

# Revision of *Bolboschoenus* (Asch.) Palla (Cyperaceae) in the Netherlands

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## Revision of *Bolboschoenus* (Asch.) Palla (Cyperaceae) in the Netherlands

In the last decades, Van der Meijden's editions of the Heukels' Flora recognized only a single taxon in the '*Bolboschoenus maritimus* group' for the Netherlands: *Bolboschoenus maritimus* (L.) Palla, formerly known as *Scirpus maritimus* L. This is probably because the previously recognized infraspecific taxa were solely based on inflorescence architecture. These characters, however, vary between and within populations, and even within clones or individuals. However, in Central Europe the study of a new character, pericarp morphology, resulted in new insights in the taxonomy of the '*Bolboschoenus maritimus* group'. A species new to science, *B. laticarpus* Marhold, Hroudová, Ducháček & Zák., has been reported to occur in the Netherlands as well.

In this study, we aimed at unravelling the occurrence, the distribution and the ecology of this new species. We studied herbarium collections, in situ populations and database records in order to make a revision of *Bolboschoenus* (Asch.) Palla in the Netherlands. We addressed possible ecological explanations for the distribution of the species found in this study by measuring dispersal traits of achenes as a proxy for differences in dispersal ecology.

We found that *Bolboschoenus laticarpus* is common and widespread in the Netherlands, and that it is the dominant species of the genus in inland freshwater fluvial systems. All other specimens belonged to *B. maritimus*, which still showed considerable morphological variation. However, we do not wish to re-establish formerly used taxonomic ranks at the infraspecific level to classify this variation. Achene traits indicated that both species are readily dispersed by hydrochory and endozoochory, but this cannot explain the differences in distribution in the Netherlands.

We provide a key for the genus *Bolboschoenus* in the Netherlands and present a distribution maps, illustrations and photos of both species. We discuss the phytosociological implications of our research based on literature and vegetation relevés with *B. laticarpus*. All revised herbarium specimens are listed in an appendix.

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## Revisie van *Bolboschoenus* (Asch.) Palla (Cyperaceae) in Nederland

Deze studie tracht inzicht te geven in de taxonomie, verspreiding en ecologie van de *Bolboschoenus maritimus*-groep, naar aanleiding van nieuwe inzichten in de taxonomie van deze groep eind jaren 90 van de vorige eeuw en de eerste 10 jaren van deze eeuw. Hiertoe hebben we herbariummateriaal van Nederlandse planten gerevisieerd. Tevens bekeken we in situ populaties om de ecologische en plantensociologische positie van met name *Bolboschoenus laticarpus* te bepalen.

Heen, vroeger ook wel Zeebies genoemd, is een bijzonder variabele soort. Planten aan de kust zijn vaak robuust, en hebben compacte, bijna hoofdjesachtige bloeiwijzen, al dan niet met een aantal zeer grote aren. In het binnenland komen juist ijlere vormen voor, met schermachtige bloeiwijzen, die bijna doen denken aan een *Cyperus*, of *Mattenbies*. Van natte duinvalleien, met name op de Waddeneilanden, zijn juist zeer kleine planten bekend, met maar één eindlingse bloeiaar, die gemakkelijk te verwarren zijn met soorten als *Stekende bies*, *Rode bies*, *Platte bies*, of zelfs *zeggen*.

In de 19<sup>e</sup> en vroeg 20<sup>e</sup> eeuw werd op grond van de variatie in met name bloeiwijzekenmerken een aantal verschillende ondersoorten, variëteiten, of vormen onderscheiden; de macrostachyate vorm, de compacte vorm, de monostachyate vorm en de typische vorm (Tabel 1). Deze worden in de meest recente bewerking van de Heukels' Flora door Van der Meijden (2005) niet meer erkend. In Nederland wordt de '*Bolboschoenus maritimus*-groep' in de 23<sup>e</sup> editie van de Heukels' Flora gezien als één soort: *B. maritimus* (L.) Palla (voorheen *Scirpus maritimus* L.). Van der Meijden baseerde zich op het van werk van Robertus-Koster in 1969. Zij concludeert dat er weliswaar duidelijke verschillen zijn tussen planten met compacte bloeiwijzen van de kust enerzijds en planten met ijle bloeiwijzen uit het rivierengebied anderzijds, maar ziet deze variatie als clinaal, waarschijnlijk in verband met milieufactoren. Eerder stelde Reichgelt in de bewerking van de Flora Neerlandica (1956), dat de verschillende tot dan toe erkende infraspecificke taxa in feite morfologische variaties zijn, die zijn te vinden binnen één en dezelfde populatie en zelfs binnen één en dezelfde wortelstok.

Sindsdien is er in Nederland geen taxonomisch onderzoek meer geweest aan dit taxon. In de laatste jaren wordt buiten Nederland, met name in Midden-Europa onderzoek gedaan aan de '*Bolboschoenus maritimus*-groep'. In een artikel van Marhold et al. uit 2004 wordt ook een nieuwe soort voor de wetenschap gepubliceerd: *B. laticarpus* Marhold, Hroudová, Ducháček & Zák. Deze auteurs onderzochten niet alleen de ecologie en de morfologie van de bloeiwijzen, maar keken ook naar dwarsdoorsneden van de achenen (nootjes). Op basis van verschillen in pericarp-morfologie kunnen veel duidelijkere scheidingen worden gemaakt binnen taxa in deze groep, dan op basis van bloeiwijze-morfologie alleen. *Bolboschoenus laticarpus* heeft een zwart, scherp driehoekig nootje. Op dwarsdoorsnede is een zeer dun exocarp en een veel dikker mesocarp zichtbaar; het exocarp bestaat uit cellen die nauwelijks hoger dan breed zijn. Bij *B. maritimus* is het nootje bruin en stomp driehoekig tot lensvormig. Het exocarp is zeer dik, en bestaat uit langwerpige aerenchymcellen die veel hoger dan breed zijn. Van *B. laticarpus* wordt door de betreffende auteurs tevens melding gemaakt in Nederland; op grond van één herbariumcollectie in het herbarium van Praag (PRA), afkomstig uit de Millingerwaard.

We wilden nader onderzoek doen naar de precieze verspreiding, biogeografie en ecologie van deze nieuwe soort, ook wilden we onderzoeken of eventueel meer soorten in Nederland voorkomen, zoals *Bolboschoenus yagara* (Ohwi) Y.C. Yang & M.Zhan en *B. planiculmis* (F.Schmidt) T.V.Egorova. We wilden onderzoeken of de grote variatie in 'Heen' in Nederland, die door Reichgelt en Robertus-Koster als infraspecifiek of clinaal werden beschouwd, op grond van nieuwe inzichten in de *Bolboschoenus maritimus* groep nu beter te classificeren valt.

Hiertoe hebben we alle herbariumcollecties in het Nationaal Herbarium te Leiden, en in een aantal kleinere herbaria onderzocht. We keken hier naar de morfologie van de bloeiwijze en van het pericarp en noteerden tevens gegevens over de locatie en ecologie. Daarnaast hebben we gekeken naar een aantal goed gedocumenteerde records op waarneming.nl, en naar gedroogd materiaal dat door enkele floristen naar ons was opgestuurd. Zie Appendix 1 voor een overzicht van alle gereviseerde collecties. Voorts bezochten we een aantal locaties van met name *B. laticarpus* in het binnenland om goed gedocumenteerd herbariummateriaal te verzamelen en een indruk te krijgen van de ecologie.

We hebben in het laboratorium onderzocht in hoeverre verschillen in dispersievermogen van de achenen de verschillen in ecologie en verspreidingsgebied, zoals we die hebben aangetroffen, zouden kunnen verklaren, met andere woorden: of er behalve een historische/geografische verklaring van het verspreidingspatroon, ook een ecologische factor is. Een soort waarvan de zaden langer kunnen drijven,

zou beter kunnen zijn toegerust op verspreiding via open zee, en een soort met zaden met grotere mechanische weerstand zou beter kunnen zijn toegerust op verspreiding via watervogels en vissen. Het drijfvermogen van achenen van *Bolboschoenus laticarpus*, een soort met relatief kleine aerenchymcellen in het exocarp, bleek veel groter dan in eerdere onderzoeken beschreven. Weliswaar hebben achenen van *B. maritimus* een groter drijfvermogen dan die van *B. laticarpus*, maar geconcludeerd kan worden dat voor beide soorten dispersie middels hydrochorie aannemelijk is. Het drijfvermogen geeft dus geen directe verklaring voor verschillen in verspreidingsgebied en ecologie, maar een hypothese zou kunnen zijn dat in het rivierengebied sneller bij toeval een goede vestigingsplaats wordt gevonden dan aan zee, en dat daarom het drijfvermogen van achenen van *B. maritimus* nog groter is. Ook voor wat betreft de hardheid van de achenen (gemeten als de weerstand tot breken), als indicatie voor het kunnen passeren van het spijsverteringsstelsel van vogels en vissen, is er weinig verschil tussen de twee soorten. Van beide soorten zijn de achenen veel harder dan van de meeste andere waterplanten die zich middels endozoöchorie verspreiden. Dat wil dus zeggen dat ook endozoöchorie een aannemelijke manier van dispersie is voor beide soorten. Andere factoren dan het dispersievermogen van de achenen spelen vermoedelijk een belangrijker rol in het verklaren van verschillen in ecologie en verspreiding, zoals bijvoorbeeld zouttolerantie van *B. maritimus*.

*Bolboschoenus laticarpus* werd door ons in het rivierengebied altijd aangetroffen in de oeverzone van kolken, wielen, nevengulen, grindgaten, en dergelijke, in een zone tussen open water en dichte riet- of lisdoddenmoerassen. De bodem is slibrijk, soms anoxisch, rijk aan ionen en voedingsstoffen en (licht) basisch. Begeleidende soorten zijn vaak andere meerjarige pioniers, zoals *Butomus umbellatus* en *Alisma plantago-aquatica*. In de successie van deze pioniermilieus naar rietmoerassen verdwijnt de soort uiteindelijk. In rietmoerassen kunnen soms nog planten worden gevonden die bijzonder lang en ijl zijn, omdat ze met riet en/of lisdodden concurreren om licht.

De meeste vegetatieopnamen van *Bolboschoenus laticarpus* die we hebben gemaakt, kunnen worden geplaatst binnen de Rietklasse (Phragmiton australis). Binnen deze klasse passen onze opnamen met hoge bedekkingen van *B. laticarpus* het beste binnen het Phalarido arundinaceae-Bolboschoenetum laticarpi, een associatie met begeleidende soorten als *Phalaris arundinacea*, *Alisma plantago-aquatica*, *Persicaria lapathifolia*, *Oenanthe aquatica*, *Lythrum salicaria*, *Phragmites australis*, *Bidens frondosa* en *Persicaria amphibia*. Andere gemeenschappen binnen het Phragmitetea waarbinnen enkele opnamen geplaatst kunnen worden zijn het Sagittario-Sparganietum, de Rompgemeenschap van Phalaris arundinaceae-[Phragmitetalia] en de Rompgemeenschap van Glyceria maxima-[Phragmitetea]. *Bolboschoenus maritimus* is een soort met vergelijkbare ecologie als *B. laticarpus* qua voedselrijkdom en bodemchemie, maar is zouttolerant. Zoutgebonden gemeenschappen met hoge bedekkingen van *B. maritimus* vallen vrijwel altijd binnen het Asteretea tripolii of in zilte overstromingsgraslanden in de Hafdistricten. De populaties van *B. maritimus* aan de inmiddels ontzilte IJsselmeerkust en waarschijnlijk ook de binnenlandse populaties, kunnen vermoedelijk ook worden geplaatst binnen het Phalarido-Bolboschoenetum. In deze associatie in Midden-Europa komen namelijk tot vier verschillende *Bolboschoenus*-soorten voor, waaronder *B. laticarpus* en *B. maritimus*.

Op basis van de analyse van herbariumcollecties en onze veldbezoeken concluderen wij dat *Bolboschoenus laticarpus* in Nederland algemeen en wijdverbreid is. Overal in het huidige stroomgebied van de Rijn, Waal, Merwede, Nederrijn, Lek, Maas en IJssel (het Fluviatiel district), evenals in het stroomgebied van de Oude Rijn en Oude IJssel, is *B. laticarpus* de dominante of meestal enige soort van het genus *Bolboschoenus*. We vermoeden dat deze soort Nederland bereikt heeft via de grote rivieren, omdat de kern van haar verspreidingsgebied in Midden-Europa ligt, en betreffende rivieren daar hun oorsprong vinden. De soort moet op grond van ecologie en biogeografie zeker niet als een nieuwkomer of exoot worden beschouwd, maar als oorspronkelijk inheems, bovendien zijn de eerste herbariumcollecties uit Nederland van deze soort bijna net zo oud als die van *B. maritimus*. Wij stellen als Nederlandse naam voor deze soort de naam 'Oeverbies' voor, deze doet recht aan de ecologische positie en is tevens een reeds in het verleden gebruikte naam. Tevens zou dan overwogen kunnen worden om *B. maritimus* weer 'Zeebies' te noemen, in plaats van 'Heen'.

De resterende collecties/records betreffen allen *Bolboschoenus maritimus*, een soort die duidelijk meer gebonden is aan de Noordzeekust, het estuariënmilieu, de Wadden en de IJsselmeerkust (voormalige Zuiderzee) en in het binnenland zeldzaam is en daar waarschijnlijk als adventief of aangeplant moet worden beschouwd. Deze soort blijft morfologisch zeer variabel; variërend van monostachyate kleine planten in natte duinvalleien, met name op de Waddeneilanden, tot robuuste

en gedrongen *compactus*-vormen en de juist weer schermvormige *maritimus* die bijna doen denken aan *B. laticarpus*. We zien echter geen aanleiding om in het verleden gehanteerde infraspecifieke taxa nieuw leven in te blazen. De tegenwoordig als relevant geziene kenmerken, met name betreffende de morfologie van de achenen, varieert namelijk niet binnen de vroeger gehanteerde infraspecifieke taxa binnen *B. maritimus*. Bovendien zijn er geen echte discontinuïteiten in de variatie in bloeiwijze.

Andere Midden-Europese soorten, zoals *Bolboschoenus yagara* en *B. planiculmis*, werden door ons niet aangetroffen, al denken we dat zeker de eerste soort (op grond van de nabijheid van het natuurlijke areaal) binnenkort zou kunnen opduiken bij (zwak) gebufferde vennetjes en pas geplagde vochtige en lemige pioniermilieus in het (zuid-)oosten van Nederland. Deze soort lijkt sterk op *B. laticarpus*, maar de nootjes zijn symmetrisch driehoekig, het exocarp is dunner en de bloeiwijze oogt 'ijler', omdat het aantal geclusterde aartjes kleiner is (persoonlijke waarneming Erik Simons en Kateřina Šumberová in Tsjechie, zie de collecties *Simons 1964* en *1966*, L en PRA). Zie voor een beschrijving van en een sleutel voor deze soorten onder anderen [Hroudová et al. \(2007\)](#).

In de Biesbosch komen beide soorten voor, vanwege de invloed van zowel de zee als de grote rivieren. Hier zijn planten verzameld met schermvormige bloeiwijzen die aan *Bolboschoenus laticarpus* doen denken, terwijl de morfologie van de achenen toch duidelijk richting *B. maritimus* wijst. Omdat we laatstgenoemd kenmerk als doorslaggevend beschouwen, hebben we ervoor gekozen om planten van deze vorm toch *B. maritimus* te noemen. Er is voor ons geen duidelijke aanleiding om deze planten te beschouwen als hybriden, al is het zeker niet uit te sluiten dat beide soorten wel degelijk zouden kunnen hybridiseren. Chromosoomgetallen van 54 en 55 komen voor bij *B. laticarpus*; bij *B. maritimus* is het aantal vrijwel altijd 55 – hybriden tussen deze twee soorten zouden dus ook met kerngewichtmetingen niet eenvoudig te detecteren zijn. Voor de hand liggende contactzones, waar in theorie hybridisatie zou kunnen optreden, zijn behalve de Biesbosch ook de IJsseldelta en de monding van de Oude Rijn, waar beide soorten naast elkaar (zouden kunnen) voorkomen.

#### *Sleutel voor Bolboschoenus in Nederland*

- 1 Nootje relatief klein, 1–3,7 × 2,0–2,4 mm, zwart tot gitzwart, glimmend, in dwarsdoorsnede driehoekig, met een dun exocarp (<½ dikte van mesocarp) bestaande uit aërenchymcellen van 1 tot 1,5(–2) keer zo lang als breed. Bloeiwijze altijd een symmetrisch scherm met een centrale cluster van aartjes en 3–6 schermstralen van perifere clusters, aartjes doorgaans 10–15 mm lang, zeer zelden tot 30 mm. Schermstralen (2–)3–4(–5) zo lang als de lengte van de aartjes in de centrale cluster. Stengel scherp of afgerond driehoekig, dit al dan niet variërend binnen één plant. Plant 40–120(–180) cm hoog: **Bolboschoenus laticarpus** Marhold, Hroudová, Ducháček & Zákř | Oeverbies

Soort van het binnenland; rivieren, kanalen, kolken, wielen, grindgaten en vergelijkbare milieus. Algemeen in het Fluviaat district, zeer zeldzaam in het Pleistoceen district en het Hafdistrict, behalve in (voormalige) riviersystemen.

- Nootje groter, 3,0–4,0 × 2,1–2,7 mm, min of meer rond, lichtbruin tot donkerbruin, eivormig, lensvormig tot stomp driehoekig in doorsnede (soms met adaxiaal kiel), exocarp >2× zo dik als het mesocarp, bestaande uit een dikke laag van aërenchymcellen, (2–)3–4× zo lang als breed. Bloeiwijze hetzij een enkele aar van 10–15 mm, (hoogte plant dan 10–40 cm, natte duinvalleien), hetzij een hoofdje met vaak macrostachyate aren, hetzij een onregelmatige scherm, met 0–3(–5) gesteelde clusters aartjes, aartjes 10–30(–45) mm lang, schermstralen 0,5–2(–4) zo lang als niet-macrostachyate aartjes in de centrale cluster. Stengel scherp of afgerond driehoekig, dit al dan niet variërend binnen één plant. Plant 40–100 cm hoog: **Bolboschoenus maritimus** (L.) Palla | Zeebies (Heen)

Soort van het kustgebied, zoute gebieden in West-Nederland, zoetwatergetijdengebied, natte duinvalleien, kwelders, inlagen, strandvlakten. Algemeen in het Hafdistrict en de IJsselmeerpolders, zeldzaam en waarschijnlijk adventief of aangeplant in het Fluviaat district en de Pleistocene districten.

## Introduction: taxonomic concepts in the Netherlands and Europe

The genus *Bolboschoenus* (Asch.) Palla (Cyperaceae) comprises 19 accepted species worldwide by current views as reflected by The Plant List 1.1 (The Plant List 2013). The genus has a nearly cosmopolitan distribution, but occurs mainly in moist temperate areas in the northern hemisphere. The distribution map produced from data in GBIF (see [www.gbif.org/species/2718273](http://www.gbif.org/species/2718273), last accessed February 29, 2016) might show a considerable collector's bias; plants of *Bolboschoenus* may have been under-collected in Asia.

In the Netherlands, a small country, the number of records in GBIF is about 32,000, which corresponds to an average of almost 1 record per square kilometer. These Dutch records constitute almost half of the total number of records in the world of this genus. They include about 400–500 herbarium specimens, but mainly consist of records in (botanical) databases like the National Flora and Fauna Database ([www.ndff.nl](http://www.ndff.nl)) and the Dutch National Vegetation Database (LVD). All these records are assigned to *Bolboschoenus maritimus* (L.) Palla, which is the only taxon of this genus recognized in the most recent Dutch Flora (Van der Meijden 2005). Before Van der Meijden's first Flora edition (Van der Meijden et al. 1983), systematics of the *Scirpus maritimus* group was considerably more complex. Here, we first provide an overview of the different concepts of *Bolboschoenus* taxonomy in the last 200 years in the European and Dutch literature.

The first major botanical works in The Netherlands (Heukels 1911; Kops et al. 1836; Vuyck 1916) followed the work of Meyer (1836), recognizing several infraspecific taxa at the variety level under *Scirpus maritimus* L. Distinction is based on inflorescence characters, such as number and length of inflorescence spikes and peduncles:

- $\beta$  *macrostachys* Vis. 1842 (*Scirpus maritimus* var. *macrostachys* Vis.: In the Netherlands, without any doubt, this name refers to *B. maritimus*, but the name of *S. m.* var. *macrostachys* actually turned out to be a synonym of *Bolboschoenus glaucus* (Lam.) S.G.Sm. (Marhold et al. 2006), a species that does not occur in the Netherlands).
- $\gamma$  *compactus* G.F.W.Meyer 1836
- $\delta$  *monostachyus* G.F.W.Meyer 1836.

In the Prodrromus Florae Batavae, De Waal (in Vuyck 1916) mentioned the nominate form as occurring more frequent in inland areas (despite its name). The *monostachyus* form is said to prefer brackish dune valleys, whereas on saline soils the *compactus* form dominates. This has been confirmed by Van Soest (1928) and Sloff & Van Soest (1938), who mentioned that in inland river systems and canals, only the nominate form of *S. maritimus* with diffuse pedunculate spikelets (= var. *maritimus/typicus*) occurs. Reichgelt (1956) mentioned four formae in the Flora Neerlandica:

- forma *macrostachys* (Willd.) Junge
- forma *compactus* (Hoffm.) Junge
- forma *monostachyus* (G.F.W.Meyer) Junge
- the typical form (nominate).

He used the lower rank of formae because he observed many intermediate character states between the infraspecific taxa, and observed that more than one form can occur in the same population, and even within a single plant.

Robertus-Koster (1969) studied the differences in seed morphology, inflorescence architecture and ecology between the compact form and the nominate (typical) form of *Scirpus maritimus* in the Netherlands. The shape of the achenes (black and triangular

versus brown and round respectively) turned out to be correlated to inflorescence architecture and geographical distribution, but populations from the tidal estuarine Biesbosch area (Provinces of Zuid-Holland and Noord-Brabant) showed intermediate characters, with more or less pedunculate inflorescences and semi-orbicular to weakly triangular achenes. She concluded that *S. maritimus* shows a clinal, probably ecologically determined variation. Consequently, in the recent Floras and standard lists from 1983 onwards, neither within *S. maritimus* nor *Bolboschoenus maritimus* no infraspecific taxa have been recognised (Van der Meijden 1990; 1996; 2005; Van der Meijden et al. 1983).

In other parts of Europe, *Bolboschoenus* has been studied intensively since the end of 20<sup>th</sup> century. For Europe, Norlindh (1972) and DeFilipps (in Tutin et al. 1980) accept only two infraspecific taxa: *Scirpus maritimus* subsp. *maritimus* and *S. maritimus* subsp. *affinis* (Roth) T.Norlindh. Subspecies *affinis* is mainly an Asian species, which in Europe is only present in the southeast, whereas the nominate subspecies accommodates all representatives of the species in Northwest Europe. Casper & Krausch (1980) further divided subsp. *maritimus* sensu Nordlindh into *B. maritimus* (L.) Palla subsp. *maritimus* and *B. maritimus* subsp. *compactus* (Hoffm.) Heyny.

Egorova (in Egorova et al. 1976) reported *Bolboschoenus planiculmis* (F.Schmidt) T.V.Egorova for the European part of the former USSR. This taxon is widespread in (Central) Europe (Hroudová et al. 2009a). Browning (in Browning et al. 1996) reported the Asian *B. yagara* (Ohwi) Y.C. Yang & M.Zhan and a putative hybrid between *B. yagara* and *B. maritimus* for Europe. This hybrid was mentioned in the Flora van Nijmegen en Kleef 1800–2006 (Dirkse et al. 2007) for the southeastern part of the Netherlands. We identified the forementioned records of this hybrid taxon in the Netherlands as *B. laticarpus*.

In a revision of the *Bolboschoenus maritimus* group, Browning (in Browning et al. 1998) reported the presence of another species for southeastern Europe: *B. glaucus* (Lam.) S.G.Sm.

In a revision by Marhold et al. (2004), the putative hybrid between *Bolboschoenus yagara* and *B. maritimus* sensu Browning et al. (1996) was published as a new species: *B. laticarpus* Marhold, Hroudová, Ducháček & Zárk. In addition to well-known diagnostic characters concerning inflorescence architecture, pericarp morphology is used as a new diagnostic character. The choice for describing this taxon as a new species is justified by distinct morphological differences combined with differences in distribution and (soil) ecology. They consider *B. laticarpus* of hybrid (allopolyploid) origin, following Browning et al. (1996). However, because of its stabilized differences in ecology and distribution – independent of putative parent species –, it is considered as a stabilized hybrid and not a primary hybrid. Marhold et al. (2004) further consider *B. yagara* and *B. planiculmis* as the most likely parent species, instead of *B. maritimus* and *B. yagara*. Marhold et al. give two arguments for this hypothesis. First, the chromosome number of *B. yagara* is  $n = 55$ . In *B. planiculmis* the chromosome number  $n = 54$  strongly prevails, while in *B. maritimus*  $n = 55$  prevails. Because in *B. laticarpus* both chromosome numbers ( $n = 54$  and  $n = 55$ ) occur, *B. planiculmis* is a more likely parent species than *B. maritimus*. Second argument is the overlapping of the distribution area of *B. planiculmis* and *B. yagara* in Eurasia.

According to Marhold et al. (2004), their new species is also present in the Netherlands: They mention a single collection (*Clevering s.n.*, PRA) from Nijmegen, Milligerwaard (sic). Since this taxon has not been recognized as a separate species in the Netherlands, its distribution in the Netherlands was hitherto unknown.

The mentioned record of *Bolboschoenus laticarpus* in the Netherlands, combined with the complex classification history of this genus (Table 1), and the striking morphological variation in Dutch populations in the field, which have so far been considered as a single species, was the reason to revise *Bolboschoenus* for the Netherlands. We aimed to find answers on the following research questions:

- Which species of the ‘*Bolboschoenus maritimus* aggregate’ do occur in the Netherlands?
- How are these species distributed, and what is their ecology and phytosociological position?
- Could differences in pericarp morphology explain distribution patterns by means of differences in dispersal capacity?
- Are intermediate specimens also present when using pericarp morphology?

Table 1. History of nomenclature of the *Bolboschoenus maritimus* group in the Netherlands. The notes in the column ‘current classification’ refer to the following references: 1. Vuijk (1916), 2. Heukels (1911), 3. Kops (1836), 4. Reichgelt (1956), 5. Tutin et al. 1980, 6. Van der Meijden et al. (1983), 7. Van der Meijden (1990), 8. Van der Meijden (1996), and 9. Van der Meijden (2005).

taxon	rank	Infraspecific taxon	author	current classification
<i>Scirpus maritimus</i>	var.	<i>macrostachys</i>	?	<i>Bolboschoenus maritimus</i> <sup>3</sup>
<i>Scirpus maritimus</i>	var.	<i>compactus</i>	?	<i>Bolboschoenus maritimus</i> <sup>3</sup>
<i>Scirpus maritimus</i>	var.	<i>macrostachys</i>	Vis.	<i>Bolboschoenus maritimus</i> <sup>1</sup>
<i>Scirpus maritimus</i>	var.	<i>compactus</i>	G.F.W.Meyer	<i>Bolboschoenus maritimus</i> <sup>1</sup>
<i>Scirpus maritimus</i>	var.	<i>monostachyus</i>	G.F.W.Meyer	<i>Bolboschoenus maritimus</i> <sup>1</sup>
<i>Scirpus maritimus</i>	var.	<i>maritimus</i>	nominate	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>2</sup>
<i>Scirpus maritimus</i>	var.	<i>macrostachys</i>	Koch	<i>Bolboschoenus maritimus</i> <sup>1</sup>
<i>Scirpus maritimus</i>	var.	<i>compactus</i>	Koch	<i>Bolboschoenus maritimus</i> <sup>2</sup>
<i>Scirpus maritimus</i>	var.	<i>maritimus</i>	nominate	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>2</sup>
<i>Scirpus maritimus</i>	forma	<i>macrostachys</i>	(Willd.) Junge	<i>Bolboschoenus maritimus</i> <sup>4</sup>
<i>Scirpus maritimus</i>	forma	<i>compactus</i>	(Hoffm.) Junge	<i>Bolboschoenus maritimus</i> <sup>4</sup>
<i>Scirpus maritimus</i>	forma	<i>monostachyus</i>	(G.F.W.Meyer) Junge	<i>Bolboschoenus maritimus</i> <sup>4</sup>
<i>Scirpus maritimus</i>	forma	<i>typicus/maritimus</i>	nominate	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>4</sup>
<i>Scirpus maritimus</i>	subspec.	<i>maritimus</i>	nominate	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>5</sup>
<i>Scirpus maritimus</i>	spec.		L.	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>6</sup>
<i>Scirpus maritimus</i>	spec.		L.	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>7</sup>
<i>Bolboschoenus maritimus</i>	spec.		(L.) Palla	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>8</sup>
<i>Bolboschoenus maritimus</i>	spec.		(L.) Palla	<i>Bolboschoenus laticarpus</i> and <i>B. maritimus</i> <sup>9</sup>

## Methods

All collections of *Bolboschoenus* from the Netherlands in the herbarium of Naturalis Biodiversity Center in Leiden (L), the Herbarium Natuurmuseum Brabant (NMBT), and the Herbarium Natuurmuseum Maastricht (MAAS) have been revised according to the recent taxonomic literature mentioned in the introduction. We also investigated plant material sent to us by Dutch botanists; part of this material is incorporated into the herbarium collections of L.

We investigated inflorescence architecture and achene and pericarp morphology, and, if available, notes on ecology. Additional observations were retrieved from photos in [waarneming.nl](http://waarneming.nl), an open access nature observations database ([waarneming.nl](http://waarneming.nl), last accessed on August 8, 2016). This resulted in a database of c. 500 records, which was used as a basis for the distribution maps using QGIS (Open Source Geospatial Foundation Project 2016). The records are shown in [Appendix 1](#).

The classification of the Floral Districts in the Netherlands used in the text follow [Van der Meijden \(2005\)](#). The abbreviations of institutional herbaria follow [Thiers \(2016\)](#).

Field work (specimen collection and phytosociological fieldwork) was carried out in the Betuwe (inland river landscape in the Province of Gelderland), South Limburg (Province of Limburg), and Hilversum areas (Province of Noord-Holland). We made vegetation relevés of *Bolboschoenus laticarpus* stands in different places and vegetation types according to the Braun-Blanquet method ([Westhoff et al. 1995](#)). In total, 20 relevés were made, which are stored in the Dutch National Vegetation Database using TurboVeg ([Hennekens & Schaminée 2001](#)), and analysed in JUICE ([Tichý 2002](#)) by manually ordering species and relevés according to recent phytosociological literature ([Hroudová et al. 2009b](#); [Hroudová et al. 1999](#); [Weeda et al. 1995](#)).

To identify differences in the species' capacity to withstand mechanical digestion in waterfowl gizzards, the hardness of the seeds of the two species was tested using an Instron 5542 device (Instron®, Nordwood, MA, USA). Fifteen seeds of dried plants collected in situ in 2015 per species were placed underneath a metal pin, which was gradually lowered at a rate of 1 cm/min while we continuously measured the force required for this downward motion. We determined the force in kg at which the seed coat cracked and used this as a measure of seed hardness. To identify differences in dispersal capacity by hydrochory, the buoyancy of seeds of both species was tested. Following [Kleyer et al. \(2008\)](#) we used two replicate treatments per species. One hundred seeds of *Bolboschoenus laticarpus* (50 per replicate) and 96 seeds of *B. maritimus* (48 per replicate) were put in plastic beakers filled with tap water and held at room temperature. Each beaker was gently shaken manually and the proportion of floating seed was determined every day for the first two weeks and once more after one month.

## Results

### *Bolboschoenus* species in the Netherlands

Using the characters given by [Marhold et al. \(2004\)](#), all the revised specimens in L, NMBT and MAAS can be divided in two groups, which can be assigned to *Bolboschoenus maritimus* and *B. laticarpus*, respectively ([Appendix 1](#)). No other species mentioned in



Hroudová et al. (2007), such as *B. yagara* or *B. planiculmis*, has been found. The two species can be distinguished on the basis of inflorescence architecture and seed morphology: *B. maritimus* usually has relatively compact inflorescences and brownish achenes, which are more or less orbicular to subtrigonal in cross section, with an exocarp >2 times as thick as the mesocarp, whereas *B. laticarpus* is characterised by a relatively long peduncles, and glossy black achenes, which are triangulate in cross section with a thin exocarp (Fig. 1). However, *B. maritimus* is highly variable (see below), and a positive identification sometimes requires the examination of the (micro-)morphological characters of the achenes – this is especially recommended for areas where both species occur.

We found two collections that are somewhat intermediate between *Bolboschoenus laticarpus* and *B. maritimus* with respect to inflorescence architecture: *Robertus-Koster, EI s.n., 1965-09-24* (Fig. 2A) and *Jansen, MT s.n., 1917-06-28*. Pericarp morphology of these collections clearly identified them as belonging to *B. maritimus*, because of their thick exocarp, consisting of aerenchymatic tissue. Size and colour of the achene also indicate *B. maritimus*, but the achenes of the two plants are somewhat keeled and their inflorescences are umbellate with long peduncles. We concluded that these two plants represent an extremely pedunculate nominate form of *B. maritimus*.

In contrast to Jäger & Werner (2012), we do not think it is possible to discriminate between *Bolboschoenus laticarpus* and *B. maritimus* by using non-floral characters alone. A complete account of the discriminating characters of both species is given in the following key to the species of *Bolboschoenus* in the Netherlands, based exclusively on the examination of material from the Netherlands, except for the dimensions of the achenes, which are based on Hroudová et al. (2007):

#### Key to the species of *Bolboschoenus*

- 1 Achene relatively small, 1–3.7 × 2.0–2.4 mm, glossy black, broadly (more or less flattened) triangulate in cross section. Exocarp thin (less than half of the thickness of the mesocarp), consisting of aerenchymous cells more or less isodiametric to 1.5(–2) times as long as wide. Inflorescence always symmetrically umbellate with a central cluster of spikelets and 3–6 rays of peripheral clusters of spikelets; spikelets usually 10–15 mm long, very rarely up to 30 mm. Peduncles of peripheral clusters (rays) (2–)3–4(–5) times as long as the length of spikelets in central cluster. Stems sharp or rounded trigonous, or varying within one plant. Plant 40–120(–180) cm tall: ***Bolboschoenus laticarpus*** Marhold, Hroudová, Ducháček & Zákr

Species of inland river systems, canals, and isolated ponds and lakes close to rivers. Common in Fluvatile District, very rare at Pleistocene and Haf Districts except for former river branches and small river systems.

- Achene larger, 3.0–4.0 × 2.1–2.7 mm, light brown to dark brown, more or less orbicular, ovate to subtrigonal in cross section (keeled abaxial ridge). Exocarp more than 2 times as thick as the mesocarp, consisting of thick layer of aerenchymous cells that are usually (2–)3–4 as long as wide. Inflorescence either a solitary spike of 10–15 mm or capitate, with macrostachyate spikelets, or semi-capitate to umbellate with 1–2(–4) pedunculate clusters of spikelets; spikelets 10–30(–45) mm long. Peduncles 0.5–2(–4) times as long as non-macrostachyate spikelets in central cluster. Plants usually 40–100 cm tall, but plants with solitary spikes then plant 10–40 cm tall. Stems sharp or rounded trigonous, or varying within one plant: ***Bolboschoenus maritimus*** (L.) Palla

Species of coastal areas, salt water systems, tidal areas, dune valleys, and coastal salt marshes ('kwelders' and 'inlagen'). Common at Haf District and IJsselmeerpolders, rare and probably adventive at Fluvatile and Pleistocene Districts.

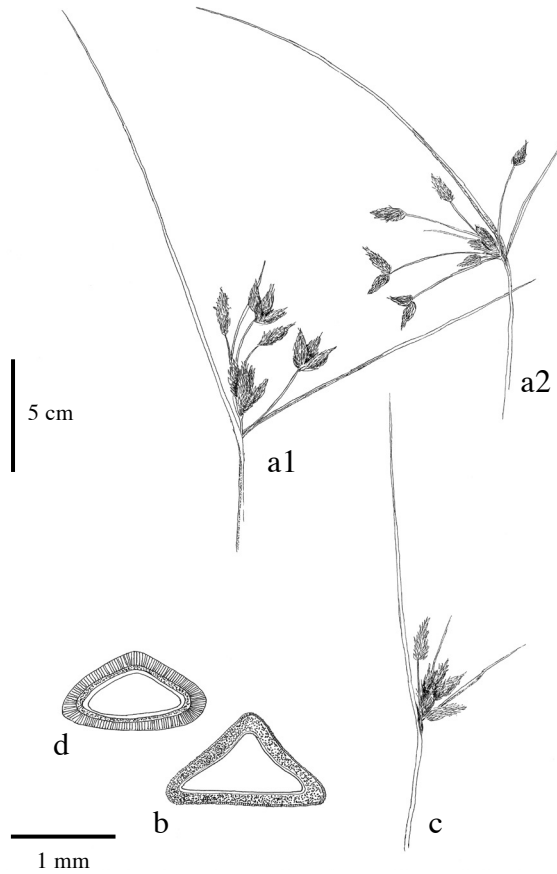


Fig. 1. *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zák (a & b) and *B. maritimus* (L.) Palla (c & d): a1. inflorescence (Slijk-Ewijk, collection Haveman, R 15.1010.003); a2. inflorescence (Dodewaard, collection Haveman, R 15.2509.002); b. achene cross-section (15.1010.003); c. inflorescence (Vlieland); d. achene (Vlieland). In the cross-section of the achenes from outer to inner: exocarp (with isodiametric or elongated cells), mesocarp (punctuated in the drawings), endocarp, and endosperm. Drawings c and d are made after a plant collected on August 31, 2015, in the '5e Kroonspolder' on Vlieland (125.870-585.085, relevé RH15.244), which after preparation of the achene was too damaged to preserve. The specimens used for drawings a and b are preserved in hb. Haveman. Illustrations: Rense Haveman, 2016.

We follow Reichgelt (1956) by not assigning formal taxonomic status to the different forms or morphotypes that occur within *Bolboschoenus maritimus* s.str. These forms seem to be correlated to site conditions, as described by several authors (Sloff & Van Soest 1938; Van Soest 1928; Vuyck 1916). In dune valleys, young dunes and marshes in the Maritime District, small, slender forms up to 40 cm tall with only one, or sometimes two, never macrostachyate, spikelets occur more often (Fig. 3). These plants can easily be confused with other Cyperaceae such as *Carex* species in subgenus *Vigneae*, *Blysmus compressus* (L.) Panz. ex Link, *Blysmus rufus* (Huds.) Link,

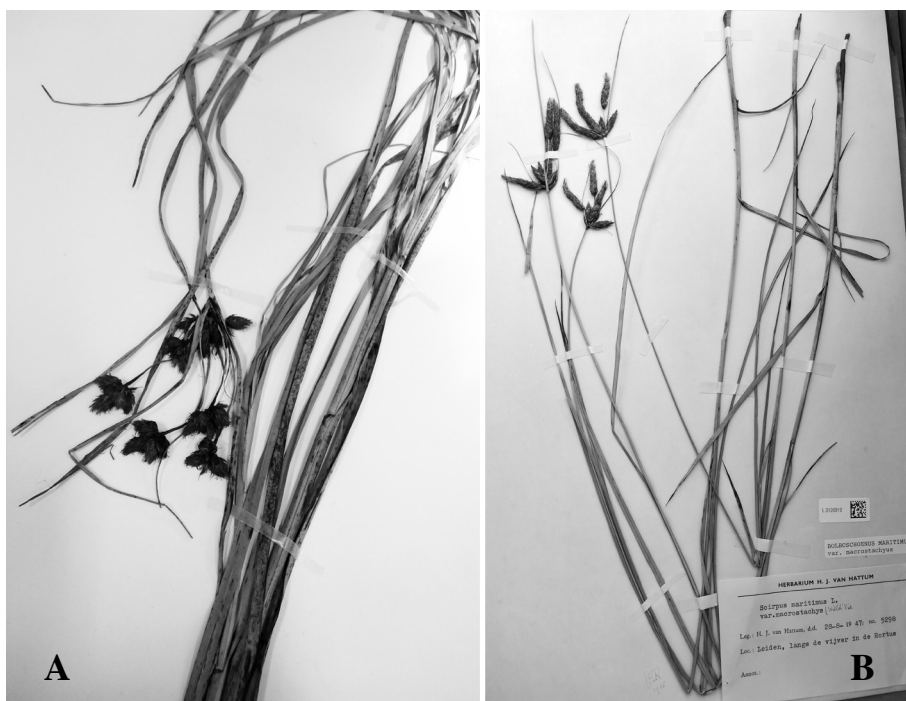


Fig. 2. *Bolboschoenus maritimus* (L.) Palla. A: Herbarium specimen *Robertus-Koster, EI s.n.*, 1965-09-24 (L) from the Biesbosch: ‘Extreme’ *maritimus* form with an inflorescence with many pedunculate clusters; B: Herbarium specimen *Hattum, HJ van 5298* (L) from Leiden: Macro-stachyate form of this species. Photos: Erik Simons.

and, especially, *Schoenoplectus pungens* (Vahl) Palla. Compact forms, often big stout plants, forming dense vegetation in habitats with >1000 mg/l Cl<sup>-</sup> (Reichgelt 1956) are indeed common in the maritime districts.

Specimens of *Bolboschoenus maritimus* that turned out not to be the monostachyate form, nor the compact form can be considered as the nominate form. Those plants have 1–3 (Fig. 4) pedunculate clusters of spikelets, but sometimes more, with even the majority of spikelets in the peripheral clusters (Fig. 2A).

The macrostachyate form (with one or more spikelets of 20–30 mm; Fig. 2B) seems to be a special feature of *compactus* and *maritimus* forms of *Bolboschoenus maritimus*. We consider macrostachyate spikelets as a character that often occurs in some forms or under ecological circumstances, in concordance with Marhold et al. (2006) and Zákravský & Hroudová (1994) who stated that the macrostachyate morphotype is an ecomorphosis triggered by habitat conditions (inundation), but of no taxonomic significance.

In *Bolboschoenus laticarpus* collections, we found only two very long (25–30 mm in Prell, HH s.n., 1944-08-13) spikelets in approximately 175 collections. Marhold et al. (2006) mention a frequency of 2.9% of macrostachyate forms in herbarium specimens of *B. laticarpus*.

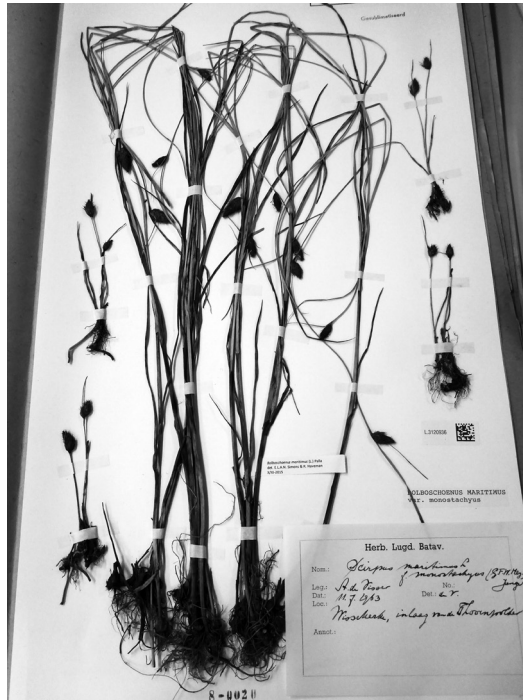


Fig. 3. *Bolboschoenus maritimus* (L.) Palla. Herbarium specimen Visser, A de s.n. (L) from Wissenkerke: Monostachyate form of this species. Photo: Erik Simons.

### Seed dispersal traits

In our opinion the distribution of the two species in the Netherlands can be, in part, explained by historical/geographical factors (influence of rivers of Central European origin) and by salt tolerance, as *B. laticarpus* is a glycophyte and *B. maritimus* a facultative halophyte (Hroudova et al. 2014).

Another factor explaining the range of the respective *Bolboschoenus* species could be differences in their dispersal capacity.

We considered only the dispersal of seeds and compared their potential to be dispersed through hydrochory, by floating on water, and endozoochory, through the digestive tract of animals, waterfowl in particular. Marhold et al. (2004) describe that *Bolboschoenus laticarpus* has a thin exocarp and little aerenchym as opposed to *B. maritimus*, suggesting lower buoyancy and thus limited potential for hydrochory.

Significantly more force was required to crack seed coats of *Bolboschoenus maritimus* than *B. laticarpus* (student's t test:  $p < 0.001$ ; Fig. 5a). Seed coats of *B. maritimus* cracked under a mass of  $12.9 \pm 2.9$  kg, while  $5.2 \pm 1.9$  kg was required for *B. laticarpus* (mean  $\pm$  standard deviation). The buoyancy test revealed that *B. maritimus* had higher buoyancy than *B. laticarpus* (Fig. 5b). Of the former, 98% of the seeds were still



Fig. 4. *Bolboschoenus maritimus* (L.) Palla. A: Herbarium specimen Ploeg, DTE van der 1572-9 from Dokkum: Inflorescence with a few more or less pedunculate clusters; B: Herbarium specimen Kern, JH 6519 (L) from Voorne: Inflorescence with 3 pedunculate clusters, still within the range of the morphological variability of this species. Photos: Erik Simons.

floating at the end of the experiment after one month, compared to only 22% of the seeds of the latter. For *B. laticarpus*,  $t_{50}$  (the time after which 50% of the seeds had sunk) was 14 days. This could not be determined for *B. maritimus*, since  $t_{50}$  for this species exceeded the duration of the experiment.

Our buoyancy test confirms that *Bolboschoenus laticarpus* has a lower buoyancy than *B. maritimus*, although buoyancy of the former was much higher than described by Hroudová et al. (1997) for *B. maritimus* subsp. *maritimus*. It should be mentioned, however, that in their experiments *B. maritimus* subsp. *maritimus* also included two taxa which are now considered to be *B. yagara* and *B. laticarpus*. The *compactus* subspecies used in Hroudová et al.'s study seems to comprise both *B. maritimus* s.str. and *B. planiculmis*.

Our results suggest that *Bolboschoenus laticarpus* is still very capable of hydrochorous dispersal and is thus easily dispersed through river systems. It could be reasoned that suitable habitat for germination are found more rapidly by chance in river systems than in oceanic systems, which could be why the more coastal *B. maritimus* has a much higher buoyancy. It is not unthinkable, however, that the thick exocarp of *B. maritimus* is not just an adaptation for long-distance transport in water, but is also a way of protection against salt.

Seed hardness was used as a proxy for the capacity to survive digestive forces in the gizzard of waterfowl, which are well-known dispersal agents for a large range of

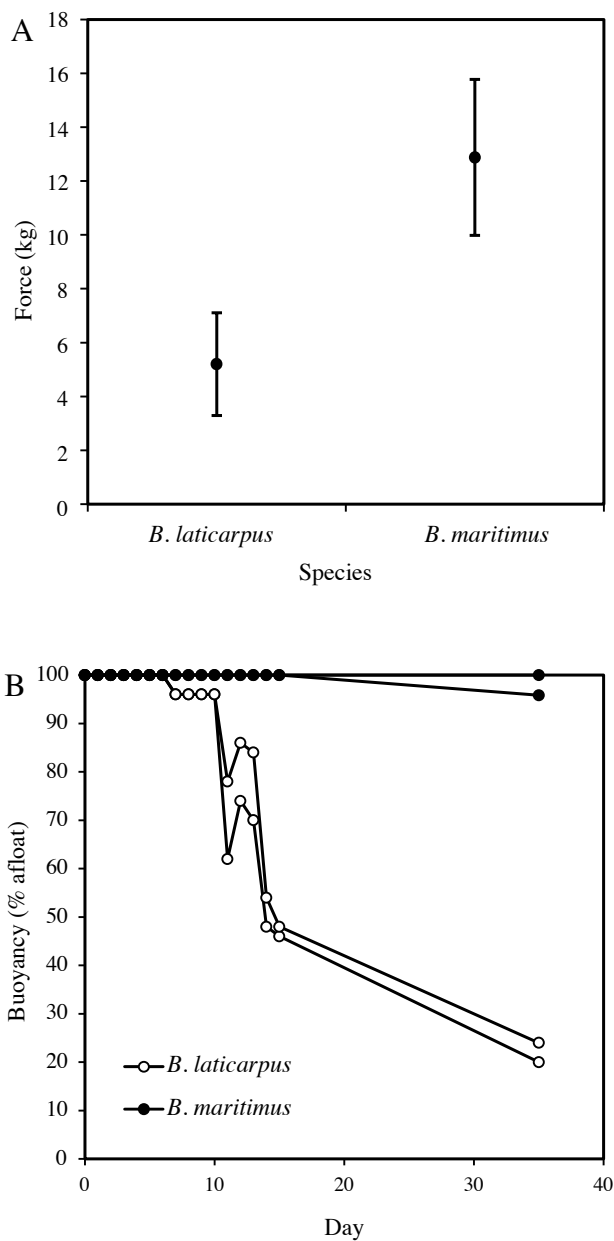


Fig. 5. Seed traits related to *Bolboschoenus* dispersal potential. The upper panel (A) shows mean seed hardness of 15 seeds of each species expressed as the mean force in kg required to crack the seed coats. Error bars represent standard deviation. The lower panel (B) shows the buoyancy of two replicates of 50 seeds (100 seeds in total) of *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zákr (open dots) and two replicates of 48 seeds (96 seeds in total) of *B. maritimus* (L.) Palla (closed dots) in water, expressed as the percentage of seeds afloat. The lines connect the measurements over time of the two replicates per species. Illustration: Erik Kleyheeg.

plant species in both aquatic and more terrestrial habitats (Soons et al. 2016). *Bolboschoenus maritimus* seeds required more force before the seed (coat) cracked than *B. laticarpus*, suggesting that it will more easily survive passage through the digestive tract of waterfowl. However, it should be noted that cracking seeds of both species required much more force than other plant species that are commonly dispersed by waterfowl (Kleyheeg 2015). This indicates that, if consumed by waterfowl, a large proportion of seeds of both species would easily pass the digestive tract intact. The same is most likely true for dispersal through the digestive tract of fish. This makes the seeds adapted to endozoochorous long-distance dispersal.

In conclusion, neither of the two dispersal traits clearly explains the distinct separation of the range of both species in the Netherlands. It therefore seems that other factors, e.g., differences in competitive strength or salt tolerance, are more important. The aerenchymous exocarp could play a role in protection against high salinity. Because the exocarp is much thicker in *Bolboschoenus maritimus* than in *B. laticarpus*, the achenes of former species are probably best protected against salt. Furthermore, the high buoyancy of the achenes of especially *B. maritimus* makes this species better adapted for hydrochorous dispersal over long distances than *B. laticarpus*, and hence better adapted for dispersal and colonization across the IJsselmeer lake.

## Distribution

The first collection of *Bolboschoenus laticarpus* in the Netherlands dates back to 1833 (Wtewaal s.n. 1833-08-15, between Werkhoven and Schalkwijk), compared to 1819 for *B. maritimus* (Anonymus s.n. 1819-07-15, St Jakobs Parochie). Therefore, we consider both species as (equally) natural in the Netherlands. Both species prefer nutrient rich, clayish soils, along rivers and canals, and in marshes. Both species are (almost) absent from the nutrient poor, dry, sandy, acidic soils of pleistocene origin in northeastern and southern parts of the Netherlands, except from rivers and canals (Fig. 6).

*Bolboschoenus laticarpus* is strictly confined to freshwater habitats, as was already described by Hroudová et al. (2007) and Marhold et al. (2004). The distribution follows the large rivers in the Netherlands: The River IJssel, including smaller branches and rivers in the IJssel system like the River Oude IJssel and the River Berkel (see Fig. 7 for a picture of *Simons 1746*, which was collected in this area), Rivers Nederrijn-Lek, Oude Rijn, Waal-Merwede of the Rhine system (originating in Central Europe), and the River Meuse (Maas, originating in France). The occurrence north of the River Rhine in the Provinces of Utrecht and Zuid-Holland is confined to the River Oude Rijn, a branch of the River Rhine which bed has silted up and which has been isolated from the Rhine by man since 1122. A collection from Sellinger (*Stouthamer s.n. 2015-11-10*) may be related to the River Eems (Ems) system, where this species also occurs (Hroudová et al. 2009a).

In the Netherlands, *Bolboschoenus maritimus* is common in maritime areas, the coastal areas of the Provinces of Zeeland, Zuid-Holland, Noord-Holland, Friesland, and Groningen. The species was also found along the borders of the freshwater IJsselmeer lake, part of the former Zuider Zee, which desalinated after 1932. Since the number of collections from the Netherlands after 1980 is limited compared to earlier decades, it is not clear to what extent the species is still occurring in this area. In the man-made

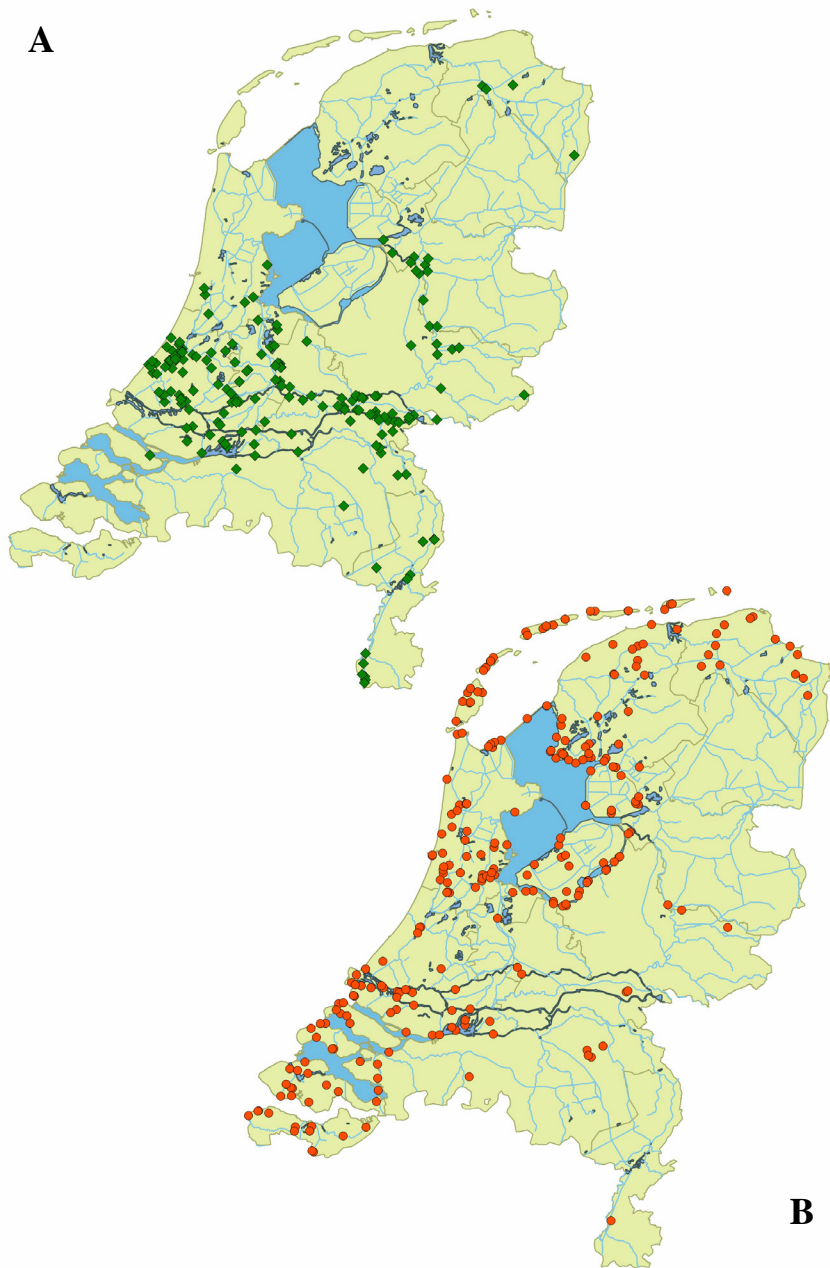


Fig. 6. Distribution of *Bolboschoenus* in the Netherlands. A: *Bolboschoenus laticarpus laticarpus* Marhold, Hroudová, Ducháček & Zár (green diamonds), B: *B. maritimus* (L.) Palla (orange dots). The distribution maps are based on the herbarium specimens we examined, but we also used a number of records provided by experienced botanists who made photos of *Bolboschoenus* plants of sufficient quality as well as records in the [waarneming.nl](http://waarneming.nl) database ([Appendix 1](#)). Illustration: Erik Simons, 2016.





Fig. 7. Plant of *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zákr near Gossel (preserved as herbarium collection *Simons 1746, L*). Photo: Erik Simons.

Province of Flevoland (a polder area reclaimed from the former Zuider Zee between 1940 and the late 1960s) *B. maritimus* seems to be the only occurring *Bolboschoenus* species. Other inland populations of *B. maritimus* are rare, and at least some of them are uninten-

tionally introduced, planted or not entirely natural in another sense. These populations tend to co-occur with (other) exotic species, e.g., *Typha laxmannii* Lepech. near Ressen (Gelderland). Some other populations in the Provinces of Noord-Brabant and Gelderland that seem more natural occur in nature restoration areas, where transport of seeds and vegetative parts by machines, soil, etc. could be an explanation for the occurrence of *B. maritimus* there. Dispersal by natural vectors (birds and fish) cannot not be ruled out though.

It is likely that *Bolboschoenus laticarpus* has colonized the Netherlands via rivers from Central Europe (River Rhine, and in lesser extent River Meuse). This is in agreement with the hypothesised allopolyploid origin of this species of two Central European parent species as stated by [Marhold et al. \(2004\)](#) and [Hroudová et al. \(2007\)](#). *Bolboschoenus maritimus*, on the other hand, seems to have reached the Netherlands by sea. Hence, it is not surprising that we found both species more or less co-occurring in the Biesbosch, a nowadays freshwater tidal area which was formerly connected to the sea.

### Ecology and phytosociological position

In contrast to *Bolboschoenus maritimus*, which is mostly confined to saline habitats, *B. laticarpus* is typical for freshwater habitats ([Hroudová et al. 2007](#), [Hroudová et al. 2014](#)). *Bolboschoenus laticarpus* was described by [Hroudová et al. \(2007\)](#) as "... a typical species of river floodplains, inhabiting riverbanks and oxbows or small streams, ditches and channels" and the distribution pattern of this species in the Netherlands ([Fig. 6](#)) matches this description well. *Bolboschoenus laticarpus* is adapted to germination in exposed, wet, and open soils ([Hroudová et al. 2007](#), [Marhold et al. 2004](#)). Establishment of *B. laticarpus* via seed is best in aerated soils, but a cold and water stratification for a minimum of three months seems to be necessary to break seed dormancy ([Moravcová et al. 2002](#)). Fluctuating water tables promote both the germination of *B. maritimus* (induced secondary dormancy after salinity decreases, [Hroudová et al. 2007](#)) and the mass-germination of *B. laticarpus* seeds, but longer drainage periods will cause severe dieback of *B. laticarpus* ([Hroudová et al. 2009b](#)).

In the Netherlands, *Bolboschoenus laticarpus* grows in the littoral zone of river ponds, oxbows, and clay or sand excavation pools and ditches in river floodplains. It typically occurs in muddy clayish soils together with other perennial pioneers such as *Butomus umbellatus* L., *Alisma plantago-aquatica* L., etc., in a gradient between open water and dense *Phragmites australis* vegetation. In high reed vegetations with *Phragmites australis* (Cav.) Steud., *Typha* species, etc., *B. laticarpus* has a slender and lax habit and grow up to 1.80 m tall. Most of the examined stands ([Appendix 2, Table 2](#), relevés 1–12) belong to the *Phragmition australis* Koch 1926, but the assignment to one of the described associations from the recent Dutch phytosociological literature ([Schaminée et al. 2010](#), [Weeda et al. 1995](#)) is not straightforward. Obviously, this is mainly caused by the confusion of the *Bolboschoenus* species in the published tables of the alliance, resulting in a doubtful delineation of the associations. Our relevés fit best in the *Alismato-Scirpetum maritimi* (Tüxen 1937) Schaminée et al. (in [Weeda et al. 1995](#)), but this association was not validly published because it was not typified (art. 3o ICPN, [Weber et al. 2000](#)). Besides, it is a superfluous name since the *Scirpetum*

triquetri-maritimae Zonneveld 1960 (sub nomine Scirpetum triquetri et maritimi) is listed as as synonym.

In a recent classification of inland *Bolboschoenus*-dominated vegetation, Hroudová et al. (2009b) distinguished a Phalarido arundinaceae-Bolboschoenetum laticarpi Passarge 1999 corr. Krumbiegel 2006 from river floodplains in Central Europe. In this association, four *Bolboschoenus* species occur. The name giving *B. laticarpus* has the highest frequency, but *B. yagara*, *B. maritimus*, and *B. planiculmis* occur in this association as well. Most frequent accompanying species are *Phalaris arundinacea* L., *Alisma plantago-aquatica*, *Persicaria lapathifolia* (L.) Gray, *Oenanthe aquatica* (L.) Poir, *Lythrum salicaria* L., *Phragmites australis*, *Bidens frondosa* L., and *Persicaria amphibia* (L.) Gray, but for neither of these species the frequency exceeds 30%. *Mentha aquatica* L., a frequent accompanying species in our table (Appendix 2, Table 2), is significantly less frequent in the table published by Hroudová et al. (2009b). However, relevés 1–12 can be assigned to the Phalarido-Bolboschoenetum laticarpi on the basis of the mentioned species. This association is characteristic for eutrophic, ion rich, base rich, (temporarily) submerged river clays. Our relevés show a typical mix of species of submerged habitats (group Potametea in Appendix 2, Table 2), helophytes (especially the Phragmitetea group), and amphibic species of temporarily submerged habitats (pioneers from the Bidentetea and less ephemeral species from the Lolio-Potentillion), which together give a good illustration of the ecological profile of *B. laticarpus*.

Relevés 13–15 (Appendix 2, Table 2) are assigned to several other Phragmitetea communities: the Sagittario-Sparganietum (relevé 13), the basal community of Phalaris arundinacea-[Phragmitetalia] (relevé 14) and the basal community of Glyceria maxima-[Phragmitetea] (relevé 15) (Weeda et al. 1995). The last relevé was made in a ditch near the limestone quarry near Winterswijk. It refers to a pioneer community that is hard to assign to a described vegetation type.

The distinction of the Phalarido-Bolboschoenetum laticarpi raises the question of the phytosociological position of *Bolboschoenus maritimus*. According to Fig. 6, this species has its main distribution in saline habitats along the coast, but it is also frequently found in more inland fen peat and marine clay areas. In saline habitats, *B. maritimus* is a typical species of the Asteretea tripolii, where it can form dense monodominant stands. This vegetation type was classified as a basal community (Westhoff et al. 1998) in the most recent overview of the Dutch vegetation. Weeda et al. (1995) described the alleged *B. maritimus* vegetation from the former brackish parts of the Fen Peat District ('Laagveendistrict') as Alismato-Scirpetum rumicetosum. The question whether these vegetation types deserve a status as independent associations is yet unclear and deserves further study. The same holds true for the *B. maritimus* dominated vegetation in the northern marine clay district ('Noordelijk kleidistrict'), which are also considered to belong to the Alismato-Scirpetum by Weeda et al. (2000). Hroudová et al. (2009b) included in their overview of Central European *Bolboschoenus* communities not only stands with *B. laticarpus* in the Phalarido-Bolboschoenetum, but also stands with *B. maritimus*, as well as stands with *B. planiculmis* and *B. yagara*. Probably, the *Bolboschoenus* vegetation from maritime clays may be included in the Phalarido-Bolboschoenetum as well, but further research is needed to prove this hypothesis.

## Remarks

Our study clearly shows that the variation in morphology and ecology in *Bolboschoenus* in the Netherlands is not continuous, as stated by [Robertus-Koster \(1969\)](#), but clustered. The morphology of the inflorescence and the pericarp, the biogeography, and the ecology clearly separates *B. laticarpus* from *B. maritimus*.

Nevertheless, *Bolboschoenus maritimus* still shows a high level of phenotypic plasticity with respect to inflorescence structure and spikelet length, and phytosociological characteristics as well. The macrostachyate and *compactus* forms seem to show a continuous intergradation towards almost nominate forms with pedunculate spikelets, as [Robertus-Koster \(1969\)](#) already concluded based on the study of Biesbosch populations. But this (extremely) pedunculate nominate form of *B. maritimus* can be distinguished on the basis of pericarp morphology from *B. laticarpus*. As noted above, both species occur in the Biesbosch area.

The known distribution of both *Bolboschoenus* species in the Netherlands ([Fig. 6](#)) may have regional collectors biases for certain areas due to the lack of herbarium specimens and observations in databases like waarneming.nl. For example, in the Achterhoek area, Province of Gelderland, the genus is probably more abundant than the distribution maps suggest and many populations of *B. maritimus* recorded in the 'Atlas van de flora van Oost-Gelderland' ([Te Linde & Van den Berg 2003](#)) will probably turn out to be *B. laticarpus*. However, up to now only very few herbarium specimens are available from this area.

We have not found other *Bolboschoenus* species in the Netherlands yet, but *B. yagara* and possibly *B. planiculmis* may be expected to occur there. We think the former could possibly occur in acid to neutral Nanocyperion or maybe Littorelletea fenens and ponds in North Limburg and East Brabant, based on proximity of the natural populations in, e.g., Germany ([Hroudová et al. 2009a](#)) and the similarity of the habitat ([Hroudová et al. 2007](#), [Hroudová et al. 2009a](#)). *Bolboschoenus yagara* resembles *B. laticarpus*, but the achenes are symmetrically triangular, the exocarp is thinner and the inflorescence looks more 'slender', because the number of (clustered) spikelets is lower (pers. obs. Erik Simons and Kateřina Šumberová in the Czech Republic, see the specimens [Simons 1964](#) and [1966](#), L, duplicates in PRA). See [Hroudová et al. \(2007\)](#) for a description of *B. yagara* and other European species.

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Figures 5–9 are pictures taken of herbarium specimens at Naturalis Biodiversity Center in Leiden (L), with permission.

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# APPENDIX 1

## Specimens examined

The specimens examined are preserved in the following herbaria: L, MAAS, NMBT. Coordinates are in Dutch grid, dates in format YYYYMMDD, e.g. 18370823 meaning August 23<sup>rd</sup> 1837. Unfortunately, few Dutch botanists used collection numbers, so there are many collections cited here in a format as, e.g., ‘Ploeg, DTE van der s.n.’, the abbreviation s.n. meaning ‘sine numero’. No date is referred to as ‘s.y.’. The abbreviation ‘hb.’ stands for herbarium and refers to private herbaria. The records have also been used for the construction of the the distribution maps of Fig. 6 and include records provided by experienced botanists, underpinned by photos of sufficient quality, as well as records in the waarneming.nl database.

### BOLBOSCHOENUS LATICARPUS

#### *Gelderland*

Abeleven, ThHAJ s.n. 18370823 langs Grift te Lent, Oude Waal Ooijpolder, 188026/430609 (L); Beijer, A de s.n. s.y. In den Ooij bij Nijmegen, 191000/430000 (L); Berg, LJ van den s.n. 20151110 Winterswijk, 250446/442397 (L); Boer, AC 1038 19520725 Pannerden, 199835/433042 (L); Brouwer, JA 3946 19580801 Rijswijk tegenover Wijk bij Duurstede, 152911/441941 (L); Clason, EW s.n. 19530727 ZO-kant Elterberg, riviertje De Wildt, 210389/431002 (L); Cool, C s.n. 19110620 Ooy, 193017/429713 (L); Dijk, E van field observation with photo 20150809 Oosterhout, 186378/432328, waarneming.nl; Eimers, N field observation with photo 20160723 Horssen, 170748/430354, waarneming.nl; Haveman, R 586162 20150925 Dodewaard, De Strang in de Hiense Uiterwaarden, 173736/435447, hb. Haveman; Haveman, R 586163 20150925 Dodewaard, Hiensche Uiterwaarden, De Strang, 174697/435347, hb. Haveman; Haveman, R 586164 20151010 Slijk-Ewijk, noordrand zandwinplas, bij pannekoekenrestaurant, 182308/434660, hb. Haveman; Haveman, R 586165 20151010 Slijk-Ewijk, 182742/432804, hb. Haveman; Haveman, R 586166 20151010 Oosterhout, Loenense Buitenpolder, 180803/433297, hb. Haveman; Haveman, R 586167 20151010 Oosterhout, Loenense Buitenpolder, 179799/433360, hb. Haveman; Hoegen, C field observation with photo 20140611 Laag-Keppel, 212238/445348, waarneming.nl; Hoogers, BJ s.n. 19620904 Ochten, Ambonnezenkamp, 167804/436975 (L); Hummelen, C field observation with photo 20151020 Heilig Landstichting, 190178/425636, waarneming.nl; Inberg, HA s.n. 20160724 Tiel, 158084/437092, NDFF; Jansen, Joh s.n. 19310719 Overasselt, 182636/419079 (L); Jansen, MT s.n. 19620828 Ochten, 168176/435582 (L); Kok Ankersmit, HJ s.n. 18730701 Hatert, in een poel, 185252/424225 (L); Muller, D field observation with photo 20151005 Gamerense waarden, 143760/424461, waarneming.nl; Ploeg, DTE van der s.n. 19620828 Ochten, 168176/435582 (L); prodromus 1124 s.y. bij Zutphen, 210649/460881 (L); Reinink, K s.n. 19860904 Kekerdom, 197701/430837 (L); Rubers, W 10827 19840801 Beusichemsewaard Lekoever bij Den Duinen, 149000/440000 (L); Simons, ELAN 1745 20150902 Wiessenbergsche Kolk, close to Hattem, 202250/497863 (L); Simons, ELAN 1746 20150905 Rijsselsche waarden, south of Gorsel, 210380/465699 (L); Simons, ELAN 1747 20150906 south of Almen, 217465/463264 (L); Simons, ELAN 1748 20150915 south of Almen, 176742/440862 (L); Simons, ELAN 1755 20151010 Weurt, Duivelskolk, 183862/430747 (L); Simons, ELAN 1756 20151016 Wageningen, Nevengeul, 174746/441518 (L); Simons, ELAN 1976 20160912 between Almen and Lochem, close to Berkel river, 220606/463971 (L); Simons, ELAN field observation with photo 20150930 Plasserwaard, 171693/439734, waarneming.nl; Simons, ELAN field observation with photo 20151123 Lienden, 164996/437210, waarneming.nl; Simons, ELAN field observation with photo 20160713 Hattem, 200968/499238, waarneming.nl; Simons, ELAN field observation with photo 20160730 Wageningen, Nude, 173296/442156, waarneming.nl; Simons, ELAN field observation with photo 20160827 Doorwerth - Doorwerthsche Waarden, 182080/441778, waarneming.nl; Simons,

ELAN s.n. 20151028 Schoutenwaard, 176077/441210 (L); Slootweg, EJ field observation with photo 20110723 Millingerwaard, 197563/432192, waarneming.nl; Soest, JL van s.n. 19250601 Doorwerth, Rijnover, 183071/441876 (L); Soest, JL van s.n. 19390701 Bemmel, 190013/433805 (L); Weeda, EJ s.n. Beekbergerwoud, 198600/465040 (L).

#### *Groningen*

Bloembergen, S 1500 19350802 verbindingsweg Paddepoel-Reitdiep, 231215/584040 (L); de Garen, C s.n. s.y. Groningen, aan de wallen, 233048/582509 (L); Hospers, A field observation with photo 20160727 Schaaphok, 245317/584450, waarneming.nl; Stouthamer, W s.n. 20151110 Selligen, 273418/552251 (L).

#### *Limburg*

Anonymus s.n. s.y. Maasoevers bij Venlo, 209145/376199 (L); Beek, A van de s.n. 19700922 Ifteren, 177713/323847 (L); Borssum Waalkes, J van 5048 19460601 Maasuitwaarden ten zuiden van Maastricht, 177357/313322 (L); Grégoire, L s.n. 19390902 Oost-Eijsden, 177627/311843 (MAAS); Grégoire, L s.n. 19570720 Maasoverlaat Bosscherveld te Maastricht, 176765/319249 (MAAS); Gubbels, S field observation with photo 20110914 Rooth, 204052/375102, waarneming.nl; Kok Ankersmit, HJ s.n. 18970701 haven Venlo, 209278/376008 (L); Ploeg, DTE van der 1572-10 19570801 Eijsden, plasje aan Maasover, 177180/310385 (L); Rieter, L s.n. 18970701 Venlo, Droogehaven, 209278/376008 (L); Rieter, L s.n. 18970715 haven Venlo, 209278/376008 (L); Simons, ELAN 1759 20151126 Sint Pietersberg Zuid, plasje ENCI, 176126/314205 (MAAS); Sloff, JG s.n. 19350805 Swalmen, Asselt, plas in de Maasweiden, 198163/359904 (L); Vergoossen, W field observation with photo 20140621 Nederweert, Schoorkuilen, 182723/363144, waarneming.nl; Vergoossen, W field observation with photo 20160804 Roermond, Stadsweide, 196930/357911, waarneming.nl; Wever, A de s.n. 19120822 Eijsden, 177180/310385 (MAAS).

#### *Noord-Brabant*

Anonymus s.n. 18480701 Biesbosch, 114129/418613 (L); Beeftink, WG s.n. 19690730 Bergse Maas bij veer ten oosten van Dussen, 127040/414572 (L); Beijersbergen, A s.n. 19760627 stuw bij Sambeek, 196375/405936 (L); Geraets, L field observation with photo 20120610 Kraaijenbergsche plassen, 184800/415758, waarneming.nl; Geraets, L field observation with photo 20151020 Kraaijenbergsche plassen, 184207/418188, waarneming.nl; Krijnen, G field observation with photo 20100709 Oosterhout, 118482/408360, waarneming.nl; Muusse, T s.n. 20150901 Brabantse Biesbosch, Hardenhoek, 112200/421100 (L); Muusse, T s.n. 20150903 Brabantse Biesbosch, Maltha, 113400/419900 (L); Piet, JJ s.n. 19410809 Achterbosch, kanaal, 167728/391473 (L); Reijerse, F s.n. 19990714 hok 192/405, 192500/405500 (L); Simons, ELAN 1951 20160710 Volkel-Houtvennen, 176645/408650 (L); Talsma, H field observation with photo 20160708 Almkerk-Woudrichem, 126658/419736, waarneming.nl; Volz, J field observation with photo 20130828 Werkendam, 120957/425342, waarneming.nl; Vuurlonen s.n. 18470701 fort Crevecoeur, 146750/416260 (L).

#### *Noord-Holland*

AZ? s.n. 18330101 bij Amsterdam, 122400/484780 (L); Langbroek, W field observation with photo 20160704 Volendam, 132571/501938, waarneming.nl; Moll, J Hb s.n. 18350701 Haarlem, 104162/488308 (L); Prell, HH s.n. 19440813 tussen Nigtevecht en Abcoude, 128425/476575 (L); Simons, ELAN 1749 20150925 's-Graveland, 137371/472271 (L); Simons, ELAN 1751 20150925 's-Graveland, 137006/474472 (L); Suringar, WFR s.n. 18530901 Haarlemmermeer, 105757/479451 (L); Tilanus, JWR s.n. 18420501 Zeeburg, 126209/487233 (L); Vonk, D field observation with photo 20140727 Haarlem-De Krim, 103748/491323, waarneming.nl.

#### *Overijssel*

Bondam, R s.n. 18470101 Kampen, 190004/507470 (L); Ch C s.n. 18920701 Zwolle, langs Almelse kanaal, 205058/502007 (L); Haveman, R 301 19890902 Overijsselse Vecht Zwolle, 206417/504851



(L); Heijden, AA van der s.n. 19770925 Den Nul, 204163/485818 (L); Hendriks, F 1008 19370101 Deventer, 207090/473825 (L); Kobus, JD 602 18770717 Deventer S.n.ippeling, 210555/473742 (L); Lako, D s.n. 18920701 Zwolle, langs de Nieuwe Wetering, 199921/505671 (L); Meulenbelt, B field observation with photo 20140621 Zwolle-Vreugderijkerwaard, 198451/503058, waarneming.nl; Reinink, K s.n. 19860813 Ramspol, 185930/513498 (L); Weeda, EJ s.n. 20110820 Zwolle, Sekdoorn, shore of sandpit, 206170/499030 (L).

#### *Utrecht*

Ameijden, UP van s.n. 19120101 Fort de Bilt, 138532/456643 (L); Bakker, D 3336 19560716 Tienhoven, 134160/464326 (L); Embden, WC van s.n. s.y. Utrecht, 136382/455660 (L); Embden, WC van s.n. s.y. Utrecht, Ezelsdijk tot Groenewegje, 137482/456993 (L); Hartsen, FA s.n. 18600902 bij de zwemschool Utrecht, 139000/455000 (L); Hoekstra, YS field observation with photo 20150621 Amersfoort-Polder Zeldert, 150779/466906, waarneming.nl; Hoogendoorn, H 559 19520608 Oudewater, Nieuwe Singel, 119849/448427 (L); Hoogendoorn, H 597 19520616 Oudewater, Nieuwe Singel, 119849/448427 (L); Hoogendoorn, H 598 19520616 Oudewater, Nieuwe Singel, 119849/448427 (L); Hospers, AM s.n. 20151009 Houten, Bedrijvenpark Rondeel, 138527/448634 (L); Hospers, AM s.n. 20151018 Steenwaard Culemborg, 142687/441432 (L); Hospers, AM s.n. 20151025 Schalkwijk, Elpad, 139255/446531 (L); Lansing, P s.n. 20120623 Tienhoven, Oostelijke binnenpolder, 135974/464895 (L); Ooststroom, SJ van 3606 19300715 Utrecht, gracht Fort Vossegat, 138760/454941 (L); Simons, ELAN 1757 20151022 Rhenen, Palmerswaard, 166798/440834 (L); Slingerland, J s.n. 19660712 Zegveld, 117865/457345 (L); Steenis, CGGJ van s.n. 19180701 Utrecht, 136382/455660 (L); Stoopendaal, W field observation with photo 20160706 Nieuwegein - Polder De Wiers / Klein Vuylcop, 136437/449250, waarneming.nl; Voo, EE van der 911 19520916 Linschoten, Lagekade, 123894/453865 (L); Witcamp, C field observation with photo 20130623 Linschoten, Lagekade, 123182/453220, waarneming.nl; Wolters, HJ s.n. 19760703 Maarssen, Amsterdam-Rijnkanaal, 130000/461000 (L); Wttewaal s.n. 18330815 tussen Werkhoven en Schalkwijk, 143000/446000 (L).

#### *Zuid-Holland*

Anonymus s.n. 19120621 Nieuwkoop 113521/462505 NHN Leiden; Anonymus s.n. 19610722 Anonymus s.n. 19120621 Nieuwkoop, 113521/462505 (L); Anonymus s.n. 19610722 Katwijk, 88557/468525 (L); Anonymus s.n. s.y. Den Haag, 81623/456908 (L); Balke, NPW s.n. 19421004 Rotterdam, Kralingerhout, 95412/439463 (L); Barkman, JJ 982 19400820 Leiden, oever kanaal, 93750/462005 (L); Batjes, H field observation with photo 20140905 Wilsveen, 89052/454522, waarneming.nl; Beefink, WG s.n. 19600809 Den Bommel, vlak ten westen van de haven, 78831/414635 (L); Benschop, A field observation with photo 20120820 Leidschendam - Duivenvoordse-Veenzijdse Polder - Achterbos, 87645/458102, waarneming.nl; Bes, J field observation with photo 20100716 Akerdijkse plassen, 88472/443941, waarneming.nl; Bevaart, J 60024 19600729 Heerjansdam, 98455/427884 (L); Bevaart, J 60026 19600808 Barendrechtse brug, 95682/427172 (L); Blom, A field observation with photo 20150929 Alblasserbos, 110050/429835, waarneming.nl; Brandes, E s.n. 20151101 Alphen aan den Rijn, Zegerplas, 106979/461744 (L); Breemen, PJ van s.n. 18950710 Den Haag, Kranenburgweg, 78295/456294 (L); Bruyn, H de s.n. 19390608 Kethel, ZH, 85584/439186 (L); Burgers, A field observation with photo 20120706 Wassenaar, Lentevreugd, 86655/464341, waarneming.nl; CP s.n. 19780731 Schoonhoven 382454, 118500/440500 (L); Courbois, M 1 20160906 c 1 km ESE of Streefkerk, 112710/434021 (L); Danser, BH 2215 19080802 Rotterdam, Spiegelnisserweg, 93371/438405 (L); Duijfjes s.n. 19610806 langs water Rijksweg Leiden-Den Haag, 90682/458194 (L); Gessele, F van field observation with photo 20140807 Oudeland van Strijen, 95874/421042, waarneming.nl; Groot, C de field observation with photo 20130820 Zevenhuizerplas, 98718/444288, waarneming.nl; Ham, W van der field observation with photo 20160804 Leidschendam - Begraafplaats Noorthey, 88185/458194, waarneming.nl; Hattink, TA 360 19730716 ZO van Haastrecht, 114169/444983 (L); Hattum, HJ van 2413 19410101 Leiden, Nachtegaallaan, 92255/465441 (L); Hattum, HJ van 305 19470101 Zoeterwoude, 94121/458624 (L); Hattum, HJ van 912 19120101 Leiderdorp richting Koudekerk, 98485/460742 (L); Heerden, A van field observation with photo 20160801 Leerdam, 131542/430105, waarneming.nl; Henrard, J Th s.n. 19140601 oever Merwede bij Gorinchem, 127448/426179 (L); Heurn, WC van s.n. 19400824 Voorschoten, 90384/460125 (L); Heurn, WC van s.n. 19400824 Voorschoten, bij Allemansgeest, 92014/460933 (L); Icke, H, s.n.

19030825 Schiebroek, 92273/442302 (L); Ittersson, van s.n. 19030812 Zoetermeer, 93870/452724 (L); Jacobs, M s.n. 19500625 Voorschoten, Hofweg, 91952/461018 (L); Janmaat, K field observation with photo 20110607 Zevenhoven-Groene Jonker, 116609/465770, waarneming.nl; Jongh, de s.n. 19550101 Oegstgeest, 92519/466526 (L); Kloos Jr, AW s.n. 19130601 Dordrecht, 106408/424012 (L); Koopmans-Forstmann, D s.n. 19100101 Den Haag, Moerweg, 80143/452523 (L); Koster, WJW s.n. 19150601 Scheveningen, Verversingskanaal, 79049/455370 (L); Laar, HJ van de 435 19580728 Boskoop, Spoolwijkседijkje, 107078/454696 (L); Lam, HJ 6707 19410715 Wassenaar, Zuidwijk, 89342/462345 (L); Lucas, JAW s.n. 19490614 Voorschoten, 90384/460125 (L); Mennema, J s.n. 19760622 Lexmond aan de Zouwe, tussen Meerkerk en Ameide, 127050/440662 (L); Mol, JL 839 19650620 Voorburg, Rode Laan, 85859/455235 (L); Ogterop, A s.n. 18960601 Hilligersberg, plassen, 93304/440738 (L); Oudemans, CAJA s.n. 18420701 Leiden, 93775/463605 (L); Overbeek, H s.n. 19750820 Lek 1 km oost van Schoonhoven, 119817/439198 (L); Overbeek, H s.n. 19750820 tussen Schoonhoven en Ammerstol, aan de Lek, 116392/438923 (L); Overbeek, H s.n. 19750826 tussen Nieuwpoort en Gelkenes langs de Lek, 118464/438943 (L); Peeters, M s.n. 19260727 Vlist, 116096/443022 (L); Quaadgras, L 706 19640705 Rijswijk, langs sloot Juliaalaantje, 82054/452022 (L); Siertsema, LH s.n. 19330725 Scheveningen, Westbroekpark, 79887/457892 (L); Siertsema, LH s.n. 19400710 tussen Delft en Vethel, 84404/442328 (L); Simons, ELAN field observation with photo 20160830 Delft, Abtswoudse Bos, 82987/443659, waarneming.nl; Sloff, JG s.n. 19170706 Hilligersberg, Bergsche plas Lommerrijk, 92992/440305 (L); Sloff, JG s.n. 19170714 Rotterdam, uiterwaard in Nieuwe Maas langs Schaarlijk, ten westen Maaskerkje, 96856/435628 (L); Sosef, MSM 13 19810825 Delft-Zuid, slootje bij wijk in aanbouw 372514, 85350/442487 (L); Thomas, P 1008 19770705 Leiden, 93138/462810 (L); Tombe, FA des s.n. 19010712 Leiden, Kronestein, 93719/461914 (L); Touw, A 1334 19570706 Leiden, slootje langs Nachtegaallaan, hoek Merelstraat, 92255/465441 (L); Touw, A 1464 19530720 Rijswijk, 82054/452022 (L); V s.n. 19020826 Willemsdorp, 102667/415722 (L); Verburg, J field observation with photo 20140611 Alphen aan den Rijn, 104849/458270, waarneming.nl; Verstraaten, R field observation with photo 20120609 Hazerswoude, 100095/459829, waarneming.nl; Vliet, B van field observation with photo 20120612 Wijngaarden, 111037/428549, waarneming.nl; Vondervoort, T vd field observation with photo 20120702 Gouda, 110132/447141, waarneming.nl; Weeda, EJ s.n. 19730801 Voorschoten, zuidrand bebouwde kom, 90546/458723 (L); Wieffering, JH s.n. 19670620 Oegstgeest, 92519/466526 (L); Wijngaarden, AJ van s.n. 19420801 Nieuwkoop, 113521/462505 (L).

## BOLBOSCHOENUS MARITIMUS

### *Flevoland*

Apperlo, P field observation with photo 20120828 Rutten, Noordoostpolder, 171730/535208, waarneming.nl; Bakker de Wit, P s.n. 18520101 Urk, 169397/519377 (L); Bakker, D 3739 19570917 kwelstrook ten zuiden van zandplaat 'Het Spijk' oostelijk Flevoland, 177600/493040 (L); Bakker, D s.n. 19550622 Noordoostpolder, Kadoeler Kanaal, 193513/519939 (L); Brandes, E s.n. 20151003 Flevoland, 154590/475386 (L); Brandes, E s.n. 20151003 Flevoland, 154647/475322 (L); Heukels, P 574 19710605 Knardijk bij lage Knarsluis Zuid-Flevoland, IVON 261453, 158249/495588 (L); Hunger, FWT s.n. 19050810 moeras ZO Urk, 169397/519377 (L); Koopmans-Forstmann, D 1931-117 19310524 buitendijks terrein, Kuinre, 185649/533045 (L); Leys, H s.n. 19680701 Lelystad, 157100/501165 (L); Leys, H s.n. 19680701 Lelystad, langs dijkje Houtribsluizen, 4e plas, wegkant, 157867/504404 (L); Linde, B te field observation with photo 20100823 Burchtkamp, ten Z van Lelystad, 160143/496533, waarneming.nl; Maijer, I field observation with photo 20120630 Almere-Kruidenwijk, 142574/487433, waarneming.nl; Maijer, I field observation with photo 20130810 Horsterwold, ZW van Zeewolde, 160636/479897, waarneming.nl; Meulenbelt, B field observation with photo 20150810 Almere-De Vaart, 145905/492264, waarneming.nl; Swart, JJ, 1278 19270612 Urk, 169397/519377 (L); Swart, JJ, s.n. 19270613 Schokland, 181248/517200 (L); Wit, HCD de 371 19300608 Schokland, 181248/517200 (L); Zinderen Bakker, EM van s.n. 19300826 Knardijk, 161767/491573 (L).

### *Friesland*

Albarda, H s.n. s.y. Leeuwarden, 182312/579603 (L); Anonymus s.n. 18190715 St Jakobs Parochie, 169530/587383 (L); Anonymus s.n. s.y. Terschelling, 151287/601645 (L); Bisschop van Tuinen, K

s.n. 18690720 Oldeboorn, 188948/562482 (L); Borssum Waalkes, J van 5098 19460701 Terschelling, Oosterend, 56342, 154557/602045 (L); Borssum Waalkes, J van 6225 19460701 Terschelling, Formerrum, kwelder, 149826/600379 (L); Breemen, PJ van s.n. 19030630 Vlieland, 126212/585839 (L); Clason, EW s.n. 19520101 Oudemirdumer Klif, 164828/538838 (L); Dolstra, J field observation with photo 20150718 Breezandijk, wadkant, 142574/559213, waarneming.nl; Haveman, R field observation with photo 20160627 Vliehors, 123665/582598, waarneming.nl; Huizenga, J field observation with photo 20100709 Ameland Lange Duinen, 173685/608473, waarneming.nl; Jacobs, M s.n. 19500612 Terschelling, Kroonpolders tussen strandpaal 3 en 4, 141986/598971 (L); Koopmans-Forstmann, D 1928-342 19280708 binnendijks terrein omgeven door basaltblokken, Stavoren, 153238/544105 (L); Koopmans-Forstmann, D 1928-446 19280731 kant van IJskeboerevaart, NW van Workum, 158209/556083 (L); Koopmans-Forstmann, D 1928-614 19280824 ten oosten van Lemmer, in sloot, buitendijks, 178710/540976 (L); Koopmans-Forstmann, D 1928-619 19280824 ten westen van Schoterzijk, in een sloot, 183221/536846 (L); Koopmans-Forstmann, D 1928-621 19280824 binnendijks, WNW Schoterzijk, 183221/536846 (L); Koopmans-Forstmann, D 1928-622 19280824 ten oosten van Lemmer, in sloot, buitendijks, 178710/540976 (L); Koopmans-Forstmann, D 1928-623 19280824 buitendijks, ten westen van Schoterzijk, 181985/537101 (L); Koopmans-Forstmann, D 1928-627 19280824 Schoterzijk, buitendijks, in plasje, 183221/536846 (L); Koopmans-Forstmann, D 1928-631 19280824 bij Schoterzijk, buitendijks, 181985/537101 (L); Koopmans-Forstmann, D 1928-767 19280916 buitendijks, vlak terrein ZW van Takozijk, 171852/541365 (L); Koopmans-Forstmann, D 1928-780 19280916 tussen Nijemirdum en Takozijk, 170429/541465 (L); Koopmans-Forstmann, D 1929-117 19290609 Lemster Hop, ten oosten van Lemmer, 177857/539691 (L); Koopmans-Forstmann, D 1929-150 19290612 sloot aan noordzijde Gaast-Parrega (niet in Parregaaster polder), 158554/559234 (L); Koopmans-Forstmann, D 1929-169 19290615 sluisput bij zanddijk, Kornwerderzand, 151532/565011 (L); Koopmans-Forstmann, D 1929-419 19290713 moeras ten noorden van spoorlijn bij Stavoren, 153511/544578 (L); Koopmans-Forstmann, D 1929-482 19290711 tussen Rode Klif en Laaxum, binnendijks, 155825/541093 (L); Koopmans-Forstmann, D 1930-403 19300628 Kornwerderzand, 151612/565104 (L); Koopmans-Forstmann, D 1930-601 19300801 oever Slotermeer, 170958/547571 (L); Koopmans-Forstmann, D 1930-606 19300801 oever Slotermeer, bij baak, 169275/546204 (L); Koopmans-Forstmann, D 1930-871 19300821 ZO van Nije Mirdum, 168144/540300 (L); Koopmans-Forstmann, D 1930-913A 19300825 oever Zandpoel (Gaasterland) ten NO van Sondel, 170878/543203 (L); Koopmans-Forstmann, D 1931-505a 19310831 NW van Bakhuizen, 158173/543523 (L); Koopmans-Forstmann, D 1931-505A/B/C 19310831 steeke ten noordwesten van Bakhuizen, 159464/542538 (L); Koopmans-Forstmann, D 1931-524 19310901 Bakhuister vaart, 158963/542905 (L); Koopmans-Forstmann, D 1931-572 19310907 weg Koudum-Heidenschap het Van, 160043/549082 (L); Koopmans-Forstmann, D s.n. 19260629 Leeuwarden, strafgevangenis H65134, 182604/579310 (L); Koster, JTh 4221 19280902 Vlieland, zuidkust, 122570/581262 (L); Koster, JTh s.n. 19690925 Schiermonnikoog, 209099/611751 (L); Koster, JTh s.n. 19690925 Schiermonnikoog, 209099/611751 (L); Ooststroom, SJ van 17309 19530710 Vlieland Kroonspolders, 4, 36, plasje westelijk uiteinde polders, 125733/585567 (L); Ploeg, DTE van der 1572-1 19520626 Buitenveld, 193246/585880 (L); Ploeg, DTE van der 1572-2 19440703 Bergum-Nieuwstad, 196412/579154 (L); Ploeg, DTE van der 1572-8 19510706 Birdaarder Straatweg, 193297/592421 (L); Ploeg, DTE van der 1572-9 19520703 Dokkum, in sloot, 195757/593377 (L); Ploeg, DTE van der 49-106 19490721 Schiermonnikoog, 205659/609209 (L); Ploeg, DTE van der 49-152 19490814 Klaarkampstermeer, 190840/590986 (L); Ploeg, DTE van der 49-279 19490903 Buitenveld, 192580/583114 (L); Ploeg, DTE van der s.n. 19580718 ten westen van Marrum, 181898/593188 (L); Ploeg, DTE van der s.n. 19640606 Hindeloopen, Stoenckherne, 156009/550636 (L); Regt, JH de field observation with photo 20110806 Oudemirdum, 161635/540243, waarneming.nl; Schulp, JA s.n. 19660801 Schiermonnikoog, moeras langs Reddingsweg, 208288/611656 (L); Siertsema, LH 627 19350826 Ameland, G55813, 171554/608418 (L); Simons, ELAN field observation with photo 20100918 Vlieland, Vallei van Malgum, 127052/587206, waarneming.nl; Sloff, JG s.n. 19180614 Gemeente Terschelling op de 'Grioe' achter Oosterend, 154557/602045 (L); Sloff, JG s.n. 19340831 Rotsterhaule, noord-oever Tjeukemeer, 184476/547445 (L); Sloff, JG s.n. 19350828 Ameland, strand tussen buitenpaal 5 en 6, 188900/608600 (L); Sloff, JG s.n. 19350830 Ameland, Oerderduinen ten oosten Stuifdijk, 188993/608630 (L); Soest, JL van s.n. 19510701 Boschplaat Terschelling, 159986/604769 (L); Stoffer, J s.n. 19590924 Groene strand, West-Terschelling, 142700/597400 (L); Suringar, WFR s.n. 18600907

Schiermonnikoog, duinvlakten, 209099/611751 (L); Talsma, H field observation with photo 20150907 Sneek, 174878/560188, waarneming.nl; Vries, G de field observation with photo 20120826 Moddergat, 199607/602318, waarneming.nl; Vries, V de 259 19370601 Vlieland stuifpolder, 125836/585566 (L); Wilde, AG de 2546 19470719 Boschplaat Terschelling, 159986/604769 (L); Wit, HCD de s.n. 19320701 Terschelling, 151287/601645 (L); Zanten, B.O. van s.n. 19510101 Terschelling, 151287/601645 (L).

#### *Gelderland*

Anonymus s.n. 18330603 Tussen Harderwijk en Elburg, 178800/489900 (L); Berg, LJ van den s.n. 20160617 Dortherbeek, 213424/471392 (L); Biermans, I s.n. 19000701 strand Elburg, 184684/495639 (L); Dirkse, G s.n. 20140723 Ressen, 187974/433866 (L); Eimers, N field observation with photo 42577 Harderwijk, Dolfinarium, 170472/484895, waarneming.nl; Jansen, MT 16578/19 19170801 veel op 't strand te Nunspeet, 179000/490000 (L); Jansen, MT s.n. 19170801 strand te Elburg, 185054/495937 (L); Kok Ankersmit, HJ s.n. 18980712 langs kanaal van Nijkerk naar zee, 160532/473374 (L); Kop, LG s.n. 19610708 Nijkerk (slootkant bij dijk), 158876/473225 (L); Meulenbelt, B field observation with photo 20150606 Nuldernaauw, 166618/480054, waarneming.nl; Nannenga-Bremekamp s.n. 19350725 Langs het IJsselmeer ten Noorden van Putten, 166000/478000 (L); Oudemans, CAJA s.n. 18350101 Harderwijk, 170634/484702 (L); RB s.n. 18640601 Harderwijk, 170000/484000 (L); Simons, ELAN 1758 20151114 Ressen, 188766/434363 (L); Simons, ELAN 1988 20161022 NW of Noordijk, N of Hoge Broekdijk E of crossing with Aaftinkdijk, 234524/463437 (L); Soest, JL van s.n. 19470709 Oude-Kerk in de Zuiderzee 462123, 182500/493500 (L); Steenis, CGJ van s.n. 19220606 zeesloot achter dijk bij Nijkerk, 160358/474183 (L) Wttewaal s.n. 18330101 tussen Elburg en Harderwijk, 178695/489664 (L); Wttewaal s.n. 18330803 langs het strand bij Harderwijk, 170000/484000 (L).

#### *Groningen*

Clason, EW s.n. 19520101 Fransum bij Aduard, 225706/588468 (L); Clason, EW s.n. 19520516 Groningen, Hoendiep, 222482/583197 (L); Clason, EW s.n. 19540101 nieuwe Eemspolder, ten N van Roodeschool, 246122/605899 (L); Clason, EW s.n. 19540101 oude arm Reitdiep tussen Garnwerd en Winsum, 228921/592669 (L); Clason, EW s.n. 19540628 Joh Kerkhoven Polder bij de Dollard, 266517/588522 (L); Duiven, JM 576 19490805 Midwolderveen-Meerland, nabij vml Huningameer, 265578/579480 (L); Heukels, P 1380 19760624 sloot ten noorden van Hefswal (gemeente Uithuizermeeden), 244836/605084 (L); Kluter, P s.n. 19520616 Beerta, 269186/577709 (L); Ludden-Middelbeek, S s.n. 19760528 Noord van Vriescheloo, westen van gemaal 'De Klieve', langs het Veendiep, 271223/569776 (L); Noord, GJ van field observation with photo 20150918 Delfzijl, 256347/595581, waarneming.nl; Noord, GJ van field observation with photo 20150925 Lauwersoog, 211290/600124, waarneming.nl; Ruben, J field observation with photo 20150801 Groningen, Reitdiep, 231006/583703, waarneming.nl; Schepper s.n. Rottumeroog, 234115/617821 (L); Vries, G de field observation with photo 20110810 Baflo, 229397/598102, waarneming.nl; Vries, G de field observation with photo 20120830 Warffum, 233011/602134, waarneming.nl; Vries, G de field observation with photo 20141001 Termunterzijl, 263141/592376, waarneming.nl.

#### *Limburg*

Wever, A de s.n. 19120822 Elsloo, aan de Maas, 181032/329000 (MAAS).

#### *Noord-Brabant*

Backer, CA s.n. s.y. Almkerk, 125500/420400 (L); Beeftink, WG s.n. 19690730 Bergse Maas bij veer ten oosten van Dussen, 127040/414572 (L); Bosch, van den s.n. 18600721 Bergen op Zoom, buitendijks, 74322/388770 (L); Ettema, N field observation with photo 20160711 Volkel-Knokerdweg, 171977/403994, waarneming.nl; Ettema, N field observation with photo 20160712 Uden-Groenewoud, 170049/407200, waarneming.nl; Ettema, N field observation with photo 20160712 Uden-Trentsedijk, 177343/409051, waarneming.nl; Geraets, L field observation with photo 20140803 Landerd, 177376/409087, waarneming.nl; Hermans, T field observation with photo 20120620 Uden, 170591/404768, waarneming.nl; Jongh, de s.n. 19510806 oever Oosterschelde ten zuiden Bergen op Zoom, 73484/383616 (L); Koster, JTh s.n. 19650924 Brabantse Biesbosch, Zuider Jonge Deen,

109837/416265 (L); Nilsen, K field observation with photo 20120929 Dintelse Gorzen, 79171/406225, waarneming.nl; Noord, GJ van field observation with photo 20150919 Werkendam, 114182/421048, waarneming.nl; Ruth, P van 14087 20080910 Chaam, Broekloop, 116000/395000 (NMBT); Sloff, JG s.n. 19250701 Nieuw Vosmeer, langs de rand van de zoetwaterput in de vluchtberg op 'De Nachtegaal', 73981/400740 (L); Sloff, JG s.n. 19340820 langs Hollands Diep ter hoogte van de Vogelvanger, 102373/414202 (L).

#### *Noord-Holland*

Abeleven, ThHAJ s.n. 18370823 oosterdoksdiijk Amsterdam, 122145/487655 (L); Anonymus s.n. 18710901 Petten, 105807/531411 (L); Anonymus s.n. s.y. Haarlemmermeerpolder, 106988/479347 (L); Ballintijn, K s.n. 20151107 Purmerbos, 127421/500136 (L); Barendse, R field observation with photo 20150821 Texel - Polder het Noorden - Utopia, 122064/571029, waarneming.nl; Barkman, JJ 981 19370705 tussen Alkmaar en Egmond a/d Hoef, aan een vaart in de weilanden, 107889/515317 (L); Biologenexcursie VU s.n. 19520606 Texel, Slufter, 116588/573037 (L); Boursse-Wils s.n. s.y. Amstelveenseweg, 118890/481805 (L); Brand, J s.n. 18900621 Zeeburg, Amsterdam, 126209/487233 (L); Buiten, N s.n. 20130605 IJmuiden aan Zee, Kennemermeer, 99133/496729 (L); Buse, LH s.n. 18370701 IJdijk bij Spaarndam, 106845/491978 (L); Butot, LJM s.n. 19440604 Schellinkhout, 136930/516328 (L); Buwalda, P s.n. 19339618 Texel, Muy, 115339/ 571048 (L); Carmiggelt, C s.n. 18920901 Nieuwer-Amstel, 121804/484788 (L); Croockewit, HWE s.n. 19320831 Geul, Texel, 110000/558000 (L); Croockewit, HWE s.n. 19430713 Limmen, 108128/509472 (L); de L & v S s.n. 19270801 de Gest, Wieringen, 130569/549276 (L); Dekker, J field observation with photo 20130726 Kennemermeer, 99054/496291, waarneming.nl; Docters van Leeuwen, WM s.n. 18990616 Huizen, zeehavens, 145288/480173 (L); Donk, MA s.n. 19290701 Texel, voorste Mui, 115339/571048 (L); Dorgelo, A s.n. 19440814 Koedijk, westoever NH Kanaal, 111558/519549 (L); Feenstra-Sluiteer, CP s.n. 19020612 Zeeburg, Amsterdam, 126209/487233 (L); Hall, van s.n. s.y. Amsterdam, 122000/486000 (L); Harshagen, IHAE s.n. 19660801 Wieringen, 126702/545958 (L); Harting, A s.n. 18570704 Wieringen, 126702/545958 (L); Harting, A s.n. 18570708 Eijerland, 119912/571463 (L); Hartsen, FA s.n. 18600828 Amsterdam, 122000/486000 (L); Hoogendoorn, H 648 19520623 Valkeveen, kust IJsselmeer, 141965/480016 (L); Hunger, FWT s.n. 19050822 Wieringen, slootkanten Stroeërkoog, 127536/548349 (L); Iersel, J van s.n. 19390504 Haarlem, bouwland, langs sloot, 104162/488308 (L); Inden, M field observation with photo 20130817 Haarlem, Bomenbuurt, 104032/489833, waarneming.nl; Kloos Jr, AW s.n. 19110701 Westknollendam, 114138/503446 (L); Kloos Jr, AW s.n. 19140701 Westknollendam, 114138/503446 (L); Kruseman, G s.n. 19260529 Halfweg, 111957/488512 (L); Leenhouts, PW 815 19510827 IJdijk tussen Blauwe Hoofd en Durgerdam, 127692/487571 (L); Leenhouts, PW 820 19510830 weg van Zunderdorp naar Ransdorp, 127263/490315 (L); Lutjebarus s.n. 19280616 Marske-polder, Wieringen, 125836/547449 (L); Meijer-Drees, E 276 19260801 Texel, 116590/566719 (L); Meijere, JCH de s.n. 18830617 Amsterdam Handelskade, 124000/487000 (L); Noord, GJ van field observation with photo 20121110 IJmuiden, Velsen, Noordzeekanaal, 103815/497483, waarneming.nl; Noord, GJ van field observation with photo 20150926 Den IJp, 121390/496856, waarneming.nl; Oudemans, CAJA 849 18720715 Heemstede, aan sloot, zilte klei, 102730/485262 (L); Popta, CML s.n. 18940614 omtrek Schoten, 104325/491273 (L); Popta, CML s.n. 18950714 bij 't Nieuwe Diep, 125673/486203 (L); Prell, HH s.n. 19430930 Ruigvaart Haarlemmermeer tegenover Schiphof, 106006/479727 (L); Sande Lacoste, van de s.n. s.y. Heemstede, ad Haarlemmermeer to Meer en Bosch, 106000/484000 (L); Siertsema, LH s.n. 19320601 rand Walenburger polder, Texel, 116098/566442 (L); Siertsema, LH s.n. 19320829 Wieringen, westelijk van Hippolytushoef, 124830/546310 (L); Simons, ELAN 1975 20160911 St Pancras, Twuyversweg, 114549/520086 (L); Simons, ELAN field observation with photo 20160911 St Pancras, Langedijk, 114885/520176, waarneming.nl; Simons, ELAN field observation with photo 20161029 Purmerend, 127704/502176, waarneming.nl; Soest, JL van s.n. 19210801 Volendam, 133290/501353 (L); Spruijt, T field observation with photo 20140804 Bakkum/Castricum NH-duinreservaat, 103439/506313, waarneming.nl; Steenis, CGGJ van 1833 19220807 Huisduinen-Den Helder, 110495/552015 (L); Steenis, CGGJ van s.n. 19260626 Koog Texel, laagtes in duinvallei, 113000/567000 (L); Steenis, CGGJ van s.n. 19260626 Muiver en Slufter Kooy Texel, 116588/573037 (L); Stoffer, J s.n. 19620901 NH Kanaal bij West-Grafdijk, 114973/507572 (L); Suringar, WFR s.n. s.y. Haarlemmermeer, 105757/479451 (L); Touw, A 963 19550703 Slufter,

Texel, 116588/573037 (L); Vermeulen, P s.n. 19270801 Texel, 116590/566719 (L); Voo, EE van der s.n. 19530906 Schellingwoude, oever IJsselmeer, 126331/488592 (L); Vroman, M s.n. 19520603 Den Helder, 112778/552551 (L); Vuyck, L s.n. 18960707 Bergerweg bij Alkmaar, 110500/517000 (L); Wouda, C field observation with photo 20131003 Koog aan de Zaan, 114811/495970, waarneming.nl.

#### *Overijssel*

Bondam, R s.n. s.y. Kampen, 189781/507053 (L); Brand, J s.n. 19280701 strand Vollenhove, 192366/520297 (L); Hunger, FWT s.n. 19050719 schokland, tussen middenbuurt en oudenkerk, 181145/515788 (L); Kok Ankersmit, HJ s.n. 18500101 Deventer, grachten zeekant, 207090/473825 (L); Koopmans-Forstmann, D s.n. 19280723 Zuiderzeekust NO van Vollenhove, 193700/523323 (L); Leys, H s.n. 19680710 Weerribben, Oldemarkt, 194000/537000 (L); Soest, JL van s.n. 19280601 Vollenhove, strand benoorden de Voorst, 192293/521286 (L); Top, WG s.n. Zwartendijk, 188916/506343 (L); Veth, JAC s.n. 19600616 Vollenhove, aan zuiderzeekust, 193700/523323 (L).

#### *Utrecht*

Koornneef, J s.n. s.y. Nieuwersluis, 129020/467653 (L); Ooststroom, SJ van 622 19260630 Spakenburg, Zuiderzeekust, 154620/474271 (L); Simons, ELAN 1973 20160909 east of Everdingen, 140073/442086 (L); Witcamp, C field observation with photo 20150830 Tull en 't Waal, 138082/445149, waarneming.nl; Zinderen Bakker, EM van s.n. 19300903 Naardermeer, Hoofdtocht tot het Spookgat, 135964/479515 (L).

#### *Zeeland*

Bakker, D s.n. 19550617 tussen Vrouwenpolder en Veere, zandig terrein achter dijk, 33766/398621 (L); Boogert, J vd 125 19740614 Slikken van Flakkee, noordelijk deel, bij zanddepot, Grevelingen, 59948/422908 (L); Braber, L s.n. 19630701 Renesse, 43498/417180 (L); Brakman, P 247 19280802 Nieuw en Sint Joosland, 34983/389681 (L); Brakman, P s.n. 19430524 kom achter de Nieuwlandse Haven, 34313/389961 (L); Buysman 187 25188007 slootkanten bij Vlissingen, 29617/386097 (L); Claessens, J field observation with photo 20150913 Het Zwin, 14800/377157, waarneming.nl; Evers, GJ s.n. 19170601 Middelburg, 32068/391601 (L); Gorter, A 1591 19370822 Terneuzen, Boerengat, 43762/372289 (L); Hoek, K 164 19730627 Kabbelaarsbank, 50165/419439 (L); Hoek, K 195 19730802 Slikken van Flakkee, 61370/419498 (L); Hoek, K 419 19740624 Slikken van Flakkee, 61370/419498 (L); Hoek, K 555 19760712 Middelpaalt (bij Brouwersdam), 47762/419377 (L); Jansen, MT s.n. 19040101 Goes, 50581/391185 (L); Knaap, F vd field observation with photo 20100626 Verdrongen Land van Saefinghe - noord van Emmadorp, 68696/371841, waarneming.nl; LHF s.n. 19690804 natuureservaat Schelpfoek, Serooskerke, 45967/413066 (L); Lako, D s.n. 18760701 Walcheren, Fort Rammekens, 34527/386256 (L); Lako, D s.n. 18830801 St Annaland, 66013/401987 (L); Lako, D s.n. 18830801 Tholen, 74052/394341 (L); Lako, D s.n. 18850801 Groede, 24104/378322 (L); Meininger, P field observation with photo 20100629 Sas van Gent, 44637/360565, waarneming.nl; Meininger, P field observation with photo 20100706 Biervliet, 36265/371983, waarneming.nl; Munck, W de s.n. 19621005 Middelpaaten, Veerse Meer, 42052/396537 (L); Ogterop, A s.n. 18940528 Biezelingen, Zuid-Beveland, 56002/388202 (L); Ooststroom, SJ van 632 19270915 dijk bij Kamperland (N Beveland), 37318/397862 (L); Ruijgrok, H s.n. 19630622 Groede, Verzonken Zwarte polder, 19415/379347 (L); Schminjer, P s.n. 18681028 oostzijde Zierikze, 53926/407812 (L); Schuringa, P s.n. 18680901 Zierikzee, 53213/407793 (L); Siertsema, LH s.n. 19360723 Ziesl Ham Zuid-Beveland, / (L); Sloff, JG s.n. 19350809 Borsselen, langs het Westeindse Weel (aan het eind van de overendse watergang), 42482/383369 (L); Vervoort s.n. 19430615 Groot Eiland bij Hulst, 58221/367851 (L); Visser, A de s.n. 19570711 Braakmanpolder, Hoek, 42882/370144 (L); Visser, A de s.n. 19580723 Nieuwvliet, Zwarte Polder, 19145/379246 (L); Visser, A de s.n. 19630711 Inlaag Thoornpolder Wissenkerke, 40695/401761 (L); Walraven, A s.n. 18540501 Sas van Gent, 43943/361033 (L); Walraven, A s.n. 18610620 Kapitalen van Biervliet, 35866/370056 (L); Walraven, A s.n. 18630601 Hoek, 42882/370144 (L); Walraven, A s.n. 18630701 Hoek, 42882/370144 (L).

## *Zuid-Holland*

Anonymus s.n. 18590901 Leiden, 93775/463605 (L); Balke, NPW s.n. 19340729 Oostvoorne, 66492/436722 (L); Beeftink, WG 749 19590901 Zuidhollandse Biesbosch, 114129/418613 (L); Beeftink, WG 797 19590909 Kwade Hoek, eerste vallei buiten oude duinreep, paal 8, 56152/428483 (L); Beek, A van de s.n. 19690501 Zuidkant van polder Goedereede en Ouddorp, 57000/424000 (L); Beijersbergen, A s.n. 19820701 Den Briel, 70993/435821 (L); Bes, J field observation with photo 20090809 Voorne-Westplaat, 62125/438157, waarneming.nl; Dorgelo, A 225-a 19160801 Oostvoorne, 66492/436722 (L); Gaasenbeek, H s.n. 19710812 Nieuw-Beyerland, dijk en oevers langs het Spui, 82665/425783 (L); Gazan, H field observation with photo 20140730 Streefkerk, 109650/435003, waarneming.nl; Gessele, F van field observation with photo 20150811 Piershil, 80006/424371, waarneming.nl; Gesselen, F van field observation with photo 20160711 Strijensas - Albert-, Pieters- en Leendertspolder (APL-polder), 99122/414086, waarneming.nl; Hattum, HJ van 5298 19470828 Leiden, vijver Hortus, 93203/463456 (L); Hek, JC de s.n. 19820501 Hardinxveld-Giessendam, griend langs Rijksweg, strand, 116470/426075 (L); Henrard, J Th s.n. 19140701 Dordrecht, De Staart, 108110/425403 (L); Henrard, J Th s.n. 19140705 Groene strand Rockanje, 63383/431934 (L); Huizing, DJJ s.n. 19531010 Moordrecht-Nieuwerkerk, autobaan, 103112/444496 (L); Hunger, FWT s.n. 18950925 Hoek van Holland, 68536/ 444383 (L); Icke, H, s.n. 19020707 Vlaardingen, 83000/434000 (L); Jansen, MT s.n. 19040619 Hoek van Holland (eilandje), 68536/444383 (L); Jansen, MT s.n. 19170628 Vlaardingen langs de rivier, 83000/434000 (L); Jansen, MT s.n. 19180101 Vlaardingen, uiterwaarden, 83000/434000 (L); Kern, JH 5234 19350727 IJsselmonde, Vondelingenplaat, 83901/433509 (L); Kern, JH 6519 19480725 Rockanje, bij het Nieuwe Water, 62937/432214 (L); Koopmans-Forstmann, D s.n. 1910-605 Hoek van Holland, eiland, 68536/444383 (L); Koster, JTh s.n. 19690915 Oostvoorne, 66492/436722 (L); Kruijne, AA s.n. 19370820 Brielle, 70993/435821 (L); MJ s.n. 19500709 De Beer' tegenover Hoek van Holland, 64317/441714 (L); Martens, R field observation with photo 20100810 Kwade Hoek west, 58295/428940, waarneming.nl; Masseling, GJ 1792 19490828 Leiden, aanleg nieuwe weg bij de Vliet tussen Leiden en Voorschoten, 92362/460876 (L); Meer, P van de s.n. 19720602 Numansdorp, Nieuwe Gors, aan de nw zijde van het bruggehoofd van de Haringvlietbrug, 87085/415463 (L); Nannenga-Bremekamp s.n. 19370626 Den Briel, 70993/435821 (L); Ooststroom, SJ van 10773 19480725 Rockanje, bij het Nieuwe Water, 62937/432214 (L); Ooststroom, SJ van 1765 19280701 De Beer, tegenover Hoek van Holland, 64317/441714 (L); Ooststroom, SJ van 4489 19310828 Oostvoorne, groene strand, ten zuiden van het verlengde der Duinlaan, 63754/437157 (L); Ooststroom, SJ van 639 19250701 Rotterdam, Waalhaven, 89983/433641 (L); Quaadgras, L s.n. 19980501 Kwintsheul, sloot in de Vogelaer, 76433/447919 (L); Reinink, K s.n. 19860828 Rotterdam, Rhoonse grienden, Golfbaan, 90607/427812 (L); Simons, ELAN 1969 20160830 Rozenburg, Nieuwe Waterweg, 75816/436784 (L); Simons, ELAN field observation with photo 20160830 Dordtse Biesbosch - Tongplaat, 108035/417683, waarneming.nl; Sloff, JG s.n. 19170721 Oostvoorne, groene strand, ten zuiden van het verlengde der Duinlaan, 63754/437157 (L); Soest, JL van 17387A 19190701 Rockanje, 62937/432214 (L); Vervoort s.n. 19370603 Schiedam, Maasoever, 86908/435002 (L); Vervoort s.n. 19430530 Rozenburg, kreek, 76648/435872 (L); Weevers, TH s.n. 18930519 Rotterdam, Ruigeplaat, 82790/431411 (L); Weevers, TH s.n. 19190701 Ouddorp Goeree, 55068/425623 (L); Wilde, AG de 202 19450722 Eiland Dordrecht (Staart), 108110/425403 (L); Sande Lacoste, CM van de s.n. 18590710 Coevorden, 246094/518905 (L).

## APPENDIX 2. Vegetation relevés

Table 2. Vegetation relevés with *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zákr.

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<b>Author</b>	ES	ES	ES	ES	RH	RH	ES	ES	ES	ES	ES	ES	ES	ES	RH	LB
<b>Demi-hectad</b>	3327	3928	6138	6138	3937	3937	3828	3338	3927	3118	4041	2715	4043	2715	3937	4127
<b>Area (m<sup>2</sup>)</b>	16	4	8	1.5	12	20	6	2	10	16	6	25	6	4	12	5
<b>Exposition</b>	-	-	-	-	-	Z	-	-	-	-	-	-	-	-	-	-
<b>Inclination</b>	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
<b>Total cover (%)</b>	80	95	90	90	95	95	80	80	60	90	80	80	50	70	99	50
<b>Cover herb layer (%)</b>	80	95	90	90	95	95	80	80	60	90	80	80	50	70	99	50
<b>Cover moss layer (%)</b>	-	-	-	-	-	-	-	-	-	1	5	-	-	-	-	-
<b>Avg. height herb layer (cm)</b>	150	100	100	120	120	180	120	150	70	120	100	100	50	100	100	150
<b>Avg. height low herb layer (cm)</b>	-	-	-	-	-	60	-	-	-	-	-	-	-	-	-	-
<b>Max. height herb layer (cm)</b>	150	100	100	120	200	250	120	150	70	120	100	100	50	100	150	150

### BOLBOSCHOENUS LATICARPUS

#### c Phragmitetea / Phragmition

<i>Mentha aquatica</i>	+	2a	2a	2a	+	2m		2b	+	+	+	1	2a	+	4
<i>Lythrum salicaria</i>	+	+				2b		+	+	+	+	1	+	+	2a
<i>Rorippa amphibia</i>	+	2a				2b		+	+	+	+	+	+	+	
<i>Glyceria maxima</i>		2a			3		2b	2a	+	+	+	2a			4



(Table 2 continued)

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Phalaris arundinacea</i>	2a	2b						2b	+			2a		3		
<i>Myosotis scorpioides</i> subsp. <i>scorpioides</i>		2a		+					+			1	+	+		
<i>Lycopus europaeus</i>			2a	2a			+	+	+		+					
<i>Galium palustre</i>		1										+				
<i>Iris pseudacorus</i>			+	+							+					
<i>Phragmites australis</i>						2b			2a			2a				
<i>Schoenoplectus lacustris</i>						3					2a		r			
<i>Alisma lanceolatum</i>									+	+			+			
<i>Rumex hydrolapathum</i>										+						
<i>Nasturtium microphyllum</i>											2a					+
<i>Sparganium erectum</i> subsp. <i>erectum</i>					2b											+
<i>Sparganium erectum</i>							2a									
<b>c Caricion gracilis</b>																
<i>Carex acuta</i>											2a	2a	+	2b	+	
<b>c Nasturtio-Glycerietalia</b>																
<i>Alisma plantago-aquatica</i>	+								+		r	+		2a		
<i>Oenanthe aquatica</i>											+					
<i>Sagittaria sagittifolia</i>													+			
<i>Glyceria fluitans</i>					2a							+				1
<i>Butomus umbellatus</i>													+	2b		
<i>Leersia oryzoides</i>												2b				
<b>c Bidentetea tripartitae</b>																
<i>Persicaria hydropiper</i>									+	2a		1		1		

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Bidens cernua</i>								+	+			+				
<i>Bidens tripartita</i>								+	+			+				
<i>Bidens frondosa</i>							+				r					
<b>c Convolvulo-Filipenduletea</b>																
<i>Solanum dulcamara</i>		+						+			+					
<i>Epilobium hirsutum</i>			2b	2a			+	+								
<i>Convolvulus sepium</i>					1						r				+	
<i>Stachys palustris</i>							+					+				
<b>c Plantaginea/Lolio-Potentillion</b>																
<i>Agrostis stolonifera</i>	2a							2a		+		2b		+		+
<i>Equisetum palustre</i>	1		+	+					1				3			
<i>Persicaria amphibia</i>		+				+				2b						
<i>Equisetum arvense</i>		+						+			+					
<i>Poa trivialis</i>	2a							2a								
<i>Elytrigia repens</i>	2a							+								
<i>Myosotis laxa</i> subsp. <i>cespitosa</i>	+							+								
<i>Eleocharis palustris</i>		2b							1		2a					
<i>Potentilla anserina</i>		2a														
<i>Lysimachia nummularia</i>																
<i>Juncus inflexus</i>			2b													
<i>Juncus articulatus</i>								2a								
<b>c Potametea</b>																
<i>Nuphar lutea</i>					3	2a					+					

(Table 2 continued)

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Lemna minor</i>					1	2m								+		
<i>Elodea nuttallii</i>						+										
<i>Callitriche platycarpa</i>											+					
<i>Nymphoides peltata</i>												2b				2a
<b>Other species herb layer</b>																
<i>Salix alba</i>			+					+	+							+
<i>Salix viminalis</i>								+								r
<i>Calamagrostis epigejos</i>				2a												
<i>Rubus</i> subg. <i>Rubus</i> (excl. <i>R. caesius</i> )																2a
<b>Other species moss layer</b>																
<i>Brachythecium rutabulum</i>																2a

**Addenda**

Relevé 1: *Carex riparia* +; Relevé 2: *Rumex conglomeratus* +, *Symphytum officinale* +, *Typha latifolia* +, *Glechoma hederaceae* r; Relevé 3: *Cicuta virosa* +, *Galium aparine* +, *Cornus sanguinea* +, *Cardamine pratensis* +, *Cardamine hirsuta* +, *Sonchus oleraceus* +, *Alnus glutinosa* +; Relevé 4.: *Myriophyllum spicatum* 1; Relevé 6: *Lemna trisulca* 1, *Salix fragilis* +; Relevé 7: *Carex paniculata* r; Relevé 8: *Funaria hygrometrica* 2m, *Sonchus asper* 1, *Carex pseudocyperus* +, *Salix x multinervis* +, *Phleum pratense* +, *Juncus effusus* +, *Rorippa palustris* +; Relevé 9: *Veronica beccabunga* +; Relevé 10: *Calliergonella cuspidata* 2m; Relevé 11: *Potamogeton pectinatus* +, *Pulicaria dysenterica* +, *Hippurus vulgaris* +, *Cirsium arvense* r; Relevé 13: *Eleocharis acicularis* 2m, *Spirodela polyrhiza* 1, *Veronica catenata* +, *Rorippa sylvestris* +, *Ranunculus aquatilis* +; Relevé 14: *Equisetum fluviatile* +; Relevé 15: *Lysimachia thyrsiflora* +; Relevé 16: *Caltha palustris* subsp. *palustris* +.