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Ephemerum cohaerens and *E. rutheanum*: persistent annual bryophytes in the Dutch Rhine floodplain

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Ephemerum cohaerens and *E. rutheanum* have been found in 12 localities in the Dutch Rhine floodplain between 2004 and 2011, mainly in the eastern reach (Upper-Rhine and Waal). The first species is very rare in western and central Europe, the latter is a European endemic known from six countries only. All localities represent the Natura 2000 habitat type 3270, 'Rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation' comprising vegetation types with a late annual development on banks of former meanders, scour holes and sand and clay pits in forelands.

The habitat requirements, life strategy and range structure in the Netherlands are discussed for both species. In several localities dominant *Ephemerum* populations exist over tens of square meters year after year. This remarkable persistence is attributed to a special combination of environmental factors and species attributes: 1) an open vegetation on well-drained mineral soil with high moisture capacity and intermediate fertility, most commonly on sandy soils with clayey layers or with a top layer of sandy clay, 2) a regular inundation regime with high and prolonged flooding up to May or early June causing a nearly annual set back of the vegetation succession, 3) a unique variant of the annual shuttle species life strategy: the species germinate from the diaspore bank with large spores and tubers and develop an extensive protonema mat first; when moisture conditions are suitable, moss plants are formed during late summer which sporulate in autumn.

Forelands of the river Rhine tributaries in the Netherlands are made up of young clayey deposits on Pleistocene gravels and sands. Terrestrial bryophytes in these forelands face annual flooding, mainly in late winter and early spring, and either strong competition by tall herbs on nutrient-rich clay or a high desiccation risk on sandy and gravelly soils during the growing season. In this highly changeble terrestrial environment most bryophytes adhere to the colonist life strategy (During 1979) exemplified by *Bryum argenteum*, the *B. dichotomum*-group, *Barbula unguiculata* and *Dicranella varia*: common generalists with a short life span, high reproductive output and small spores. More typical riverine species depend on intermediate soil texture and disturbance regimes that prevent dominance by competitive herbs. These conditions occur in Natura 2000 habitat 3270, 'Rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation' (EC 2007). In the Netherlands it comprises vegetation types with a late annual development on banks of former meanders, scour holes and sand and clay pits in forelands. Characteristic vascular plants are small, short living and often have persistent seed banks, such as *Eleocharis acicularis*, *Cyperus fuscus*, *Limosella aquatica, Potentilla supina* and *Pulicaria vulgaris*. Typical bryophytes are *Physcomitrella patens* and *Riccia cavernosa*. These species have an annual shuttle strategy: they anticipate vegetation gaps and bare soil by regenerating from the soil diaspore bank (During 2001). In 2004 extensive mats of an *Ephemerum* species were found in this habitat, first believed to be the very rare *E. cohaerens* but later identified as the even rarer European endemic *E. rutheanum* (Holyoak 2010). In the following years several new localities of both species were discovered, mainly in the forelands of the river Waal, the main tributary of the Rhine system in the Netherlands.

We present data on the distribution and ecology of both *Ephemerum* species in the Netherlands and discuss their life strategy and range structure in Europe.

Study area

The study area encloses the Rhine system from the German border at 15 m a.s.l. to Gorinchem city, 80 km downstream at 2 m a.s.l. where the system enters the fresh-water tidal area (Fig. 1). Most scour holes, (former) sand and clay pits and meander cutoffs in this area have been searched in late summer and autumn between 2009 and 2011.

The Rhine system was embanked between 1150 and 1300 (Van de Ven 2004). Since then, flooding has been restricted to the area between the dikes, about 1–2 km wide. The river channel was fixed during the 18th and 19th centuries by means of groynes and revetments. Embankment has led to higher sedimentation rates in the forelands and a raised floodplain level (Wolfert 2001). Numerous scour holes bear witness of the many dike breaches during the 19th century and earlier.

The eastern reach of the Rhine system is characterised by a highly sinuose, laterally meandering river (Upper-Rhine, Upper-Waal) characteristic for the area where the thickness of Holocene clay deposits covering Pleistocene sands and gravels is less than the depth of the river (Wolfert 2001). The annual amplitude of the river water table is 600–700 cm (1971–1990 period; Middelkoop et al. 2003) with low water tables in the forelands in summer and high water levels during flooding resulting in a set back of the vegetation succession on margins of scour holes and other foreland waters almost every year. This area is covered by Natura 2000 site Gelderse Poort (NL9801024).

The lower reach of the Rhine is a downstream migrating river of low sinuosity (Middle-Waal), associated with a lower gradient, a low elevation above sea level and thick clay deposits (Wolfert 2001). The annual amplitude of the river water table is much lower than in the eastern reach: about 200–400 cm (Middelkoop et al. 2003). The forelands in this westernmost part of the study area belong to Natura 2000 site Uiterwaarden Waal (NL2000011).

Occasional searches for *Ephemerum* in the forelands of the other two Rhine tributaries, Lower Rhine and IJssel, were so far unsuccesful. The Lower Rhine is regulated by locks causing much smaller water table fluctuations in this reach of the Rhine system than in the Upper Rhine and Middle Waal.

Taxonomy and reproduction

Taxonomy

Until recently, *Ephemerum rutheanum* has been maintained as a distinct European species by Meinunger and Schröder (2007). They discuss its confusing taxonomy in the literature and give three extant German localities. In 2010 D. T. Holyoak reviewed the European *Ephemerum* species and concluded that his *E. hibernicum*, described from Ireland (Holyoak and Bryan 2005), in fact belongs to *E. rutheanum*. Moreover, he proposes the new combination *E. crassinervium* subsp. *rutheanum* (Holyoak 2010). Clearly, *E. rutheanum* is very close to *E. crassinervium*. Awaiting genetic analyses and additional information about the occurrence of the American *E. crassinervium* subsp. *crassinervium* in Europe (mentioned by Bryan 2007), we prefer to treat *E. rutheanum* as a species.

Holyoak (2010) gives a key to all European *Ephemerum* species. *Ephemerum cohaerens* and *E. rutheanum* are variable species and not always easy to distinguish. Young, non-fruiting plants are sometimes impossible to identify morphologically. Both species have a costa but in *E. rutheanum* it not always reaches the leaf base. In the field, well-developed *E. rutheanum* patches are recognizable by the linear leaves with upwardly pointing, often flexuose leaf tips not unlike *E. serratum* (Fig. 2; Holyoak and Bryan 2005, Fig. 4D). *Ephemerum cohaerens* has broader, ovate-lanceolate leaves with more gradually contracting, outwardly pointing leaf tips (Fig. 3; Urmi et al. 2007). 'Shouldered' leaves are common in *E. cohaerens* but occur in well-developed *E. rutheanum* as well.

Chloronema and rhizoidal tubers

Both *Ephemerum cohaerens* and *E. rutheanum* have more or less fastigiated chloronema branches as described by Pressel et al. (2005). Especially well developed dense protonema mats show this distinctive branching pattern. The chloronema branches usually end in sharp tips, though in *E. cohaerens* also rounded chloronemal tips were seen. Below ground both species have the typical caulonematal/rhizoidal tubers described by Pressel et al. (2005). These look like swollen rhizoids with brown pigmented walls. Some have spine-like side branches ending in a sharp tip. The branches are up to four cells long, end branches however can be up to seven cells long. Not all branches have sharp ends; in the studied plants tubers with spines are more numerous in *E. rutheanum* than in *E. cohaerens*. No discriminating differences between the tubers of both species were observed. The tubers are formed before the sporophytes mature and so may act as an alternative way of perennation on sites susceptible to inundation prior to sporophyte maturation. The persistent occurrence of both species at Dutch floodplain localities may well be due to the presence of these tubers.

Distribution

In Europe, *Ephemerum cohaerens* is mainly a lowland species in the temperate zone with a western and central dis-

Figure 1. Map of the study area in the centre of the Netherlands with the Rhine tributaries Upper-Rhine, Lower-Rhine, Waal and IJssel as well as the Meuse river (all lower case) and a 5 × 5 km grid. A selection of cities in upper case. *Ephemerum* localities: *E. cohaerens* (open square: 1843 record; solid squares: 11 post-2000 records); *E. rutheanum* (7 open circles).

tribution (Ahrens 2000, Smith 2004). It has been found in 15 countries from Ireland in the west to Rumania in the east. Most finds are in the upper reaches of large rivers such as Danube, Rhine and Rhone and their tributaries with a main flooding period in early spring caused by meltwater discharge in high mountains. *Ephemerum rutheanum* is a

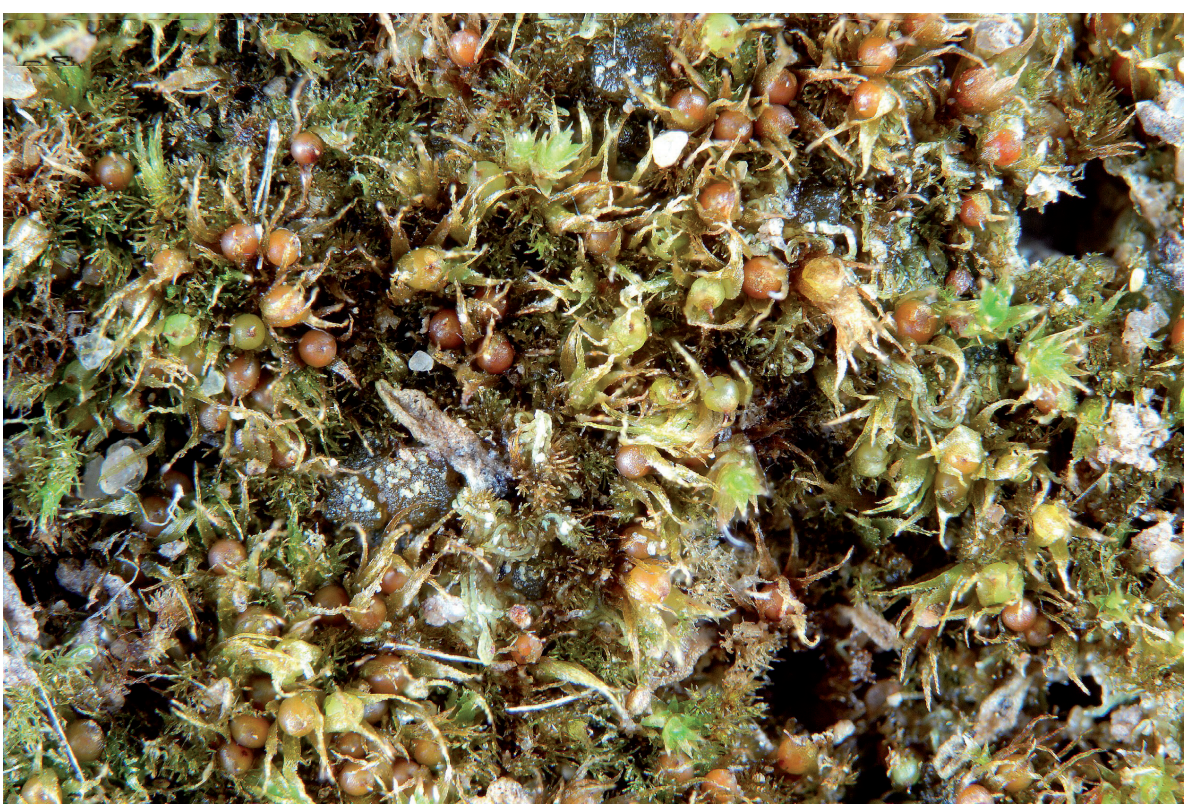

Figure 2. *Ephemerum rutheanum*. Huissen locality. Photo by D. Haaksma.

Figure 3. *Ephemerum cohaerens*. Slijk-Ewijk locality. Photo by D. Haaksma.

lowland species known from Ireland, Wales, the Netherlands, Germany, Poland and France (Holyoak 2010). The association with floodplains of rivers originating in high mountains is less obvious.

Until recently *Ephemerum cohaerens* was considered to be extinct in the Netherlands after its first discovery by S. M. van der Sande Lacoste in November 1843 on the Merwede river bank near Papendrecht, east of Rotterdam (Fig. 1). The collection in L consists of 12 small slices of sandy clay showing protonema spots with scattered fruiting plants and single shoots of *Bryum argenteum* and *Drepanocladus aduncus* (Fig. 4).

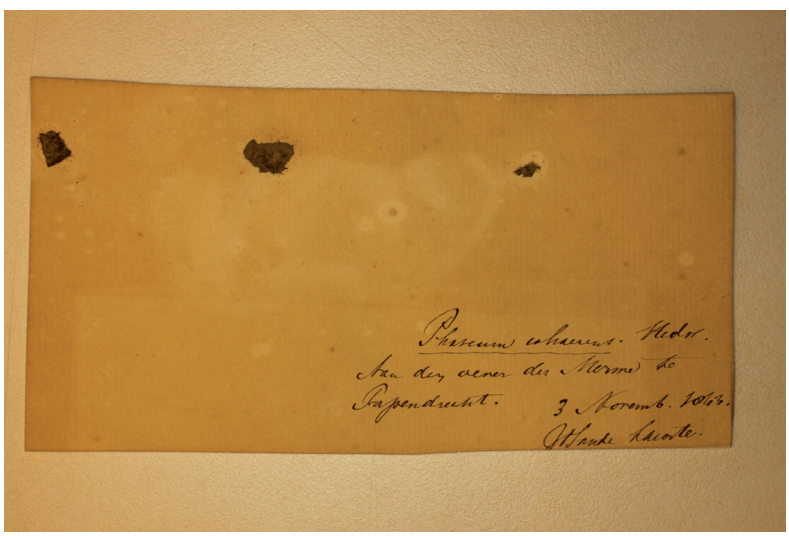

Figure 4. Part of the 1843-collection of *Ephemerum cohaerens* by S.M. van der Sande Lacoste in L. Photo by L. B. Sparrius.

Table 1 presents data on all localities found between 2004 and 2011. It includes Keeken in adjacent Germany within 1 km from the Dutch–German border, discovered in 2003 by U. W. Abts (Meinunger and Schröder 2007) and reconfirmed here by the first author in 2009. Most localities occur within the Natura 2000-site Gelderse Poort between the cities Arnhem–Nijmegen and the German border (Fig. 1). The localities with large populations (>25 m) often contain both species, but with quite different amounts. The very large Huissen populations consists mainly of *E. rutheanum* with scattered patches of *E. cohaerens*, whereas the opposite holds for the equally large Haalderen and Kekerdom populations (Table 1).

Ecology

Topsoil features

For each locality the topsoil texture in patches of *Ephemerum* was described using a 25 cm long gouge auger. Generally, the topsoil is layered as a result of inundation events with a major contribution of (coarse) sands compared to clay. Based on these descriptions three texture types are distinguished (Table 1): 1) type SC: more or less homogeneous sandy clay with a water table deeper than 25 cm including profiles with layers of coarse and fine sand alternating with 1–3 cm thick clay horizons and covered by a thin sandy clay layer. This is the most frequent type of topsoil of unshaded, more or less sloping banks of scour holes and sand pits with *Ephemerum* (Fig. 5a); 2) type FS: homogeneous fine sand with a water table within 25 cm. This type was found only once on a flat shore of a former sand pit (Fig. 5b); 3) type RM: root mats of willow (*Salix* spp.) encrusted with clay on sandy clay. These conditions occur on the highest and outermost bank zone where it is shaded by willow or poplar (*Populus* spp.)(Fig. 5c).

Inundation regime and vegetation zonation

The time, duration, frequency and depth of flooding within the Rhine floodplain vary greatly between location and years, periodically setting back vegetation succession (Siebel and Blom 1998). The typical zonation pattern of localities with large populations of *Ephemerum* results from annual inundation of the river bank zone at least up to early June. This is illustrated by the Huissen locality, a scour hole with *Ephemerum rutheanum* dominance over more than 100 m of margin every year (Fig. 6). The uppermost zone is dense marsh vegetation mostly no longer flooded as from early May (Fig. 6A). In early June a one to several meters wide adjacent zone with scattered marsh plants, such as *Lythrum salicaria* and *Mentha aquatica,* is uncovered. This will become the uppermost part of the *Ephemerum* zone. The lower part is still flooded (Fig. 6B). In the course of June this lower zone is often still too wet to allow protonema growth. *Eleocharis acicularis* is the first species that recolonizes the wet, sandy bank (Fig. 6C). During July and August an open and low vegetation develops here, including extensive chloronema mats of

Table 1. Data on localities (town or village) of *Ephemerum cohaerens* (Ec) and *E. rutheanum* (Er) in the Netherlands and adjacent Germany (D). Columns Ec and Er give frequencies within the occupied area (compare column Length): D = dominant, F = frequent, O = occasional, R = rare. Column Topsoil gives soil texture types: FS fine sand with high water table (<25 cm), RM clay-encrusted root mat of willow, SC coarse and fine sands with clay horizons and low water table (>25 cm).

Locality	Ec	Er	Position (UTM grid)	Dates	Habitat	Length (m)	Topsoil
Papendrecht	R		31U 618950-5742950	1843	river bank	?	SC
Haaften	F		31U 651930-5742800	2010–2011	sand/clay pit bank	10	SC,RM
Dreumel		O	31U 667570-5749020	2009–2011	sand/clay pit bank	30	SC
Slijk-Ewijk	F		31U 690100-5752160	2009–2010	scour hole margin	5	SC,RM
Oosterhout	R	O	31U 695450-5750310	2009–2011	scour hole margin	80	SC,RM
Ooij	R		31U 700240-5749430	2011	pasture	1	SC
Haalderen	D	O	31U 701550-5752160	2009–2011	scour hole margin	25	SC
Huissen	O	D	31U 702750-5757190	2004–2011	scour hole margin	140	SC
Angeren	R		31U 703250-5756660	2004	sand/clay pit bank	1	SC,RM
Gendt		R	31U 704720-5750730	2004	sand/clay pit bank	1	SC
Kekerdom	F	R	32U 293600-5750720	2009–2011	sand/clay pit bank	220	SC,RM
Pannerden	R	O	32U 296830-5751930	2009–2011	sand/clay pit bank	100	FS,RM
Tolkamer	R		32U 300020-5749530	2011	sand/clay pit bank	1	RM
Keeken (D)	R		32U 299280-5747860	2003–2011	scour hole margin	5	RM

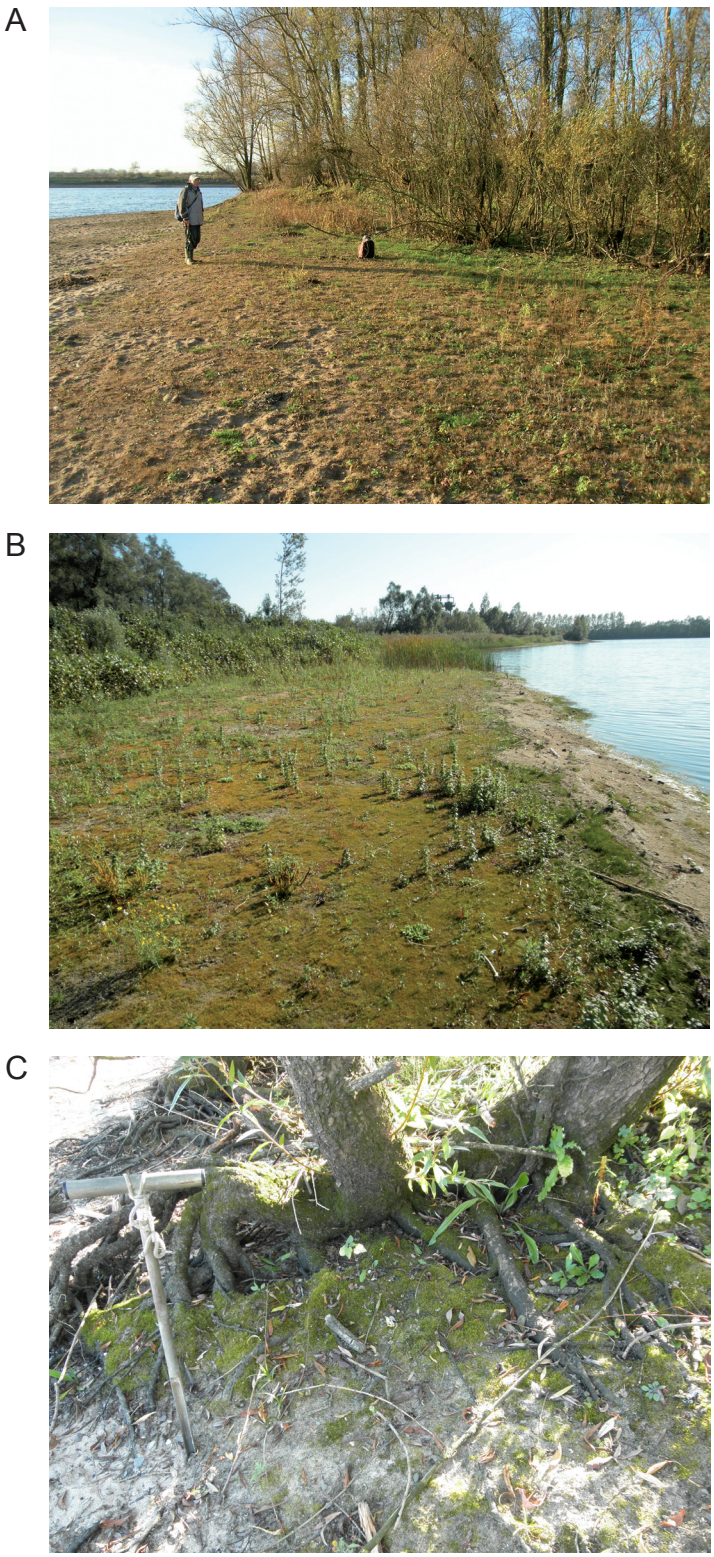

Figure 5. *Ephemerum* habitats with different topsoil texture. (A) Type SC: sandy clay with water table >25 cm (Kekerdom locality; 14 November 2009) (B) Type FS: fine sand with water table <25 cm (Pannerden locality; 30 September 2011), (C) Type RM, root mat of willow (Tolkamer locality; 30 September 2011). Photos by R. J. Bijlsma.

Figure 6. Inundation stages for the scour hole Grote Bloem (Huissen locality) in different seasons. (A) 1 May 2005 (inaccessible); (B) 2 June 2010; (C) 29 June 2010; (D) 9 October 2004. Photos by R. J. Bijlsma.

Ephemerum but mostly without moss plants. *Eleocharis* often dies back in this period. The appearance of sporulating plants depends on summer conditions but generally starts in late August. Massive sporulation occurs in September. Eventually, the *Ephemerum* zone extends from the low and open marsh vegetation to well above the mean water line in summer, avoiding bare sandy soil (Fig. 6D).

Associated species

In most *Ephemerum* localities two vegetation relevées were made in distinct parts of the zonation. Table 2 and 3 present the most frequent vascular plant species and bryophytes associated with both *Ephemerum* species.

An indicator species analysis (PC-ORD for Windows ver. 4.25; McCune and Mefford 1999) with relevées grouped according to *Ephemerum* species (duplicating relevées with both species), yielded six indicator species with significance level <5% (based on 1000 permutations): *Drepanocladus aduncus* ($p < 0.008$) for the *Ephemerum cohaerens* habitat and *Bidens tripartita* ($p < 0.049$), *Lythrum salicaria* ($p < 0.003$), *Myosotis scorpioides* ($p < 0.016$), *Pulicaria vulgaris* ($p < 0.013$) and *Tripleurospermum maritimum* ($p < 0.043$) for the *Ephemerum rutheanum* habitat. This slight difference in habitat based on both relative abundance and relative frequency of associated species can be explained by the topsoil texture type RM (root mat) which is always associated with *Ephemerum cohaerens* (Table 1). This sheltered and well-drained habitat (Fig. 5C) is optimal for *Drepanocladus aduncus* and suboptimal for marshland species (*Lythrum*, *Myosotis*) and species of well-illuminated habitats such as *Pulicaria*.

The open herb layer (mean cover 46%) of the *Ephemerum* habitat consists not only of species typical of nutrient-rich habitats with prolonged inundation (*Bidention*/*Chenopodion*) but also of periodically wet (*Lolio–Potentillion*) habitats or otherwise periodically disturbed vegetation on compact, nutrient-rich (*Polygonion*) or moist, rather nutrient-poor soils (*Nanocyperion*) (Table 2). Compared to the typical *Bidention* habitat in the Netherlands, the *Ephemerum* vegetations have relatively more

Table 2. Data on associated vascular plant species with frequency >10%. Species are ordered by frequency. Nomenclature after Van der Meijden (2005). Life form after Hill et al. (2004): Gn = non-bulbous geophyte, Hc = hemicryptophyte, Ph = phanerophyte, Th = therophyte (annual plant, including Hz = annual hydrophyte). Characteristic species for the syntaxonomical units *Bidention* (Bid; including *Chenopodion*), *Nanocyperion* (Nan), *Polygonion* (Pol) and *Lolio-Potentillion* (Lol) are indicated with a K (after Sýkora et al. 1996, Lemaire et al. 1998, Weeda et al. 1998).

Herb layer species	Frequency	Mean cover	Life form	Bid	Nan	Pol	Lol
Mentha aquatica	81	4.9	Hc				
Plantago major	81	8.9	Hc			K	K
Agrostis stolonifera	63	9.9	Hc				K
Lythrum salicaria	59	6.5	Hc				
Myosotis scorpioides	56	6.7	Hc				
Bidens tripartita	52	1.3	Th	K			
Eleocharis acicularis	52	18.4	Hc				
Juncus bufonius	48	2.2	Th		K		
Salix alba	48	4.2	Ph				
Gnaphalium uliginosum	44	1.9	Th		K		
Poa annua	44	1.4	Th			K	K
Conyza canadensis	41	2.0	Th				
Juncus compressus	30	7.1	Gn				K
Medicago lupulina	30	5.4	Th				
Potentilla supina	30	4.3	Hc	K			
Taraxacum officinale	30	1.9	Hc				
Cirsium arvense	26	2.4	Gn				
Lycopus europaeus	26	1.1	Hc				
Plantago lanceolata	26	2.6	Hc				
Potentilla anserina	26	11.4	Hc			K	K
Pulicaria vulgaris	26	3.3	Th	K			
Bellis perennis	22	1.0	Hc				
Equisetum palustre	22	2.2	Gn				
Juncus articulatus	22	1.2	Hc				
Rumex maritimus	22	1.2	Th	K			
Trifolium repens	22	1.8	Hc				
Veronica catenata	22	1.0	Th				
Calystegia sepium	19	1.0	Gn				
Centaurium pulchellum	19	1.0	Th				
Solidago gigantea	19	3.0	Hc				
Chenopodium rubrum	15	2.0	Th	K			
Lysimachia nummularia	15	3.3	Hc				
Populus nigra	15	2.3	Ph				
Rorippa sylvestris	15	1.3	Hc				K
Artemisia vulgaris	11	2.3	Hc				
Cyperus fuscus	11	1.0	Th	K			
Epilobium tetragonum	11	1.0	Hc				
Galium palustre	11	1.0	Hc				
Jacobaea paludosa	11	1.7	Hc				
Matricaria discoidea	11	1.0	Th			K	
Myosoton aquaticum	11	1.0	Hc				
Potentilla reptans	11	7.7	Hc				K
Rorippa palustris	11	1.0	Th	K			
Tanacetum vulgare	11	1.0	Hc				
Tripleurospermum maritimum	11	1.0	Hc				

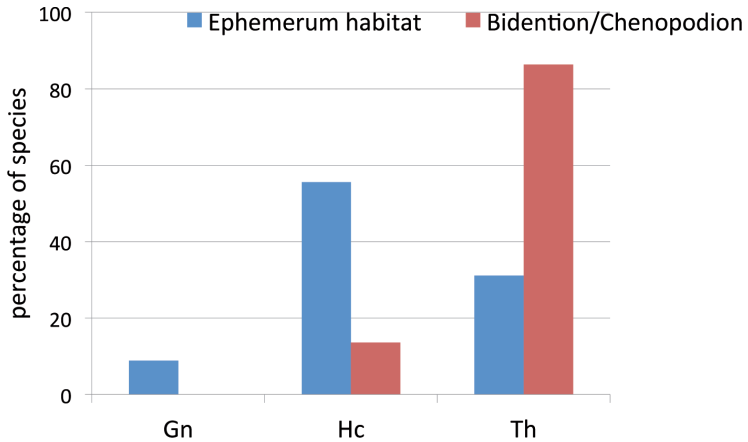

Figure 7. Percentage distribution of vascular plant species over life forms in *Ephemerum* habitat (Table 2) compared to *Bidention* habitat in the Netherlands (Weeda et al. 1998, Table 29.1). Only species with frequency >10% have been considered. Life forms (after Hill et al. 2004): Gn = non-bulbous geophyte, Hc = hemicryptophyte, Th = therophyte. The assignment of species to life forms follows Hill et al. (2004) or Ellenberg (1991) for continental species.

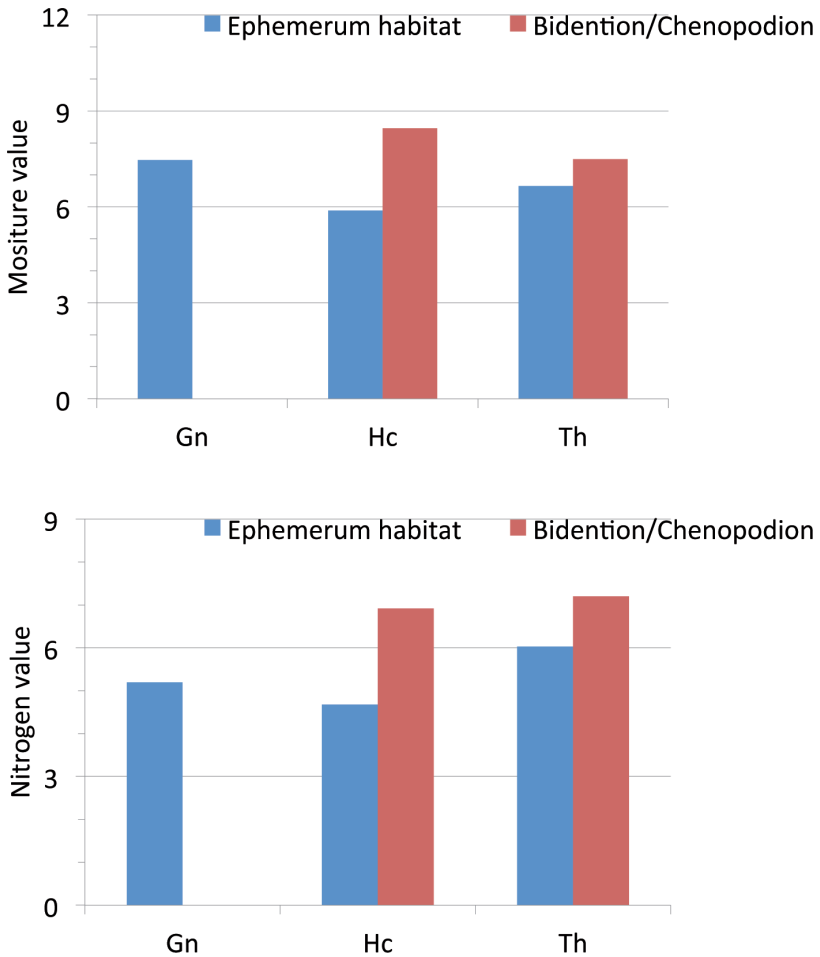

Figure 8. Frequency-weighted Ellenberg values for moisture and nitrogen per life form of vascular plants in *Ephemerum* habitat compared to *Bidention* habitat in the Netherlands. The moisture value ranges from 1 (extreme dryness) to 12 (submerged) and the nitrogen value from 1 (extremely infertile) tot 9 (extremely rich). Ellenberg values according to Hill et al. (2004) or Ellenberg (1991) for continental species.

hemicryptophytes than therophytes (Fig. 7). Moreover they have lower frequency-weighted Ellenberg indicator values for nitrogen and moisture and nitrogen (Fig. 8). The latter indicate intermediate moisture conditions (Hill et al. 2004). The relatively high number of hemicryptophytes in the *Ephemerum* habitat points to better conditions for establishment and growth of perennial life forms compared to typical *Bidention*.

The moss layer (mean cover 48%) is rather species-poor with most other species with low frequency and cover (Table 3). The chloronema of *Ephemerum* often dominates (Fig. 9) leaving little room for colonists such as *Bryum* species. Only the perennial stayer *Drepanocladus aduncus* is likely a successful colonizer of the *Ephemerum* habitat: it occurs in alle relevées with a mean cover of 20%, just as both *Ephemerum* species (Table 3), with an optimum in *E. cohaerens* habitat, especially on root mats (see above). The annual shuttle species *Physcomitrella patens* and *Riccia cavernosa* have their optimum in the typical *Bidention* habitat on clay and occur only incidentally in *Ephemerum* habitats.

Discussion

Habitat requirements

On the west European continent *Ephemerum cohaerens* has a scattered southern distribution with a centre in the Upper-Rhine area in Germany south of Mannheim including the Strasbourg area in France (Alsace). Smaller centres are the Boden Sea area in southern Germany and the French departments Savoie and Isère east of Lyon (Rhône-Alpes) (Hugonnot et al. 2007, Meinunger and Schröder 2007). Here, *E. cohaerens* has been found in a variety of habitats including pastures, arable fields, sand, gravel and loam pits, quarries, reservoir, lake and river margins on clayey or loamy, neutral or base-rich soils (Ahrens 2000, Hugonnot et al. 2007). These authors emphasize the ephemeral behaviour of the species and the temporary nature of the localities.

Ephemerum rutheanum shows no overlap in distribution with *E. cohaerens* in Germany where it has been found after 1995 on a ditch-side, a lake margin and in an arable field (Meinunger and Schröder 2007). Holyoak

Figure 9. Huissen locality, bank of scour hole Grote Bloem (compare Fig. 6). Herb layer with among others *Cyperus fuscus*, *Eleocharis acicularis*, *Potentilla supina* and *Pulicaria vulgaris* and a more or less closed moss layer of *Ephemerum rutheanum*. Photo by R. J. Bijlsma.

and Bryan (2005) describe the habitat of *E. rutheanum* as periodically inundated sites in the catchments of three rivers in Ireland. The species has been found there on a range of topsoil conditions including mud, sandy mud, claymud and clay, either unshaded, partly shaded by herbs or rather strongly shaded by *Salix* bushes. In one Irish locality *E. rutheanum* and *E. cohaerens* were found growing together. Large populations of *E. rutheanum*, covering tens of square meters, have been found in the inundation zone of two Irish localities (Holyoak and Bryan 2005).

In the Rhine floodplain in the Netherlands both *Ephemerum* species share the same habitat which is much more restricted than described for *E. cohaerens* in Germany and France. However, the smaller Dutch habitat range may be the result of a strong focus of our survey on sand/clay pits and scour holes in forelands. Indeed, in 2011 *E. cohaerens* was found by M. Zwarts in very small quantities in a pasture gap in the Waal forelands (Ooij locality; Table 1). The most remarkable difference between the Dutch and other continental records so far, is the persistent dominance over tens of square meters year after year, in localities such as at Huissen, Haalderen and Kekerdom (cf. also Holyoak 2010).

Persistent dominance apparently requires an open vegetation on well-drained mineral soil with high moisture capacity and intermediate fertility. This is the case in sandy soils with clayey layers or with a top layer of sandy clay (topsoil texture type SC). *Ephemerum* was never found on poorly-drained, heavy clay where the typical *Bidention* species *Limosella aquatica*, *Physcomitrella patens* and *Riccia cavernosa* have their optimum as well as many bryophyte colonists of nutrient-rich soils such as *Dicranella varia*, *Pohlia melanodon* and the very rare *Physcomitrium eurystomum*. On clay, root mats (texture type RM) provide drainage. On pure sand, a high water table guarantees moisture availability (texture type FS).

A relatively low nutrient availability (compared to typical *Bidention* sites) is indicated by a few species with an optimum in *Nanocyperion* communities on inland loamy soils (Table 2). In the westernmost Haaften locality *Ephemerum cohaerens* was found together with *Bryum knowltonii* and *Weissia brachycarpa* which indicate base-rich and less nutrient-rich conditions. In Ireland Holyoak even found *Ephemerum serratum* and *Archidium alternifolium* in *E. rutheanum* localities (Holyoak and Bryan 2005): species of very nutrient-poor, often acidic soils, never found in the Rhine floodplain in the Netherlands. The remarkable absence or low frequency of common nitrophilous *Bidention* herbs, such as *Persicaria* spp., *Bidens* spp. (apart from *B. tripartita*), *Rumex palustris*, *Chenopodium* spp. and *Atriplex* spp. further points to a relatively low soil fertility.

The second requirement for persistent dominance of *Ephemerum* in the Dutch sites is a regular inundation regime with high and prolonged flooding up to May or early June causing a nearly annual set back of the vegetation succession, accompanied by slight topsoil erosion or sedimentation.

The third requirement is that conditions related to topsoil texture (moisture availability) and inunundation regime occur over a sufficiently large area.

Life strategy

All *Ephemerum* species are considered as annual shuttle species as defined by During (1979). This strategy

Table 3. Data on associated bryophytes with frequency >10%. Species are ordered by frequency. Nomenclature and life strategy after Siebel and During (2006). Life strategy: as annual shuttle species, col = colonist, ecol = ephemeral colonist, fug = fugitive, sta = perennial stayer. Characteristic species for the syntaxonomical units *Bidention* (Bid) and *Polygonion* (Pol) are indicated with a K (after Sýkora et al. 1996, Weeda et al. 1998).

Moss layer species	Frequency	Mean cover	Life strategy	Bid	Pol
Drepanocladus aduncus	100	21.6	sta		
Ephemerum cohaerens	70	16.9	as		
Bryum barnesii	48	3.6	col		
Bryum argenteum	41	2.9	col		K
Ephemerum rutheanum	41	17.0	as		
Leptobryum pyriforme	41	7.5	ecol		
Physcomitrella patens	26	1.6	as	K	
Bryum rubens	22	6.3	ecol		
Barbula unguiculata	19	2.8	col		
Bryum klinggraeffii	19	5.4	ecol		
Funaria hygrometrica	15	8.5	fug		
Dicranella varia	11	1.7	col		
Pohlia melanodon	11	3.0	col		

is applied by species using different tactics. One tactic is triggered by extreme drought events such that ponds and lakes dry out and the diaspore bank in the soil of their bottoms becomes exposed and can be released. *Physcomitrium sphaericum, Micromitrium tenerum* and *Riccia huebeneriana* are well-known examples (Furness and Hall 1982, During 1989, Eckstein 2006). Another tactic is applied by *Physcomitrella patens*, a species that develops in late summer and autumn on dried up bare mud and clay at nutrient-rich sites. It has no persistent protonema or tubers but a high growth rate which enables fast colonization and early sporulation.

Apparently, *Ephemerum cohaerens* and *E. rutheanum* adhere to yet another tactic. They germinate from the diaspore bank with large spores (about 60–70 µm; Holyoak and Bryan 2005, Smith 2004) and tubers, and first develop an extensive protonema mat. When moisture conditions are suitable, plants are formed during late summer which sporulate in autumn. Under adverse conditions no moss plants are formed and only chloronema mats remain with scattered non-sporulating plants. In the westernmost Haaften locality with a moderate water table amplitude (Middle-Waal), protonema and old, often somewhat weathered plants of *E. cohaerens* were found in June just after the submergence period, suggesting that protonema and some plants had survived flooding. Chloronema growth may be rapid as suggested at the same site where chloronema and young plants were found on bare soil where three weeks earlier the topsoil with *E. cohaerens* had been removed.

We are not aware of differences in strategy between the two *Ephemerum* species and cannot but explain the remarkable different contributions to the moss layer of the Huissen and Pannerden localities (with mainly *E. rutheanum* and rare *E. cohaerens*) compared to the Haalderen and Kekerdom localities (mainly *E. cohaerens* with scattered *E. rutheanum*) as a result of chance events.

Range structure

In Europe, both *Ephemerum* species occur mainly in (former) inundation zones of floodplains and river catchments. We speculate that waterfowl, fishermen and other visitors of these primary habitats contribute to the dispersal along secondary man-made habitats such as reservoirs, ponds and ditches. In the Netherlands a spectacular (exponential) increase of breeding greyleg geese (*Anser anser*) occurred from almost extinct to 100–150 breeding pairs in 1977 (Voslamber 2002) to about 25 000 in 2005 (<www.sovon.nl>) with a yearly increase of about 20% after 2000. Forelands including scour hole and sand pit margins are now intensively grazed by geese in summer and autumn, probably resulting in an intensified dispersal of *Ephemerum*.

We do not know how old the recently discovered populations are. The largest Huissen locality was discovered in 2004 when *Ephemerum* already occupied all potential habitats. This 15 m deep scour hole was formed during a catastrophic dike breach in December 1769 when about 70 villages became flooded. The second largest locality is the Haalderen scour hole formed by two consecutive dike breaches in March 1784. The large Kekerdom locality is a bank of a meander cutoff that was enlarged as a sand pit. The only certainly man-made *Ephemerum* habitat is the 20th century sand pit of the Pannerden locality in the Gelderse Poort area (Fig. 5B) where *E. rutheanum* and *E. cohaerens* occur, showing that both species are capable of succesfully occupying new habitat.

The concentration of localities in the eastern reach of the Rhine system (Fig. 1) may be explained by a combination of factors. Firstly, the shallow clay layer covering Pleistocene sands and gravels compared to the downstream area with thick clay layers (Wolfert 2001). Erosion of the shallow clay layer enables the occurrence of sandy soil textures which are an important component of *Ephemerum* habitat. Secondly, the sinuosity of the Rhine tributaries in this area resulted in a wide riverbed and many meander cutoffs and scour holes which are the principal habitat of both *Ephemerum* species. Finally, the increased amplitude of the Upper-Rhine and Middle-Waal in the 20th century compared to the early 1800th century (Middelkoop et al. 2003) due to human impact on the landscape has contributed to the availability of drawdown zones in the river forelands. The former sand and clay pits and scour holes with large populations of *Ephemerum* all rest in sandy subsoil in contact with the groundwater. The groundwater table is strongly influenced by the river water level causing large water table fluctuations as compared to water bodies resting on clay. This habitat therefore is very similar to the drawdown zone of reservoirs.

Natura 2000

Ephemerum cohaerens is considered endangered on the European Red List of bryophytes (ECCB 1995). *Ephemerum rutheanum* can be considered as a European endemic (Holyoak 2010). The recently discovered large persistent populations of these species in inundation zones of the Dutch Rhine floodplain prove Natura 2000 habitat type H7230 'Rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation' a stronghold for these very rare European bryophytes.

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