

# *Eleocharis ovata* and its alien allies in the Netherlands

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## Key words

alien species  
wetlands  
*Eleocharis*  
*Ovatae* series  
cryptic species  
*Eleocharis obtusa*  
*Eleocharis ovata*  
*Eleocharis engelmannii*

**Abstract** – A revision of Dutch herbarium specimens of *Eleocharis* series *Ovatae* shows that two exotic species from North America have also been recorded in the Netherlands since 2011–2012: *Eleocharis obtusa* and *E. engelmannii*. The number of localities of these species is steadily increasing. The native species, *E. ovata*, nowadays only occurs on the Ewijkse Plaat along the River Waal, west of Nijmegen. This population appears to be viable, but it is in a highly dynamic environment close to the river, and might disappear again. The current Red list status 'Sensitive' with trend 'unchanged or increased' is due to confusion with these two exotic species, and may therefore be far too optimistic for this species. Although reported as absent from the Iberian Peninsula, the occurrence of *E. ovata* in Spain is reinstated.

All three species are quite similar in terms of morphology and ecology, but can be distinguished from each other on the basis of the fruits (the width of the persistent stylopodium in relation to the dimensions of the achene), the length of the perianth bristles, the number of stamens and the number of stigmas on the style (2 or 3).

*Eleocharis ovata* seems to be bound to large rivers and occurs in vegetations belonging to the *Bidention tripartitae*, but is also found on loamy to sandy and rather oligotrophic shores of shallow ponds. The two alien species are found in *Bidention tripartitae*, *Nanocyperion flavescens* or *Littorelletea uniflorae* vegetations, or transitions between them, but the information on habitats for these two species is limited. For the time being they seem to be bound to slightly poorer soils than *E. ovata*.

**Samenvatting** – Na een revisie van het Nederlandse herbariummateriaal van de *Eleocharis Ovatae* serie blijken twee uit Noord-Amerika afkomstige exotische soorten, die recent gemeld zijn voor België, sinds 2011–2012 ook aanwezig in Nederland: *Eleocharis obtusa* en *E. engelmannii*. Het aantal vindplaatsen van deze soorten neemt gestaag toe. De inheemse soort, *E. ovata* (Eivormige waterbies), komt nogal onbestendig voor, en is momenteel alleen nog aanwezig op de Ewijkse Plaat, in de Waal ten westen van Nijmegen. Deze populatie lijkt levensvatbaar, maar bevindt zich wel in een hoog dynamisch milieu, en zou dus ook snel weer (bovengronds) kunnen verdwijnen. De huidige status 'Rode Lijst – Gevoelig', met trend 'onveranderd of toegenomen' komt voort uit verwarring met de twee exoten, en is dan ook veel te optimistisch voor deze soort. In de loop van ons onderzoek stuiten we ook op een collectie van *E. ovata* uit Spanje. Hiermee hebben we kunnen vaststellen dat de soort, in tegenspraak met moderne literatuur, ook voorkomt op het Iberisch schiereiland.

De soorten lijken nogal op elkaar, maar kunnen worden onderscheiden op grond van de vruchten (de breedte van de persistente stijlvoet ten opzichte van de rest van het nootje), de lengte van de perigoonborstels, het aantal meeldraden en het aantal stempels (2 of 3).

*Eleocharis ovata* lijkt vooral gebonden aan grote rivieren en komt daar voor in het *Bidention tripartitae*, maar is vroeger ook aangetroffen op lemige tot zandige en wat schralere venoevers. De twee uitheemse soorten zijn, voor zover er gegevens op de herbariumcollecties zijn genoteerd, aangetroffen in vegetaties die behoren tot de verbonden *Bidention tripartitae*, *Nanocyperion flavescens* of *Littorelletea uniflorae*.

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## INTRODUCTION

*Eleocharis* R. Br. (Cyperaceae) is a genus comprising about 250 species (Govaerts et al. 2007), with a more or less worldwide distribution, having the largest concentration of species in the New World. The Flora of North America reports 67 species (Galen Smith et al. 2002), whereas only a small number of species is recognized in Europe. Walters (1980) reports 15 species and Jiménez-Mejías & Luceño (2011) recognize 17, of which 4 introduced. Six taxa have been recorded in the Netherlands (Reichgelt 1956, van der Meijden 2005).

*Eleocharis* is characterized by several morphological reductions. The plant consists of a cluster of unbranched stems, each terminating in an inflorescence consisting of a single spike (called 'spikelet' in almost all literature on this genus). Leaves are reduced to tubular basal sheaths, which occasionally bears a tiny blade. Despite the overall morphological simplicity, there is significant variation within the genus regarding how this reduced morphology is shaped and organized. Hence, most taxa are distinguished based on a limited number of characters.

Infrageneric classification has been complex, with subdivision into sections or subgenera, sometimes including series of which some are even divided into subseries (Svensson 1929, 1932, 1934, 1937, 1939, and later González-Elizondo & Peterson 1997). Many of those groups turned out to be non-monophyletic (Roalson et al. 2010). No infrageneric taxa have been mentioned in the Flora Europaea (Walters 1980), or in standard works for the Netherlands (van der Meijden 2005, Reichgelt 1956).

*Eleocharis* series *Ovatae* Svenson (in subgenus *Eleocharis*, section *Eleogenus* (Nees) Benth. & Hook. f.) is a well-supported clade nested in a badly resolved clade on the (sub)section level (Roalson et al. 2010).

*Eleocharis* series *Ovatae* comprises six species, of which five are restricted to North-America and one can be considered a circumboreal species (Galen Smith et al. 2002). They are wetland species, generally caespitose annuals with a fibrous root system. However, in North-America plants have been observed with ascending rhizome-like roots, and it seems likely that such plants survive the winter (Galen Smith et al. 2002). All species have brown, smooth, biconvex achenes, with compressed stylopodia (also called 'tubercles'), and a base chromosome number of  $n = 5$ . Stylopodium base dimensions and perianth bristle characters are taxonomically the most important and reliable. Stamen and stigma numbers are difficult to observe and are often variable within species. Information on style dimensions or illustrations of styles are absent from modern treatments. The style is caducous and specimens are usually collected and identified with ripe fruits, and hence without styles. Anthers are often caducous, and the remaining filaments are often not easily distinguished from the perianth bristles.

Until recently, the only known species of *Eleocharis* series *Ovatae* in the Netherlands was *E. ovata* (Roth) Roem. & Schult. (Reichgelt 1956, as *E. soloniensis* (Dubois) H. Hara). It has always been an extremely rare ephemeral species in the Netherlands, appearing on muddy, loamy or clayey shores of rivers, former river branches, fens and ponds. The first herbarium specimen of *E. ovata* dates from 1848, collected by T.H.A.J. Abeleven near Weurt, in the Province of Gelderland, on the banks of the River Waal. From the 1850s onward, however, the large rivers in the Netherlands were 'normalized' (van Heezik 2007), resulting in a drastic reduction of suitable habitats (muddy banks) for this species. This could explain the rarity of this species ever since, as the bottoms of temporarily drained fishponds, another important habitat for annual wetland species in Europe (Prach et al. 1987,

Deil 2005), are hardly present in the Netherlands. After more than a century and a half, in 2012, the species was found again close to the aforementioned locality on the 'Ewijkse Plaat', the location of a river wetland restoration project by E. Slootweg. This population is probably not older than a few decades, as local works for nature restoration were carried out in 1989. Before that year, suitable habitat was probably not available. Collections of other populations in the Netherlands have been made at three other localities in Middle-Limburg and in the Sliedrechtse Biesbosch (Province of Zuid-Holland) between 1994 and 2002. At two out of those three localities, wetland restoration by means of topsoil removal had taken place, resulting in ephemeral pioneer communities. Hitherto, in total only 11 herbarium collections from 4 Dutch localities are known. The population on the Ewijkse Plaat, estimated to consist of up to 40 plants (waarneming.nl), seems to be the only extant one in 2018, with no records in 2019.

However, from 2011 onwards, some new populations of *Eleocharis ovata* were reported from Friesland, eastern Noord-Brabant and northern Limburg, away from the known localities and in different, non-fluvial habitats. Since Verloove (2015) recorded two closely related species of North American origin of this series in Belgium (*Eleocharis obtusa* (Willd.) Schult. and *E. engelmannii* Steud.), the identity of those new populations in the Netherlands aroused suspicion to us and other Dutch botanists. After examination of herbarium specimens in L and WAG (herbarium acronyms follow Thiers (2019+)) and some field work, the aforementioned North American species turned out to be present in the Netherlands as well. What turned out to be the first Dutch specimen of *E. obtusa* was collected by H. J. Jager in 2011 near Drachten (Province of Friesland) and a year later, J.H.P. Bruinsma collected the first Dutch specimen of *E. engelmannii* Steud. at Son (Province of Noord-Brabant). At present, there are four populations for each of these two non-native species (Fig. 1).

## RECOGNITION, DISTRIBUTION AND ECOLOGY OF THE SPECIES

*Eleocharis ovata* (Roth) Roem. & Schult., *Systema Vegetabilium* 2, ed. 15 [= ed. 16]: 152. 1817.

Basionym: *Scirpus ovatus* Roth, *Tent. Fl. Germ.* 2(2): 562. 1793; *Catal. Bot.* 1: 5. 1797.

*Scirpus soloniensis* Dubois, *Meth. Eprov.*, ed. 2: 249. 1833. – *Eleocharis soloniensis* (Dubois) H. Hara, *J. Jap. Bot.* 14: 338. 1938.

*Eleocharis ovata* (Roth) Roem. & Schult. var. *heuseri* Uechtr., *Jahresber. Schles. Ges. Vater. Cult.* 44: 80. 1866.

Therophyte. Caespitose herb, culms ascendant (previously treated as var. *heuseri* Uechtr.) to erect, 5–24 cm tall, 0.3–0.9 mm wide, round to subcompressed, shallowly ridged, glabrous, light green. Fibrous roots, rhizomes absent. Leaf sheaths 1–3, light brown to orangish red (at base), distal leaf sheath 0.6–3.2 cm, apiculate to mucronate (rudimentary leaf lamina).

Inflorescence a single spike, ovoid to ovoid-globose 2.5–10 × 1.5–4 mm; densely flowered, apex blunt to obtuse. Basal 2 glumes empty; basal most glume subamplexicaul; fertile glumes ovate, c. 1.5 × 0.5 mm, apex acute to obtuse, membranous, abaxially green when young, turning dark brown to blackish brown when ripe, darker than in *E. obtusa* and *E. engelmannii* (Fernald 1899), adaxially blood-red to purple, margin narrowly hyaline. Perianth bristles 6, c. 1.5 × as long as achene (including stylopodium), retrorsely spinulose. Stamens 2, anthers c. 0.5 mm.

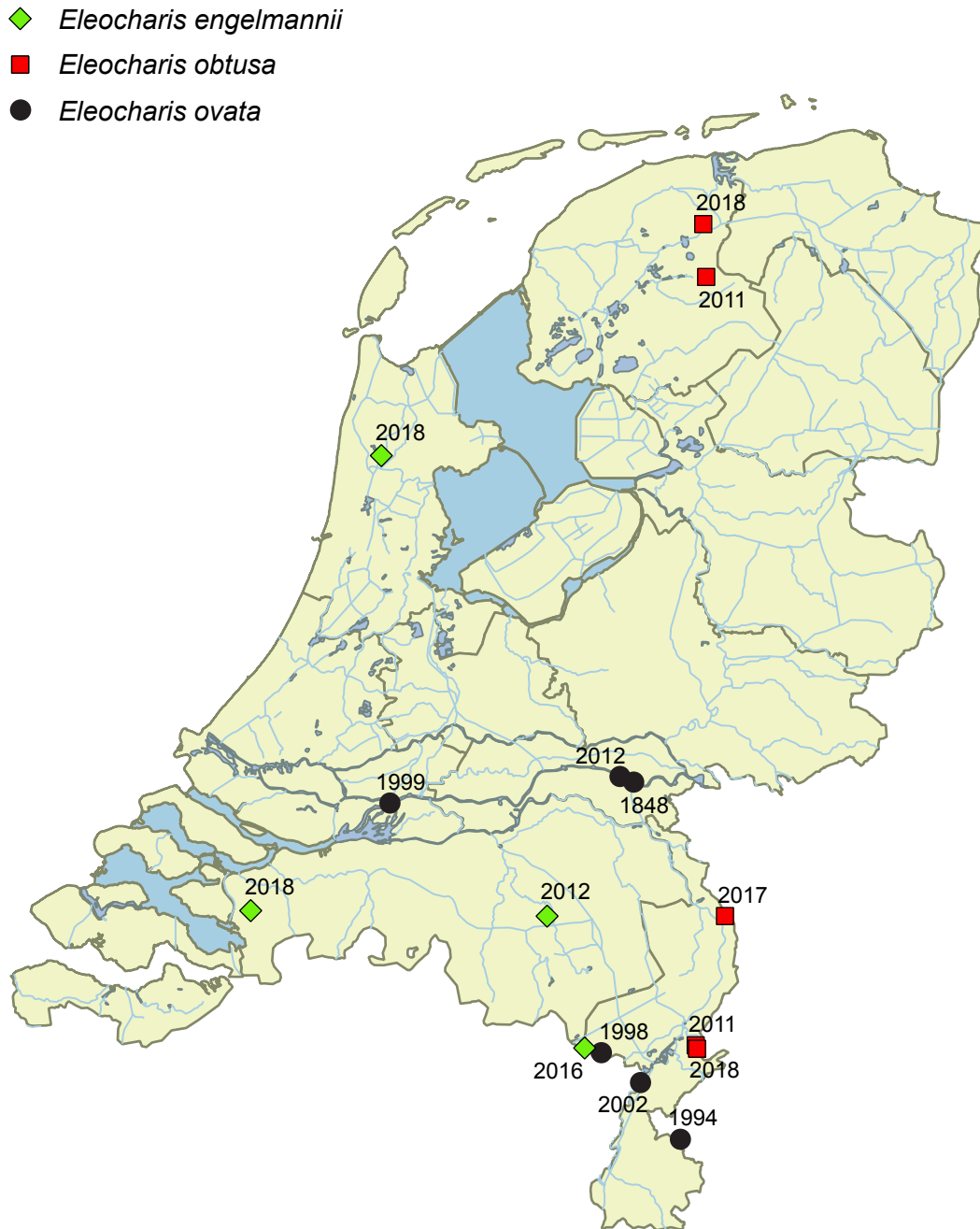


Fig. 1. Distribution map of the three species belonging to *Eleocharis* R.Br. series *Ovatae* Svenson in the Netherlands based on herbarium specimens preserved in the herbarium of Naturalis Biodiversity Center (L and WAG). The localities are labelled with collection year of the specimens. The herbarium specimens were georeferenced and the information was entered into the Naturalis database BRAHMS.

Style 2-branched. No information on style dimensions is known from literature, but Fig. 2 shows a bifid style of approximately the same length as an unripe achene (unfortunately, in our herbarium specimens, no styles were present). Achene biconvex, white when unripe, but turning glossy brown at maturity, obovoid, c.  $0.8 \times 0.5$  mm, smooth; stylopodium deltoid in side view, when ripe c.  $1/3$  as long and c.  $1/2$  as wide as achene, dorsiventrally compressed, apex acuminate. Fl. and fr. July–October. — Fig. 2.

Chromosome number:  $2n = 10$ .

Habitat — Pioneer vegetations on sandy, loamy or more often clayish soil of shallow ponds, fens and lakes falling dry (late) in the summer. In the Netherlands, it has predominantly been

found in eutrophic environments, in vegetations belonging to the *Bidenton tripartitae*, sometimes with *Nanocyperion flavescens* elements. However, a collection from Schinveld/Russcherbeek (*van Moorsel s.n.* (L) describes a loamy sandy soil with *Juncus bulbosus* L., *J. articulatus* L., *Baldellia ranunculoides* (L.) Parl., *Agrostis stolonifera* L., *Potamogeton pusillus* L. and *Alisma plantago-aquatica* L., clearly indicating more meso- or oligotrophic conditions. In Central Europe, the species is often found in vegetation on fishpond bottoms with a species composition that can be classified as the *Eleocharition ovatae* (Šumberová & Lososová 2011).



Fig. 2. *Eleocharis ovata* (Roth) Roem. & Schult., Ewijkse Plaat (Province of Gelderland), 2012. Left: habit. Right: (unripe) achenes. Photos: Erik Sloomweg.

**Distribution** — More or less circumboreal. Europe, but absent from Great Britain and Ireland, and Fennoscandia. According to Jiménez-Mejías & Luceño (2011) it is present in Malta and Albania. However, the only record from Malta (Gozo Island) in the Dutch herbaria we found (K. U. Kramer & L. Y. T. Westra 5352, U [U.1239312]), proved to be a very caespitose form of *E. palustris* (L.) Roem. & Schult., possibly other such collections from Malta have also been mistaken for *E. ovata*. According to Jiménez Mejías & Luceño (2008) the species does not occur in the Iberian Peninsula, but we found at least two specimens belonging to *E. ovata* from Spain: *Eliás s.n.* (U [U.1239311]) from Buggedo in Castilla y León and *Merino s.n.* (U [U.1239315]) from La Guardi de Pontevedra in Galicia, on the shore of the river that forms the border with Portugal, making it likely it can be found in Portugal as well. Further distribution — Japan, Kazakhstan, Russia (Lunkai & Strong 2010), Canada, USA (Galen Smith et al. 2002).

**Distribution in the Netherlands** — Province of Gelderland: First record for the Netherlands collected in Weurt, close to Nijmegen by Abeleven in 1848 (see Appendix). Since 2012, a more or less stable population at the 'Ewijkse Plaat'. Province of Limburg: Russcherbeek, Areven and several collections from the Stevolplas, close to the River Meuse. Province of Zuid-Holland: A single collection from the Biesbosch (Rhine & Meuse estuaries), first recorded and collected by A. Boesveld in 1999 and probably present there until 2009. We doubt the species can quickly reappear there. No information on seed longevity of this species is present in the LEDA plant trait database (Kleyer et al. 2008), but the data of other species of *Eleocharis* that are present, suggest that the seedbank is transient.

Most localities are situated in the Meuse-Rhine river corridor, connecting the Netherlands, as an 'outpost', to the Central- and West-European distribution area.

According to Sparrus et al. (2014), the Dutch Red List status for this species is 'gevoelig' ('Near Threatened', following IUCN terminology). At the time the Red List was constructed, the number of records was overestimated, because the records of the non-native species *Eleocharis obtusa* and *E. engelmannii* had been identified as *E. ovata*.

Given that the species is extremely rare (known from just one locality) and ephemeral in the Netherlands, and declining in many parts of Europe, the status Critically Endangered would make more sense in a next edition of the Dutch Red List. Apart from that, there is a possibility that the non-native congeners could outcompete *Eleocharis ovata*.

***Eleocharis engelmannii* Steud., Synopsis Plantarum Glumacearum 2: 79. 1855.**

*Eleocharis ovata* (Roth) Roem. & Schult. var. *engelmannii* (Steud.) Britton, J. New York Microscop. Soc. 5: 103. 1889.

*Eleocharis obtusa* (Willd.) Schult. var. *engelmannii* (Steud.) Gilly, Iowa State Coll. J. Sci. 21: 92. 1946.

*Eleocharis engelmannii* Steud. var. *detonsa* A. Gray ex Patt., Cat. Pl. Illinois: 46. 1876.

*Eleocharis engelmannii* Steud. f. *detonsa* (A. Gray ex Patt.) Svenson, Rhodora 31: 208. 1929.

*Eleocharis ovata* (Roth) Roem. & Schult. var. *detonsa* (A. Gray ex Patt.) Mohlenbr., Ill. Fl. Illinois, Sedges: Cyperus to Scleria, ed. 2: 195. 2001.

*Eleocharis monticola* Fernald, Proc. Amer. Acad. Arts 34: 496, f. 45–50. 1899.

Therophyte. Caespitose herb, culms erect, 10–24 cm tall, 0.8–2.2 mm wide, round to subcompressed, shallowly ridged, glabrous, light green. Fibrous roots, rhizomes absent. Leaf sheaths 1–3, deep purple red (at base), distal leaf sheath up to 4 cm, apiculate to mucronate (rudimentary leaf lamina).

Inflorescence a single spikelet, ovoid to ovoid-cylindric 4–18 × 2–4 mm; densely flowered, apex bluntly acute to obtuse. Basal 2 glumes empty; basal most glume subamplexicaul; fertile glumes ovate, c. 1.5 × 0.5 mm, apex acute to obtuse, membranous, abaxially green when young, turning dark brown when ripe, adaxially blood red-purple, margin narrowly hyaline. Perianth bristles 6, c. as long as achene (including stypodidium) or shorter, or absent (hence the variation/forma 'detonsa'), retrorsely spinulose.

Stamens (2–)3, anthers c. 0.5 mm. Style (2–)3 branched. Achene biconvex, white when unripe, but turning glossy brown at maturity, obovoid, c. 1 × 0.8 mm, smooth; stylopodium deltoid in side view, when ripe about as wide as achene, c. 0.2 × 0.8 mm, dorsiventrally compressed, apex acuminate. Fl. and fr. July–December. — [Fig. 3](#).

Chromosome number: 2n = 10.

Habitat — Pioneer vegetations on sandy or loamy soil of shallow ponds, fens and lakes falling dry (late) in summer. The plants in Heerhugowaard were found in a new residential area, in disturbed soil near a recently excavated ditch. Not much is known yet on the phytosociological position of this species in the Netherlands. The label of *Simons & Gonggrijp 2121* (WAG), indicates *Lythrum portula* (L.) D.A. Webb, *Isolepis setacea*, *Callitriche brutia* (L.) R.Br., *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zák., *Scirpus georgianus* R.M. Harper, *Typha latifolia* L., and *Carex scoparia* Willd. as accompanying species.

Distribution — Canada, USA ([Galen Smith et al. 2002](#)). In Europe now recorded from Belgium, The Netherlands, and Germany ([Plieninger 2001](#), [Verloove 2015](#)), but possibly overlooked elsewhere.

Distribution in the Netherlands — First record for the Netherlands is a collection made by J.H.P. Bruinsma in 2012 in Son, north of Eindhoven, Province of Noord-Brabant (*Bruinsma s.n.*, L [L.2058156]). The first and the third authors collected the species at or very close to the same location in 2017. They described the location on the label of the aforementioned collection *Simons & Gonggrijp 2121* as a former military terrain which has become a suburban village. In 2018, W. Lammers found the species near Halsteren, which is also located in the Province of Noord-Brabant, but more than 100 km west of Son. In 2016, T.O.V. Muusse found the species close to Weert in the Province of Limburg, c. 50 km southeast of Son. The most recent find was made by the third author and the local group of the Dutch Association of Field Biology (KNNV Alkmaar–Den Helder) in Heerhugowaard, Province of Noord-Holland, c. 160 km northwest of Son.

Two of the accompanying species annotated on the label of *Simons & Gonggrijp 2121*, *Scirpus georgianus* and *Carex scoparia*, are species native to (Eastern) North America. The presence of three North American species at the locality in Son

points towards a common introduction pathway. *Scirpus georgianus* and *Eleocharis engelmannii* could have been introduced in Europe by military troops ([Plieninger 2001](#), [Verloove 2015](#), [2019](#)). This is most likely the case here, because the locality is situated on a former military terrain and there has been a lot of military activity in the Eindhoven area since the Second World War. Introduction by military activity might also be the case for the two other localities in the southern part of the Netherlands where *E. engelmannii* occurs. However, introduction by military troops is unlikely for the occurrence in Heerhugowaard. Possible introduction pathways to this locality could have been the transportation of seeds by human-transported soil or dispersal of seeds by birds (avichory).

Note — The absence, reduction, or caducity of perianth bristles and / or the absence of spines on bristles is supposed to be an adaptation to tidal environments for some Cyperaceae formerly placed in *Scirpus* ([Schuyler 1972](#), [Strong 1994](#)). This is true for *Eleocharis diandra* C. Wright and *E. aestuum* Hines ex A. Haines, but *E. mutata* (L.) Roem. & Schult., often occurring on tidal mud flats has robust and spiny bristles. *Eleocharis engelmannii*, a species that also has more or less reduced perianth bristles, could hardly be considered having a tidal ecology, rendering the relation between the habitat and the reduction of bristles highly questionable.

***Eleocharis obtusa* (Willd.) Schult., Mant. 2: 89. 1824.**

Basionym: *Scirpus obtusus* Willd., Enum. Pl. 1: 76. 1809.

Therophyte. Caespitose herb, culms ascendant to erect, 10.5–24 cm tall, 0.8–0.9 mm wide, round to subcompressed, shallowly ridged, glabrous, light green. Fibrous roots, rhizomes absent. Leaf sheaths 1–3, deep purple red (at base), distal leaf sheath 2.5–4.0 cm, apiculate to mucronate (rudimentary leaf lamina).

Inflorescence a single spikelet, ovoid to ovoid-cylindric 4–9 × 2–4 mm; densely flowered, apex blunt to obtuse. Basal 2 glumes empty; basal most glume subamplexicaul; fertile glumes ovate, c. 1.5 × 0.5 mm, apex acute to obtuse, membranous, abaxially green when young, turning dark brown when ripe, adaxially blood red-purple, margin narrowly hyaline. Perianth bristles 6, c. 1.5 × as long as achene (including stylopodium), retrorsely spinulose.



Fig. 3. *Eleocharis engelmannii* Steud. Left: habit at Son (Province of Noord-Brabant), 2017. Right: (unripe) achenes, Heerhugowaard (Province of Noord-Holland), 2018. Photos: Sipke Gonggrijp.



Fig. 4. *Eleocharis obtusa*. (Willd.) Schult. Left: habit at De Hamert - Nieuwe Heerenven Zuid (Province of Limburg), 25-08-2017. Right: achene at Boukoul (Province of Limburg), 21-08-2013. Photos: Nick van der Ham (left), Sipke Gonggrijp (right).

Stamens (2–)3, anthers c. 0.5 mm. Style with (2–)3 branches. Achene biconvex, white when unripe, but turning glossy brown at maturity, obovoid, c. 0.8 × 0.5 mm, smooth; stylopodium deltoid in side view, when ripe c. 1/3 as long and c. 1/2 as wide as achene, dorsiventrally compressed, apex acuminate. Fig. 4. Fl. and fr. July–October. — Fig. 4.

Chromosome number: 2n = 10.

Habitat — Pioneer vegetations on sandy, loamy soil of shallow ponds, fens and lakes falling dry (late) in summer. All localities are nature restoration projects. At present, not much is known about the ecology of this species in the Netherlands, but this species seems to be more restricted to mesotrophic and oligotrophic environment than *Eleocharis ovata*. The latter species has been recorded in oligotrophic, mesotrophic, and eutrophic environments. *Simons et al. 2083* (WAG) mentions: ‘Muddy shore of pond falling dry in (late) summer, on loamy more or less oligotrophic soil, rich in sulphate. Together with *Nanocyperion* species

(*Cyperus fuscus* L., *Juncus bufonius* L. (= *J. ranarius* Songeon & E.P. Perrier), *Gnaphalium luteo-album* L.), *Bidention tripartitae* species (*Bidens radiata* Thuill., *B. tripartita* L., *Persicaria* species, *Rumex maritimus* L.), and *Littorelletea* species (*Elatine hexandra* (Lapierre) DC., *Eleogiton fluitans* (L.) Link (= *Isolepis fluitans* (L.) R.Br.), *Baldellia ranunculoides* subsp. *ranunculoides*.’ In Italy, the species has become naturalised and grows as a weed in rice fields (Koch 1952, Pignatti 1982).

Distribution — Canada, USA, Hawaii included (Galen Smith et al. 2002). Europe: Italy (Koch 1952, Walters 1980), Switzerland (Desfayes 2007), Belarus (Dzhus 2014), and Belgium (Verloove 2015).

Distribution in the Netherlands — The first record for the Netherlands was collected by H.J. Jager, who found the species close to Drachten (Province of Friesland) in August 2011. Later in this year it was found in Swalmen (Province of Limburg). So far, the species has only been found in these two provinces. The localities in Limburg are in proximity to the Meuse valley, but are not

Table 1. Diagnostic characters of the three *Eleocharis* species treated in the present study. The symbol # means ‘number (of)’.

species	stylopodium			# stigmas	# stamens	length of perianth bristle	colour of basal leaf sheaths	habit
	shape	width (in mm)	width / achene width					
<i>E. ovata</i>	deltoid, equilateral in side-view	0.3–0.5	2/3	2	2	greatly exceeding achene length (1.5 x)	light brown-orange	thin slender stems
<i>E. obtusa</i>	wider than high	0.5–0.9	7/10–9/10	(2–)3	(2–)3	exceeding achene length	(wine-)red	thick erect stems
<i>E. engelmannii</i>	much wider than high, depressed	0.5–0.9	9/10	(2–)3	(2–)3	at most equaling stylopodium length; some perianths absent	(wine-)red	stout plant with thick erect stems

situated in the river bed or on river deposits. The localities in Friesland are not close to any (large) river system.

There are several possible pathways of introduction for new populations of *Eleocharis obtusa* in Europe and the Netherlands. First, around military bases, introduction could have been by unintentional transport of achenes by persons and vehicles. This process may be 'ongoing'. For example, in Belgium, the species mostly occurs in areas that are, or have been used as, military training areas (Verloove 2015). In the Elsenborn Military Camp *Eleocharis obtusa* was accompanied by, among other species, the North American *Scirpus georgianus* (Lambinon & Mause 2010), the same species that was found at the *E. engelmannii* locality at Son.

A second option is transport of seeds or viable plant parts with plant or soil material for commercial trade. In Belarus, *Eleocharis obtusa* was found in cranberry plantations (Dzhus 2014), where it was found growing together with other (invasive) species originating from North America. These plantations were planted with cranberry (*Vaccinium macrocarpon* Aiton) imported from Wisconsin, USA, in the 1980s. It is beyond doubt that *E. obtusa* and the other North American species have unintentionally been introduced in these plantations by the import of cranberry planting stock. The population of *E. obtusa* in Swalmen is close to a *V. corymbosum* farm. *Vaccinium corymbosum* L. is also native to North America and it is almost certain that also in this case *E. obtusa* was introduced by importing North American planting stock.

A third option is hydrochory and/or avichory, a more natural way of seed dispersal by water or birds from other European populations. For the Netherlands, this is likely the case for the populations in Limburg, which are situated more or less close to the River Meuse. These populations may originate from populations of *Eleocharis obtusa* that occur in the northeastern part of Belgium close to the Belgium/Dutch border in Limburg (Verloove 2015).

### KEY TO THE THREE ELEOCHARIS SPECIES

The key to the three *Eleocharis* species treated in the present study is based on the keys by Galen Smith et al. (2002), Verloove (2015), and the examination of Dutch herbarium specimens. The diagnostic characters are listed in Table 1.

1. Stylopodium about as wide as achene, 0.5–0.9 mm wide. Basal leaf sheaths red to wine red. Culms erect, 0.8–2 mm wide, often robust, 10.5–23 cm tall. Stamens predominantly 3. Styles predominantly 3-branched ..... 2
1. Stylopodium about 2/3 as wide as achene or less, 0.3–0.5 mm wide. Basal leaf sheaths light brown to orange. Culms ascendant to erect, up to 0.9 mm wide, often slenderer, 5–24 (–35) cm tall. Stamens predominantly 2. Styles 2-branched ..... *Eleocharis ovata*
2. Stylopodium 1/3–1/2 as long as achene, at least 2/3 as long as wide. Perianth bristles exceeding stylopodium in length ..... *Eleocharis obtusa*
2. Stylopodium at most 1/4 as long as achene, 1/10–2/5 as long as wide. Perianth bristles at most equally long as stylopodium, or (partially) absent ..... *Eleocharis engelmannii*

### REMARKS

The presence of two alien species of the *Eleocharis* series *Ovatae* from North America raises the question whether other species belonging to this North American group (see Fernald 1899, Galen Smith et al. 2002, Svensson 1929) could emerge in Europe as well. They are:

- *Eleocharis diandra* C. Wright occurs in northeastern North American lakeshores and estuaries. The species resembles *E. ovata* in having 2 stamens, bifid styles, and a depressed stylopodium, which is 1/3–1/2 as long as wide and less than 2/3 as wide as the achene. It differs from *E. ovata* by its reduced perianth bristles.
- *Eleocharis aestuum* Hines ex A. Haines resembles *E. diandra* and has an almost identical distribution, but differs in morphology in having no or only 2–4 perianth bristles, non-depressed stylopodia, and stramineous or whitish achenes (Haines 2001).
- *Eleocharis lanceolata* Fernald from the southern states in the Mississippi Basin, Texas, and California, resembles *E. engelmannii* and *E. obtusa*, but differs from these species in having slender, almost capillary culms, acuminate-lanceolate spikes, and elongated stylopodia.

Of these three species, *Eleocharis lanceolata* seems to be confined to warmer climates than the North-West European climate. In their areas of origin, *E. diandra* and *E. aestuum* grow in similar climates as occurring in North-West Europe, but these two species are quite rare in North America (Haines 2001).

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## Appendix

### Herbarium specimens examined

The herbarium specimens that were examined for this study are listed below.

Herbarium acronyms are according to [Thiers \(2019+\)](#). The abbreviation 's.n.' stands for 'sine numero', i.e. specimens without a collection number.

*Eleocharis ovata* — *R.C.M.J. van Moorsel s.n.* (L), 10-9-1994. Ruscherbeek. 50°58.8' N, 5°59.8' E; *E.L.A.N. Simons 921* (WAG), 19-7-2012. East of Ewijk. 51°52.62' N, 5°46.08' E Alt: 12m; *R. Barendse s.n.* (L), 0-8-1998. Het Areven, bij Stamproy. 51°11.70' N, 5°41.44' E; *A. Boesveld s.n.* (L), 30-9-1999. Sliedrechtse Biesbosch. 51°48.69' N, 4°51.07' E; *R. Barendse 1630* (L), aug-1998. Het Areven bij Stamproy. 51°11.70' N, 5°41.44' E; *T.H.A.J. Abeleven 1116* (L), 0-10-1848. Waaloever te Weurt bij Nijmegen. 51°52' N, 5°49' E; *J. Klinckenberg s.n.* (L), 19-8-2002. Stevensweert: Maasplas. 51°07.29' N, 5°50.62' E; *E.L.A.N. Simons 2101* (WAG), 14-10-2017. Ewijkse Plaat, close to Beuningen. 51°52.64' N, 5°46.06' E; *E.J. Slootweg s.n.* (L), 19-7-2012. Beuningen, uiterwaarden. 51°52.65' N, 5°46.07' E; *G.M. Dirkse 8548* (L), 27-7-2012. Beuningse uiterwaarden. 51°52.65' N, 5°46.07' E; *E.J. Weeda s.n.* (L), 5-9-2002. Midden-Limburg, Stevensweert, bij Molenveld. 51°07.3' N, 5°50.6' E.

*Eleocharis engelmannii* — *J.H.P. Bruinsma s.n.* (L), 4-12-2012. Son, waterberging Sonniuspark. 51°31.91' N, 5°28.74' E; *E.L.A.N. Simons 2121* (WAG), 4-11-2017. Son, Sonniuspark. 51°31.91' N, 5°28.74' E; *T.O.V. Muusse s.n.* (WAG), 3-9-2016. SW of Weert, Weert - Kettingdijk. 51°12.45' N, 5°37.54' E; *W. Lammers s.n.* (L, WAG), 2-7-2018. Halsteren - Het Laag. 51°32.43' N, 4°18.27' E; *S. Gonggrijp 226* (L), 28-8-2018. Heerhugowaard. 52°40.08' N, 4°48.46' E.

*Eleocharis obtusa* — *E.J. Weeda s.n.* (L), 20-9-2011. Swalmen, Blankwater. 51°12.66' N, 6°03.78' E; *H.J. Jager s.n.* (L), 31-8-2011. Azeven. 53°06.5' N, 6°08.1' E; *E.L.A.N. Simons 2083* (WAG), 18-8-2017. East of Wellerlooi, Hamert, Nieuwe Heerenven. 51°31.77' N, 6°11.02' E; *J. Huizenga s.n.* (L, WAG), 18-6-2018. Twijzelmieden, between Buitenpost and Twijzel. 53°14.32' N, 6°07.53' E; *N. Eimers s.n.* (L), 27-8-2018. Asenray - Elmpterbroek 51°12.14' N, 6°04.08' E.