the Kotouč locality because the Central European persistence of *P. marchica* is now known to be in such a perilous state?

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