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THE DIASPORE BANK OF HORNWORTS (ANTHOCEROTAE, BRYOPHYTA) AND ITS ROLE IN THE MAINTENANCE OF POPULATIONS IN CULTIVATED FIELDS

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*SUMMARY — A study was carried out in the vicinity of Bern (Switzerland) as part of more extensive biological investigations on hornwort populations (*Anthoceros agrestis *Paton and* Phaeoceros carolinianus *(Michx.) Prosk.). From soil cores taken in profiles between 1.5 and 50 cm at three different positions in a wheat stubble-field (I), in an adjacent field covered with catch crop (II) and in a hay meadow (III), 15 different bryophytes and at least two fern taxa emerged. The floristic composition of the diaspore reservoir differs considerably from that on the corresponding surface and between the fields from different localities (I, II vs. III). No significant difference, however, was found in the number of viable hornwort spores present in the diaspore bank between fields with (I, III) or without (II) gametophytic occurrence above-ground at the time of sampling. These results and long-term observations at selected sites suggest that the hornwort spore bank plays a crucial role in the maintenance of their populations. Implications for the conservation of endangered hornwort populations are presented and appropriate cropland farming is recommended.*

KEYWORDS: Anthoceros, Phaeoceros, *Switzerland, diaspore bank, arable fields, agricultural management, conservation*

ZUSAMMENFASSUNG — Die Diasporenbank der Hornmoose (Anthocerotae, Hepaticae) und ihre Rolle bei der Erhaltung der Populationen in Äckern

*Die vorliegende Arbeit wurde in der Umgebung von Bern als Teil ausgedehnter populationsbiologischer Untersuchungen an Hornmoosen (*Anthoceros agrestis *Paton und* Phaeoceros carolinianus *(Michx.) Prosk.) durchgeführt. Aus Bohrkernen von Bodenprofilen zwischen 1.5 und 50 cm Tiefe an je drei Stellen in einem Weizen-Stoppelfeld (I), in einem benachbarten Acker mit Gründüngung (II) und in einer ca. 5 km entfernten Heuwiese (III) keimten 15 verschiedene Moose und wenigstens 2 Farne. In der floristischen Zusammensetzung des Diasporenreservoirs unterscheiden sich I und II deutlich von III und alle drei wiederum beträchtlich von der aktuellen Flora an den entsprechenden Stellen. Es gibt aber keine signifikanten Unterschiede bezüglich der Zahl der keimfähigen Hornmoos-Sporen in der Diasporenbank zwischen den Feldern mit aktuellem Vorkommen (I, III) und jenem ohne (II). Diese Ergebnisse und Langzeitbeobachtungen an ausgewählten Orten deuten darauf hin, dass die Sporenbank der Hornmoose für die Erhaltung ihrer Populationen eine zentrale Rolle spielt. Es werden Folgerungen für den Schutz gefährdeter Hornmoos-Populationen vorgestellt und dafür geeignete Ackerbaumethoden empfohlen.*

Introduction

The loss of and threat to species and populations of all kinds of organisms is a general trend in our century in most parts of the world (e.g., Plachter 1991; Urmi & al. 1993). It is doubtless a consequence of human impact (e.g., Von Salis 1992) among which we find agricultural management. Previous studies dealing with the two hornwort taxa occurring in Switzerland have demonstrated that they are likewise affected by modern methods of cropland farming (Bisang 1992). Comparing the present-day distribution of *Anthoceros agrestis* and *Phaeoceros carolinianus* with herbarium records and bibliographical data on their distribution from the beginning of this century, a population decline has to be assumed (Bisang 1992). This applies especially to *Phaeoceros carolinianus* which has therefore been classified as «endangered» in the Red Data List of Swiss Bryophytes (Urmi & al. 1992).

The present study is part of more extensive biological investigations on hornwort populations. The aim is to increase the knowledge about their life cycles, to evaluate the main factors of

agricultural practice affecting them and to supply basic information for conservation measures. The understanding of the species' life history and population ecology is a prerequisite to develop effective conservation strategies (e.g., Cornelius 1991).

Study sites and methods

Nomenclature follows Corley & al. (1981) and Corley & Crundwell (1991) for mosses and Grolle (1983) for hepatics and hornworts except where otherwise indicated.

Study sites. The study was conducted in the vicinity of Bern, Switzerland, in three fields currently under agricultural cultivation (Fig. 1). Two adjacent fields I and II, bordering on a park wood at their western end, are located in Bern, Enge-Viererfeld, 600.1/201.4 (co-ordinates of *Landeskarte der Schweiz*), at 560 m a.s.l. Field III lies at a distance of approximately 5 km at Muri, Bodenacker, 602.4/197.5, at 530 m a.s.l., and is enclosed by forest along three sides. At the time of sampling, field I was a wheat stubble-field. Field II, a former rye field, was covered by 'catch crop' (crop covering the soil over winter to reduce leakage of nitrate) and field III was an artificial hay meadow due to crop rotation. The soil of the investigated fields can be classified as sandy loam according to the 'International scheme of particle size classes'. The bryophyte taxa of the surface vegetation of both localities were recorded (Tab. 2). The species of the neighbouring fields I and II were not recorded separately but the low cover and abundance of bryophytes under the catch crop of field II was noted. The bryophyte vegetation on the surface can be ascribed at all study sites to the Pottietum truncatae Waldheim (Ahrens 1992). Well developed hornwort populations bearing sporophytes grew at site I and III, including *Phaeoceros carolinianus* at the latter. No hornworts were observed at site II in autumn 1991.

Sampling. Three positions were chosen arbitrarily within each field where soil samples were taken in profiles (Fig. 1: a, b, c) in October 1991 using a root auger of 8 cm diameter. From the soil cylinders obtained, blocks with a base of *ca.* 5.5 x 5.5 cm and a height of 3 cm were cut out at depths of 1.5, 5, 10, 15, 20, 30, and 40 cm, and at one position (Ia) at 50 cm (Tab. 1). The cores were used to avoid contamination with soil from other depths. Because some cylinders

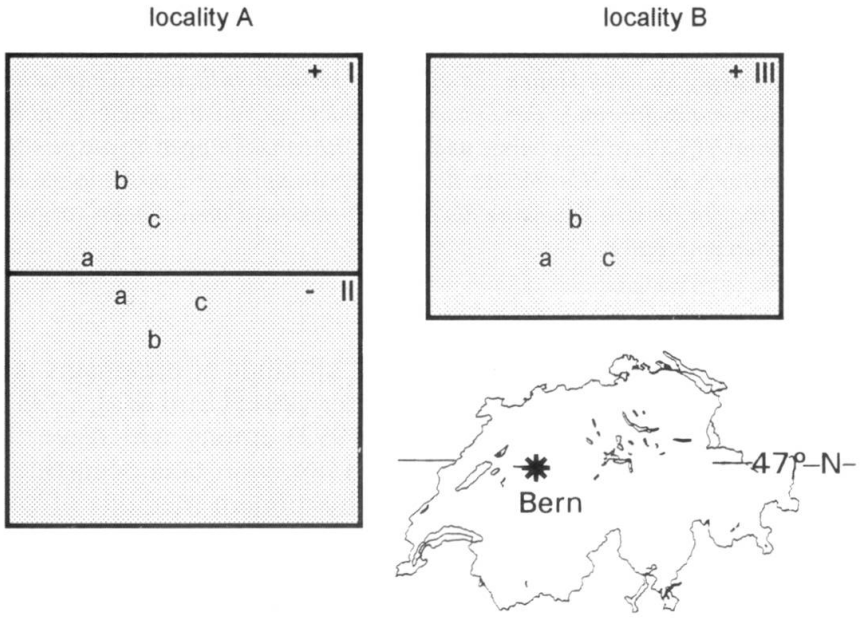

FIGURE 1. Location of study sites and sampling design. Profiles a, b, c in fields I, II, III. + / -, with/without gametophytic hornwort population in autumn 1991.

were compressed during digging, the actual depths of the soil samples may vary slightly between the profiles (Tab. 1). The samples were stored in plastic bags until further treatment in the laboratory (1 - 2 days). Thin soil layers (ca. 0.5 cm thick) were spread out on sterilized wet sand in Petri dishes of 9 cm diameter (two replicates from each core).

Field	I	I	I	II	II	II	III	III	III
Profile	a	b	c	a	b	c	a	b	c
Depth 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
2	5	5.5	5	5	6	6	5	5	5
3	10	9	9	9	10	10	10	10	9.5
4	15	15	15	15	15	15.5	14	15	18.5
5	20	22	20	20	20	20	20	20	25
6	28	29	30	30	29	29	30	29	30
7	38		38	41			40		33.5
8	50								

TABLE 1. Depths [cm] of the analysed soil samples from different profiles (a, b, c) in three cultivated fields.

Cultivation. The soil samples were cultivated in closed Petri dishes. Two replicates from the profiles a of all study sites (a, a*) and one set of replicates from profiles b and c of all study sites were kept at room temperature (22 - 24 °C) under long day conditions of 16 : 8 hours in light produced by a fluorescent tube. The soil was kept moist by addition of sterilised deionised water. The samples were moved weekly to avoid growth effects due to the slightly unequal light conditions on the development of the cultures.

To test the influence of cultivating conditions on the germination of diaspores in soil samples, one set of replicates from each field was kept in a glasshouse (b*) and one set was kept outdoors (c*) in the Botanic Garden at Zürich. The former is a temperate house with natural light and a temperature of about 13 °C during day and 9 °C during night, respectively, and an air humidity between 60% and 80%. At that place, it was impossible to keep the moisture in the Petri dishes balanced due to rather high radiation during sunny days. The soil thus dried up easily and developing bryophytes usually died within a few days. The outdoor cultivation turned out to be problematical since the plastic Petri dishes were opened or even overturned during heavy rainfalls or storms and, therefore, had to be excluded from further analysis.

The sterilisation of soil samples intended to be used as controls (to test for possible contamination of the cultures with air-borne spores) was not successful due to a technical defect with the autoclave. In those 'test' cultures, however, no weedy species (e.g., *Funaria hygrometrica*) were observed. Additionally, very few gametophytes and protonemata developed in the soil cores from the lowermost depths during the whole experimental period. It is thus concluded that a contamination of the cultivated samples is negligible.

Screening. The cultures were checked at intervals of about one month. The development of bryophyte gametophytes including protonemata, fern prothallia and, if present, algae was observed using a dissecting microscope, but without a detailed identification of individual species. Occasionally germinating phanerogams were removed. Hornwort gametophytes and fern prothallia were counted individually. The former were transferred into separate cultures in order to prevent spores from the developing capsules germinating. Despite the above-mentioned problems with the greenhouse cultures, it is assumed that it was possible 'to catch' the germination of hornworts in those due to frequent observation. The sporelings were counted and mean values of b and b* calculated which are presented in Tabs 3 and 4. Otherwise, the cultures kept in the glasshouse could not be investigated further. The final screening took place approximately $7^1/_2$ months after the start of the experiment. The species composition of each sample was determined, if necessary, by microscopical investigation of the specimens, and the dominant species was noted. In some cases, it was impossible to identify the plants to species level (see Results). Voucher specimens of all species from the soil samples and from the surface vegetation of the study sites are deposited in Z.

	Field I		Field II		Field III	
	D	S	D	S	D	S
Anthoceros agrestis	+!	+!	+!	-	+!	+!
Bryum rubens	+	+	+	+	+	+
Dicranella staphylina	+	+	+	+	+	+
Pottia truncata	+	+!	+	+!	+	+!
Phascum cuspidatum	?	+!	?	+!	?	(+!)
Ephemerum (cf.) *minutissimum*	+!	+!	+	+!	+!	+!
Eurhynchium hians	(+)	+	(+)	+	+	+
Dicranella schreberiana	+	-	+	-	+	+
Ditrichum cylindricum	+	-	+	-	+	+
Pohlia melanodon	+	+	-	+	-	-
Phaeoceros carolinianus	-	-	-	-	+	+!
Riccia sp.						
(= *R. sorocarpa* above-ground)	-	+!	-	+!	+	+!
Weissia cf. *controversa*	-	-	-	-	+	+
Bryum klinggraeffii	+	-	+	-	+	-
Bryaceae indet.	-	-	-	-	+	-
Leptobryum pyriforme	+	-	-	-	-	-
Bryum violaceum	-	+	-	+	-	-
Bryum argenteum	-	-	-	-	-	+
Pleuridium subulatum	-	-	-	-	-	+
Brachythecium rutabulum	-	-	-	-	-	+
Number of species						
(without *Phascum cuspidatum*)	11	9	9	8	13	14
species in common	7		5		11	
differing species	6		7		5	

TABLE 2. Bryophyte taxa occurring in the diaspore bank (D) and on the surface (S) of three cultivated fields. ! = with sporophytes (column D: in culture); (+) = sparse occurrence.

Loc. A		Profiles			
Field	depth	a	a*	b	c
I	1	0	0	0	2
I	2	0	0	1	0
I	3	0	0	0	0
I	4	0	0	1	0
I	5	0	1	0	2
I	6	0	0	0	0
I	7	1	1	-	-
I	8	0	0	-	-
total		1	2	2	4

Loc. A		Profiles			
Field	depth	a	a*	b	c
II	1	0	1	2	0
II	2	1	2	2	0
II	3	1	1	2	0
II	4	0	0	2	0
II	5	1	0	0	0
II	6	0	1	0	0
II	7	0	1	-	-
total		3	6	8	0

Loc. B		Profiles			
Field	depth	a	a*	b	c
III	1	0	0	1	1
III	2	0	3	0	0
III	3	0	2	0	0
III	4	0	2	0	0
III	5	0	0	0	0
III	6	0	0	0	0
III	7	0	0	0	0
total		0	7	1	1

TABLE 3. Number of hornwort sporelings in soil samples of different depths and profiles (a - c; a* = replicate of a) in three cultivated fields. Depths (1 - 8) see Table 1.

Results

Identification of bryophyte species (see Tab. 2)

Ephemerum sp. All plants bearing sporophytes could unambiguously be identified as *Ephemerum minutissimum* Lindb. Separation of closely related species, however, is impossible if they are sterile.

Pottia sp. This includes most probably *Phascum cuspidatum* since it was not possible to ascribe with certainty the juvenile pottioid plants from the cultures to one of the two genera. The latter was more or less common in the surface vegetation at all study sites. The occurrence of more than one *Pottia* species in the diaspore bank cannot be excluded although only *Pottia truncata* was found above-ground, being very abundant and copiously producing sporophytes in all fields.

Bryum spp. *Bryum* species of the *erythrocarpum* complex (*B. klinggraeffii*, *B. rubens*, *B. violaceum*) were identified by means of their rhizoidal tubers. There might have been other species of this complex appearing from the soil samples that did not produce rhizoidal gemmae. If that was the case they have been merged into the above mentioned taxa. It is impossible to distinguish their gametophytes, especially when grown under unnatural conditions.

Weissia sp. The identification of *Weissia* taxa remains uncertain if there are no sporophytes at hand.

Riccia sp. The only species observed in the surface vegetation (site III) was *R. sorocarpa*. The cultivated plants could not be definitively ascribed to this species but may belong to it. They developed very narrow, band-shaped, sterile thalli without the thickenings in the epidermal layer characteristic for this taxon. However, this feature is sometimes lacking in plants from Central Europe grown under natural conditions as well.

Development of plants in culture

Hornwort spores, including one *Phaeoceros* spore (IIIa*, depth 5 cm), germinated from the second until the fourth month of cultivation, except one that appeared after seven months. The very young sporelings started as globose cell masses producing rhizoids on all sides. Flattening of the thallus occurred with increase of the number of cells. Gametangia, and in *Anthoceros agrestis* often sporophytes, were formed a few weeks after germination. In most of the soil cores from 0 to 22 cm, protonemata of mosses and of *Riccia* started to grow within the first month of the experiment and increased in abundance afterwards. Gametophores established subsequently and rhizoidal gemmae were soon observed (often in large quantities) in species of *Bryum* and *Dicranella*. Most of the bryophyte species arising from the soil samples remained sterile. Only *Anthoceros agrestis* and occasionally *Ephemerum minutissimum* Lindb. produced sporophytes (Tab. 2: !). Antheridia developed in one specimen of *Bryum rubens* (IIc, depth 30 cm).

Field	I	II	III	total
Depth 1	2	3	2	7
2	1	5	3	9
3	0	4	2	6
4	1	2	2	5
5	3	1	0	4
6	0	1	0	1
7	2	1	0	3
8	0	-	-	0
total	9	17	9	35

TABLE 4. Number of hornwort sporelings in soil samples from various depths of three different cultivated fields. The number per depth and field is the sum of sporelings in the samples of corresponding depths of profiles a - c. Depths (1 - 8) see Table 1.

Composition of the diaspore bank

Fifteen different bryophyte species emerged from the diaspore bank during the period of the experiment

(Tab. 2). Additionally, large quantities of two types of fern prothallia established in the soil cores of all fields.

The bryofloristic composition turned out to differ considerably between above- and below-ground at all study sites: The number of taxa common to both the diaspore bank and the surface vegetation compared with the number of taxa differing between them is 7 vs. 6 in field I, 5 vs. 7 in field II and 11 vs. 5 in field III, respectively (Tab. 2). A comparison of the diaspore reservoir of individual fields gives evidence of distinct differences in bryophyte species composition between fields of different localities. A detailed analysis of the species diversity and its variation within and between sites and with regard to depth will be presented later (Bisang, unpubl.[1]).

Despite the fact that gametophytes occurred in fields I and III but not in field II at the time of sampling, most hornworts germinated in the soil samples from field II (Tabs 3 and 4). The difference between fields, however, proved not to be significant (Kruskal-Wallis-Test, analysis of variance by ranks; $P = 0.24$). The mean number of gametophytes that appeared per sample with a surface of about 64 cm^2 (Petri dishes of 9 cm diameter) is 0.4. This corresponds to an average of at least 63 viable hornwort spores per m^2 of soil surface in the field.

Spatial structure of the diaspore bank

Too few hornwort gametophytes appeared in the investigated soil samples to perform statistical analysis within study sites (Tab. 3). Nevertheless, when the numbers of sporelings of corresponding depths from all profiles in all fields are summarized, a significant difference between the total number of sporelings in samples from 0 to 25 cm and in those from below 25 cm was revealed (depths 1 - 5: 31 vs. depths 6 - 8: 4; Tab. 4). A similar pattern related to depth was found for fern spores and for moss protonemata. In all profiles of all sites, significantly fewer prothallia emerged (W-test: $p < 0.05$, Riedwyl 1975) and protonemata appeared later and showed a tendency to grow more slowly in the soil cores from the lowermost depths between 28 and 50 cm (Bisang, unpubl.).

Discussion

Development of plants in cultures

As no growth cabinet was available to keep the cultures at a suitably low temperature (*ca.* 10 - 15 °C), killing of bryophytes by fungi was feared (see During & ter Horst 1983, p. 58). Nevertheless, fungi were observed only in one sample. Growth of algae and bacteria, however, was considerable in some samples (*Vaucheria* sp., *Botrydium* sp., *Nostoc* sp.) and may have influenced the growth of bryophyte gametophytes.

Anthoceros agrestis was one of the two species that produced sporophytes in culture. Its capsules were sometimes found in culture vessels where only one spore had germinated indicating self-fertilization.

The relatively low number of hornworts that established in culture may indicate few viable spores being present in the soil or unfavourable external conditions for germinating. Renzaglia (1978, p. 51) found spores of *Anthoceros punctatus* s.l. extremely difficult to germinate in culture contrary to other Anthocerotalean taxa. With the data of the present study at hand, it is not possible to decide why few hornworts appeared, but it is of little importance as long as the resulting figures are used in a comparative manner only.

Composition of the diaspore bank

Differences in the species composition above- and below-ground were revealed in comparable studies of diaspore banks for both bryophytes (During & ter Horst 1983; During & van Tooren 1987; Jonsson 1993; Kohn & Schmidt 1994; Smith 1987) and vascular plants (see review in Fischer 1987, p. 37).

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[1] All unpublished data referred to in this paper are deposited at the 'Institut für Systematische Botanik' of the University of Zürich.

Viable fern spores are reported to be present in the soil of a variety of habitats that are remote from sporophyte populations (During & ter Horst 1983; During & al. 1988; Clymo & Duckett 1986). The obviously large dispersal capacity of ferns is supposed to be related to the height of spore release above ground (During & ter Horst 1983).

The differences between individual profiles within fields are probably due to a clumped distribution of spores in the soil (During 1987). Various factors may account for the considerable floristic differences between the fields of comparable ecological conditions lying at a distance of about 5 km. Although the general environmental conditions such as climate, inclination, soil characteristics (Bisang, unpubl.) and land use (arable fields with crop rotation) are similar at all study sites, there may be variation at a more local scale or even micro-scale. For example, in the light and moisture conditions due to the close proximity of field III to a forest, or caused by the agriculture management. Field III was kept as a meadow in the year of sampling whereas fields I and II were cereal-fields. Changes in arable farming practice or other historical factors could have influenced species composition as well. During & al. (1988) report a greater below-ground species diversity in forested as against to open sites. Finally, despite the growing evidence that spores of a number of bryophyte species may be transported over long distances (e.g., Bremer & Ott 1991; Miles & Longton 1992; Stoneburner & al. 1992), the subsequent successful establishment of gametophores from air-borne spores seems to be quite rare in nature (Longton & Schuster 1983).

The plants in culture of *Anthoceros agrestis* and *Phaeoceros carolinianus* were presumably derived from spores present in the soil since both taxa usually copiously produce sporophytes. This holds true for a number of other species, such as *Riccia* sp., *Ephemerum minutissimum* and *Pottia truncata* which are commonly encountered with capsules on the surface of the study sites. The majority of plants, however, has probably arisen from asexual propagules such as rhizoidal tubers (*Bryum* spp., *Dicranella* spp.) or gametophyte fragments (e.g., *Eurhynchium hians*). Earlier studies also indicate that vegetative propagative units probably predominate in bryophyte diaspore banks (During & al. 1988, Smith 1987).

Anthoceros appeared in soil samples from field II where gametophytes were lacking during at least one year. This and other species that established in culture without occurring in the modern surface vegetation are assumed to have persistent diaspore banks, probably comparable with one of the persistent seedbank types defined by Thompson & Grime (1979). No direct evidence on *Phaeoceros carolinianus* could be obtained from the present investigation since only one spore germinated in culture. Long-term studies, however, demonstrate the importance of a store of viable spores: *Phaeoceros carolinianus* has re-appeared in stubble-fields of selected sites where it was not observed during a period of several years (Bisang, unpubl.). In accordance, long-lived spores of *Phaeoceros laevis* were reported by Proskauer (1958). There is evidence that spores of a number of bryophyte species, especially of 'Annual Shuttle Species' sensu During (1979), remain viable in the soil «for quite a long time» (During & ter Horst 1983; During 1987; Jonsson 1993).

Although present both in the corresponding diaspore bank and in the neighbouring field I, gametophytes of *Anthoceros agrestis* were not observed in field II with catch crop in autumn 1991. This suggests that farming practice is an important factor influencing the growth of hornworts. Results of long-term studies further support this conclusion. Hornwort gametophytes were significantly more frequently encountered in fields with cereals than in other crops (95% vs. 8 to 50%, $p < 0.05$; Bisang, unpubl.).

Spatial structure of the diaspore bank

Management is considered to be responsible for the abrupt decline in the number of diaspores of bryophytes and ferns between 25 and 28 cm. The fields are ploughed to a depth of 20 to 25 cm which results in a continuous stirring and inverting of the soil profile above. Animal activity, soil erosion and soil movement by water are probably important mechanisms causing the transport of propagules into and within deeper layers in arable fields also as was presumed, for example, by Harper (1977) and During & al. (1988) for other habitats. In one of the few

studies dealing with the store of bryophyte propagules in deeper soil layers, the abundance of *Sphagnum* shoots was shown to decrease with increasing depth (Clymo & Duckett 1986). Dyer & Lindsay (1992) report that «bryophytes were usually most common in the upper soil levels». A reduction of the diaspore density with depth applies also for many species of vascular plants (for a review see Urbanska 1992) and for the majority of fern spore banks examined so far (Schneller 1988; Dyer & Lindsay 1992).

Conclusions

The present results indicate that the bryophyte diaspore reservoir is essential for the local survival of a number of species. It may provide an escape in time during unfavourable conditions and a source for rapid colonisation (Furness & Hall 1981; Kohn & Schmidt 1994; 'being there' strategy according to During 1990, p. 173). This was shown for both hornwort taxa that survived unsuitable cultivation as propagules in the soil. It may imply for those bryophyte species with limited ability of dispersal over intermediate and long distances and/or subsequent successful terrestrial establishment, that the chance for a recolonisation after extinction above-ground is small, if they are not present in the diaspore bank. Therefore, it is likely that the long-term persistence of certain species depends to a considerable degree on the presence of their propagules in the soil.

Implications for practical conservation measures

The results of the presented investigation of the diaspore bank in agricultural fields and of the long-term observations mentioned above imply that appropriate agriculture practice is crucial for the survival of hornworts, especially for *Phaeoceros carolinianus*, in regions like Central Europe where they are confined to cultivated fields. It should allow the ephemeral bryophytes to complete their life cycles, including the development of mature sporophytes which ensures a continuous spore reservoir in the soil. This has to be achieved by management agreement with farmers comprising financial compensation of extra effort and of potentially reduced profits. Necessary measures are, first, ploughing in late autumn to allow for sporophyte production. The long-term studies have shown that many methods of modern cropland farming, e.g., the accented furrowing of potatoe-fields or the tillage with heavy machines in general, create unfavourable growing conditions for hornworts. It is thus recommended to favour growing of cereals as they can be cultivated without the use of heavy agricultural machines in a more or less traditional way, with limited supplementary work and usually with moderate crop reduction. Crop rotation, even if occasionally alternating with conventional production, could be continued since there is evidence that hornwort spores are able to survive unsuitable cultivation in the diaspore bank during several years. The application of artificial fertiliser and of herbicides should be limited as long as their negative effect on bryophytes cannot be excluded.

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