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SHORT COMMUNICATION

Distribution, ecology and morphology of three *Ceratocystis* hybrids in the Province of Fryslân, the Netherlands (*Carex*, Cyperaceae)

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Key words

Carices
hybrids
Carex demissa × *C. oederi*
Carex ×*fulva*
Carex ×*pauliana*
distribution
ecology
habitus
morphology

Abstract – Recently the hybrid *Carex* ×*pauliana* [*C. hostiana* × *C. oederi*] has been found for the first time in the Province of Fryslân (formerly called: Friesland; since 2004 officially: Fryslân) in the Netherlands. In this article the authors pay attention to the distribution, habitus, ecology and morphology of this very rare hybrid. A comparison is made with the related hybrids *C.* ×*fulva* [*C. hostiana* × *C. demissa*] and *C. demissa* × *C. oederi*.

Samenvatting – Recentelijk is de hybride *Carex* ×*pauliana* [*C. hostiana* × *C. oederi*] voor het eerst gevonden in de provincie Fryslân in Nederland. In dit artikel besteden de auteurs aandacht aan de verspreiding, habitus, oecologie en morfologie van deze zeer zeldzame hybride. Voorts wordt ze vergeleken met de verwante hybriden *C.* ×*fulva* [*C. hostiana* × *C. demissa*] en *C. demissa* × *C. oederi*.

Om te bepalen tot welke van de drie hybriden een plant gerekend moet worden, beoogt de volgende sleutel behulpzaam te zijn:

1. Snavel van het urntje met een wit vlies aan de top (kenmerk overgeërfd van *C. hostiana*); kafjes met een brede vliezige rand: *C. hostiana* hybriden 2
1. Snavel van het urntje zonder een wit vlies aan de top; kafjes met een smalle wit-vliezige rand . . . . . *Carex demissa* × *C. oederi*
2. Stengels 18-55 cm; urntjes 3-4 mm lang, snavel 1-1.6 mm lang . . . . . *Carex* ×*fulva*
2. Stengels tot 25 cm; urntjes korter dan 4 mm, snavel korter dan 1 mm . . . . . *Carex* ×*pauliana*

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INTRODUCTION

The genus *Carex* L. (Cyperaceae) comprises c. 2000 species worldwide (Reznicek 1990). The exact number of species is difficult to ascertain as new species are being described all the time and it also depends on taxonomic insights. Consultation of the World Checklist of Monocotyledons (now incorporated in the World Checklist of Selected Plant Families (WCSP)) on the internet, on 1 August 2017, revealed 1969 species worldwide (Govaerts et al., continuously updated). Koopman (2015) mentioned for Europe 224 *Carex* species, 85 subspecies, 26 varieties, 25 introduced species and 295 hybrids. In the Netherlands we have to deal with 61 taxa of *Carex* and 28 hybrids (Koopman 2010). Hybridisation within *Carex* takes place in a few sections, especially: *Canescentes* (Fr.) H. Christ, *Ceratocystis* Dumort., *Phacocystis* Dumort., and *Vesicariae* (O. Lang) H. Christ (Wallace et al. 1975, Cayouette & Catling 1992). This article focusses on three hybrids within section *Ceratocystis*. The nomenclature in this article follows Koopman (2015).

In preparation of a publication about the current distribution of the association Cirsio dissecti-Molinietum Sissingh & De Vries ex Westhoff 1949 in the Dutch Province of Fryslân, all known places with this vegetation type were investigated during 2016 and 2017 (Hosper & Timmerman in prep.). Special attention was paid to all locations of *Carex hostiana* DC., one of the distinctive species of the Cirsio dissecti-Molinietum, mentioned by

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Van der Kloot (1939) and Van der Ploeg (1977). It is remarkable that on all present sites of *Carex hostiana*, the species *C. demissa* Hornem., and often also *C. oederi* Retz., grows as well. The hybrid *Carex* ×*fulva* Gooden. [*C. demissa* × *C. hostiana*] is also found on all these locations of *C. hostiana*, except in It Kobbelân (km-square 11.23.31).

CAREX SECTION *CERATOCYSTIS* AND ITS HYBRIDS

In the Netherlands, the following species belong to *Carex* section *Ceratocystis*: *Carex demissa*, *C. flava* L., *C. hostiana*, *C. lepidocarpa* Tausch and *C. oederi* (Van der Meijden 2005). *Carex flava* and *C. lepidocarpa* are very rare and more calcareous species, in former times they were almost restricted to southern Limburg. The other three species are scatteredly distributed over the country (Koopman & Więcław 2019). *Carex hostiana* is the rarest one of these three species in the Netherlands, as well as in the Province of Fryslân.

With five species within section *Ceratocystis* there are 5 × 4/2 = 10 hybrids possible and they all exist in Europe (Więcław & Koopman 2013, Więcław 2014, Więcław & Wilhelm 2014, Koopman 2015). Six of these hybrids occur in the Netherlands, but none are common there (Koopman & Więcław 2019). Of both *Carex* ×*ruedtii* Kneuck. [*C. flava* × *C. lepidocarpa*] and *C.* ×*xanthocarpa* Degl. [*C. flava* × *C. hostiana*] only a single herbarium collection from the Netherlands is known; both collections were made in South Limburg and are preserved in L. *Carex* ×*alsatica* Zahn [*C. demissa* × *C. flava*] is restricted to the southern provinces, but known there from only a few sites (Koopman 2010, Koopman & Więcław 2019).

The other three hybrids within section *Ceratocystis* have a more scattered distribution pattern in the Netherlands, like their parental species. Koopman (2010) mentioned *C.* ×*fulva* from several sites in eight provinces, based on herbarium material in L (Koopman & Więcław 2019). *Carex* ×*pauliana* F.W. Schultz was mentioned by Kern & Reichgelt (1954) from the Provinces of Overijssel and Gelderland, also based on herbarium material in L (Koopman & Więcław 2019). According to Koopman (2010), no recent finds of this hybrid has been recorded. However, Hofstra et al. (2016) showed that this hybrid still occurs in the Lemselermaten (Province of Overijssel), where it was first found in 1944 by V. Westhoff. Where both parental species grow together, the hybrid is relatively often generated, but it is possibly overlooked because of the striking similarity with both parents.

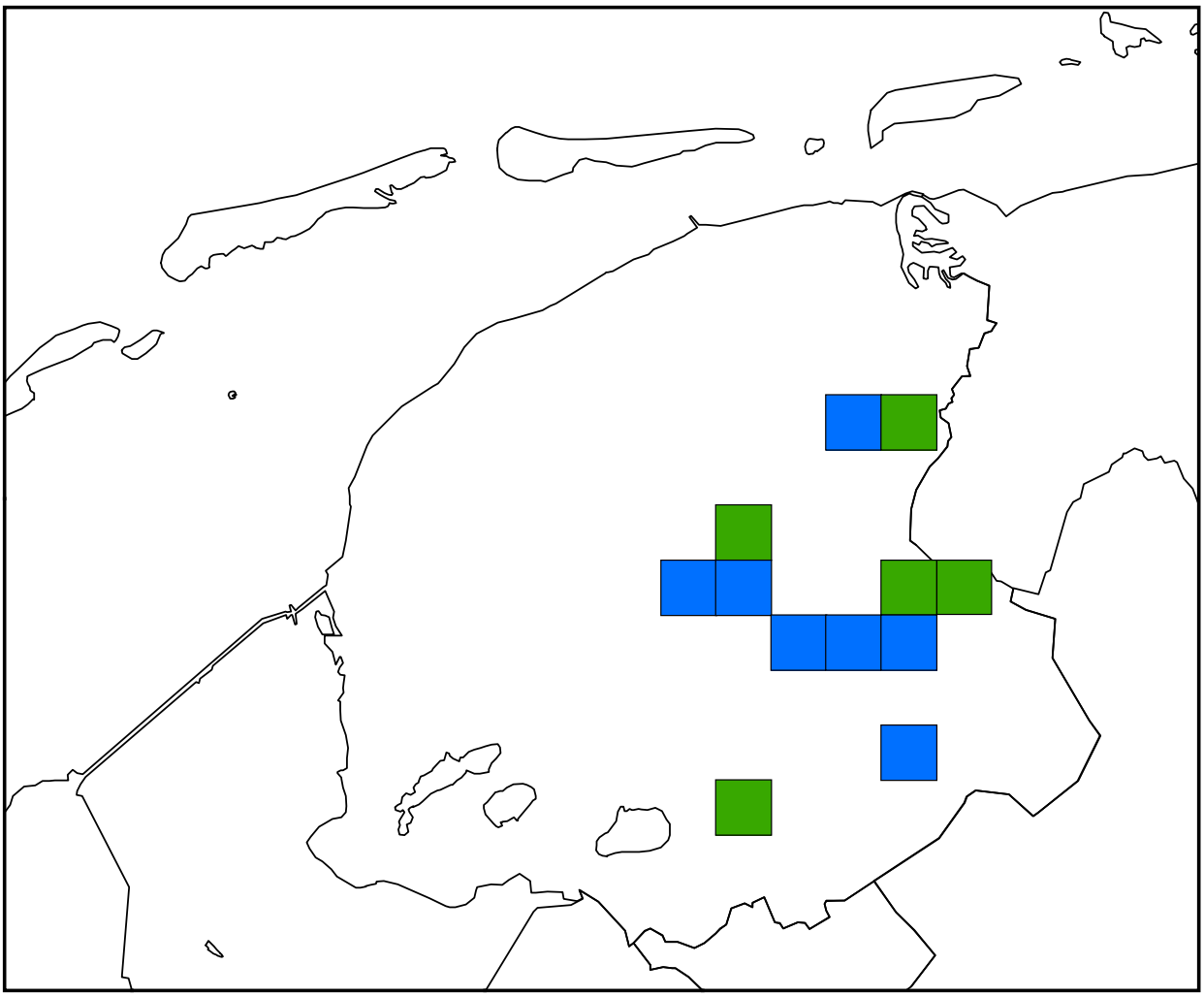

Fig. 1. Distribution of *Carex* ×*fulva* Gooden. in the Province of Fryslân, the Netherlands: Atlas squares with recent finds (■) and atlas squares with finds made by Van der Ploeg (1977) that have recently been confirmed (■).

CERATOCYSTIS HYBRIDS IN THE PROVINCE OF FRYSLÂN

Carex ×*fulva* Gooden. [*C. demissa* × *C. hostiana*]

Carex ×*fulva* was not reported for the Province of Fryslân by Kern & Reichgelt (1954). However, there are 17 collections from Fryslân in L, 16 of these have been made by D.T.E. van der Ploeg & F. Rudolphy during 1952–1981, so more than from any other province (Koopman & Więcław 2019). The oldest one, from 1952, was obviously not seen by Kern & Reichgelt (1954). Van der Ploeg (1977) mentioned this hybrid for seven atlas squares in the eastern Pleistocene part of Fryslân, as shown by the blue squares in Fig. 1. In all these seven atlas squares this hybrid has been found recently. It is noteworthy that Van der Ploeg (1977) mentioned *C. hostiana* from exactly the same seven atlas squares in Fryslân, and additionally also from 11.13. However, it is peculiar that Van der Ploeg (1977) did not mention *C.* ×*fulva* from 11.13, as there is a collection with material in Leiden from this square made by Franke & Van der Ploeg in 1954; see Appendix.

Since 2015, Hosper & Timmerman (in prep.) have made an inventory of the current locations of *C.* ×*fulva* in Fryslân, where they have found it at 18 sites (km-squares) in twelve atlas squares (blue and green squares together in Fig. 1). So for seven atlas squares (blue) this hybrid was already reported by Van der Ploeg (1977) and it still occurs there. Besides it has recently been found in another five atlas squares (green) by a targeted search. In the Appendix all known records of the three hybrids are listed. The list includes several records of *C.* ×*fulva* dating from between 1977 and 2015. Probably the hybrid has grown continuously in Fryslân.

Carex ×*pauliana* F.W. Schultz [*C. hostiana* × *C. oederi*]

Carex ×*pauliana* has never been recorded before from Fryslân, neither by Kern & Reichgelt (1954) nor by Van der Ploeg (1977). In July 2017, it was found there for the first time by A. Timmerman. Currently it is known from two sites in Fryslân (Fig. 2).

Carex demissa × *C. oederi*

Carex demissa × *C. oederi* was first reported for Fryslân by J.F. Neve (Van Ooststroom & Reichgelt 1964, Van der Ploeg 1977; red square in Fig. 3: 11.46) in 1963 from Hoornsterzwaag. According to herbarium material in L, Van der Ploeg found it also in 1985 in the Boornbergum Krite (grey square in Fig. 3: 11.24; Appendix). There are three collections of this hybrid from the 21st century (green squares in Fig. 3; Appendix). So, currently it is known from five sites in Fryslân.

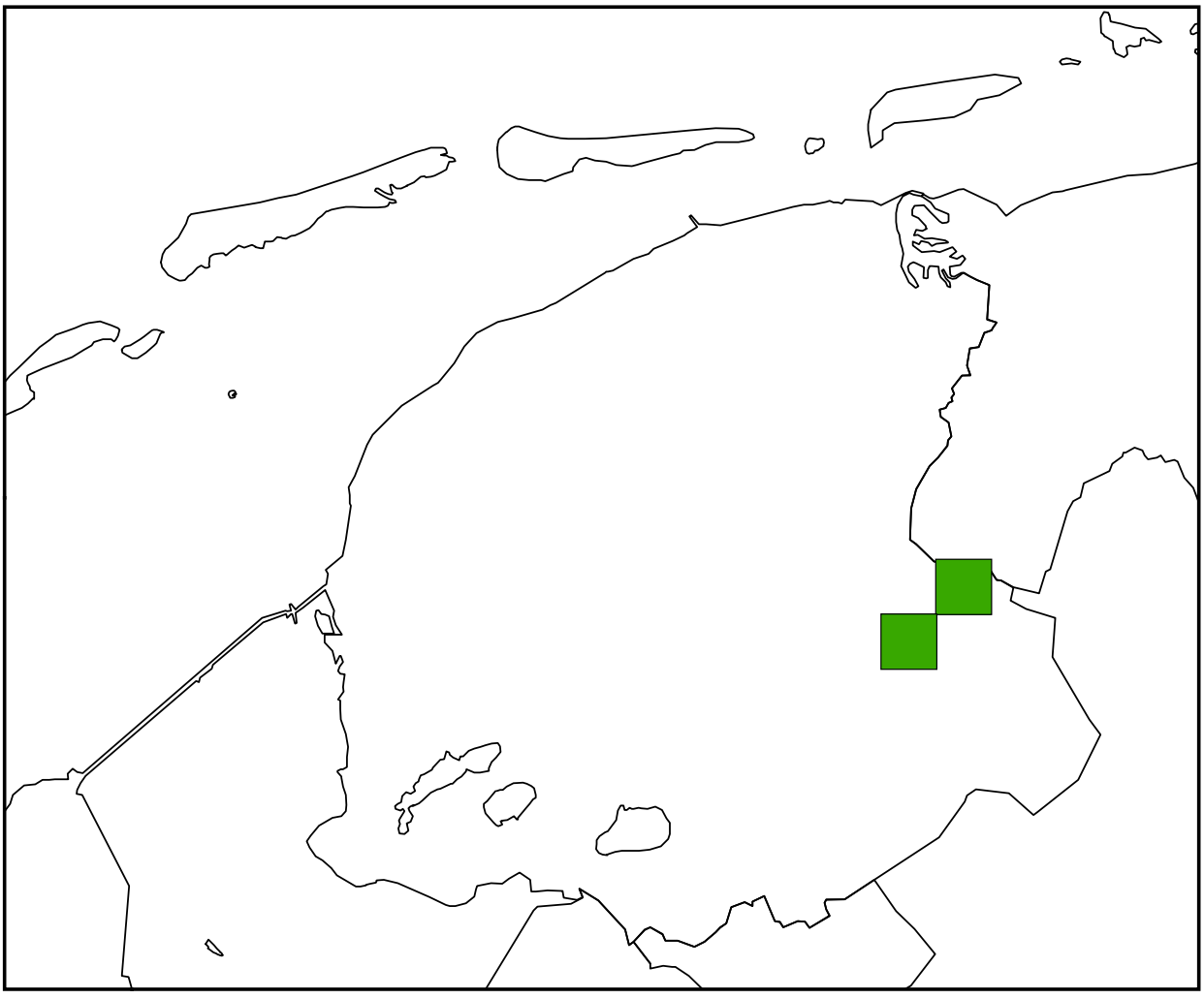

Fig. 2. Distribution of *Carex* ×*pauliana* F.W. Schultz in the Province of Fryslân, the Netherlands: Atlas squares with recent finds (■).

HABIT OF THE HYBRIDS

The characteristic features of the hybrid *Carex* ×*fulva* are intermediate to both parents, but its habit mostly resembles *C. hostiana*. Remarkable for this hybrid is the open tussock, which is similar to that of *C. hostiana*, but its colour is lighter yellow-green and its lowest bract is longer than the one in *C. hostiana*. The flowering and fruiting stems of the hybrid exceed the basal leaves. Contrasting with *C. demissa* is the upright position of the inflorescences. In addition, the hybrid is sterile and often forms larger tussocks than *C. demissa* due to vegetative propagation.

In moist habitats, in older and younger fen meadow communities (Cirsio dissecti-Molinietum) where *Carex oederi* was abundantly growing, a hybrid was found that is also sterile, but differs from *C.* ×*fulva* in size, colour, and width of the bracts. This hybrid is smaller than *C.* ×*fulva* and has shorter stems. It is also darker green and has wider and spreading bracts. The plants are compact and the inflorescences are stiff and equal in length to the leaves. This material appears to belong to *C.* ×*pauliana* [*C. hostiana* × *C. oederi*].

In the nature reserve where this hybrid was found, a few years ago a plot of former farmland was excavated and its topsoil was removed. In the vegetation along a recently dug ditch, with abundant *Carex demissa* and even more *C. oederi*, occurred a very compact green hybrid with sterile utricles and very short stems. This hybrid has been identified as *C. demissa* × *C. oederi*.

ECOLOGY OF THE HYBRIDS

In the Province of Fryslân the three *Cerastocystis* hybrids are almost exclusively found in the Cirsio dissecti-Molinietum, which is characterised as a plant community of unmanured (i.e., not fertilised), moist meadows with relatively alkaline groundwater. The growth of the vegetation of this plant community is limited by a lack of phosphate (Hosper 1981). The management of this vegetation type consists of yearly mowing and the subsequent removal of the cut vegetation in August. The Cirsio dissecti-Molinietum is found on clay-on-peat soils (without orchids, *Carex pulicaris,* nor *C. oederi*) and on loamy, sandy peat soils (with orchids, *C. pulicaris*, and *C. oederi*). In the past, vast Cirsio dissecti-Molinietum vegetations were found in the Lage Midden of Fryslân in the transition zone between the soils of Pleistocene origin and those of Holocene origine. These vegetations occurred mostly in areas with groundwater levels at ground level in summer and in areas inundated with mineral water from the Frisian collector basin. They may also have occurred

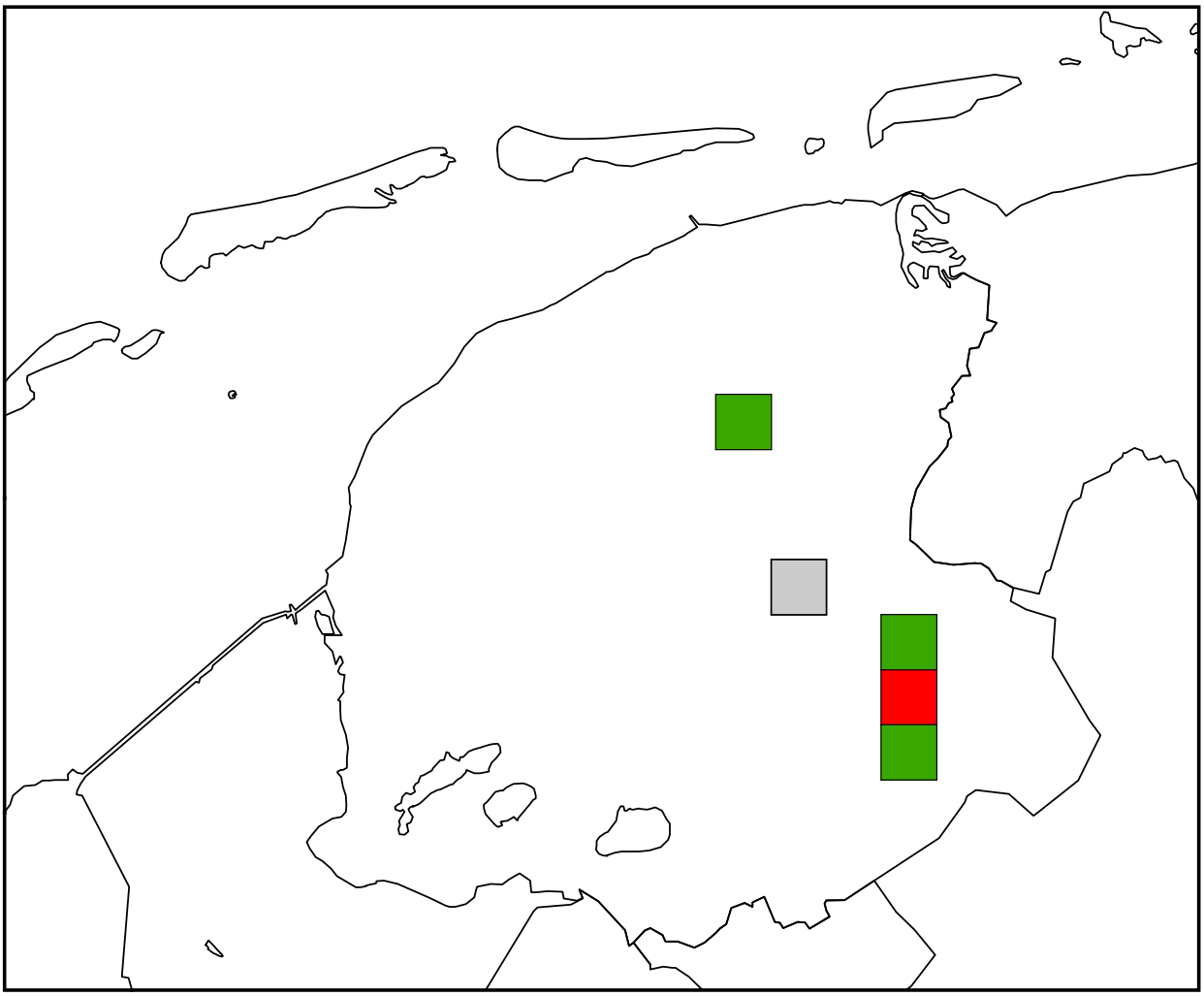

Fig. 3. Distribution of *Carex demissa* Hornem. × *C. oederi* Retz. in the Province of Fryslân, the Netherlands: Atlas squares with recent finds ( ) and atlas squares with finds made by Van der Ploeg (1977) ( ) and Van der Ploeg (1985) ( ).

on the sides of the upper and middle part of river valleys, and with even higher species diversity (Van der Kloot 1939). As a consequence of irrigation with water from the Frisian collector basin since 1920 and the ensured empoldering, the reduction of groundwater levels, and the fertilisation with synthetic fertilisers since 1950, well-developed Cirsio dissecti-Molinietum vegetations have mostly disappeared from the Holocene part of Fryslân (Fokkema et al. 1984).

Nowadays, the most valuable relicts of the Cirsio dissecti-Molinietum are situated in the Pleistocene part of Fryslân, i.e. in the stream valleys of the Rivers Boorn, Tjonger, and Linde, and in the original valley of the River Oude Ried, a tributary of the River Lauwers. However, some relicts of this plant community, but with impoverished diversity, are still surviving in the Lage Midden of Fryslân. The largest area, with plenty of *Carex hostiana*, still remains in the Unlân fan Jelsma nearby Goïngahuizen. *Carex buxbaumii* Wahlenb. also used to grow here, but it has not been found there since 2000.

The three aforementioned *Ceratocystis* hybrids are found in these carefully conserved relicts of the Cirsio dissecti-Molinietum. Of these three hybrids, *Carex* ×*fulva* has by far the widest distribution. Everywhere where *C. hostiana* occurs, *C.* ×*fulva* may be found as well, especially in the transition to the drier subassociation of the Cirsio dissecti-Molinietum, subass. nardetosum.

It is remarkable that *Carex* ×*pauliana* is only found in Cirsio dissecti-Molinietum vegetations with a natural landscape relief, where *C. hostiana* occurs and where *C. oederi* is frequently present nearby, mostly as a result of regeneration measures. *Carex oederi* occurs on open, moist soils with a sparse vegetation of pioneers as a result of turf stripping and topsoil removal in the past. *Carex* ×*pauliana* meets the ecological conditions of *C. hostiana*, i.e. a loamy, peaty, sandy soil and alkaline groundwater. *Carex* ×*pauliana* occurs in the lowest, wettest parts of Cirsio dissecti-Molinietum vegetations on sites which were turf stripped about ten years ago, but it is also found in adjacent or nearby old Cirsio dissecti-Molinietum vegetations.

The most recent location of the hybrid *Carex demissa* × *C. oederi* is at the slope of a channel, which was dug two years ago to drain precipitation and groundwater. The soil of the slope consists of loamy sand and is very humid. Especially *C. oederi*, being a pioneer, is abundantly present there. The occurrence of the hybrid might be overlooked. Its distribution is, therefore, incompletely known and has to be investigated in more detail.

MORPHOLOGY OF THE HYBRIDS

These three hybrids have in common that the utricles are empty or only 10 to 20 (to 30)% of the utricles are well-developed (Więcław 2014). When ripe, the hybrid female spikes become straw-coloured. With the combination of these two features, empty utricles and the typical straw-colour, these hybrids are relatively easy to recognise in the field. When in the field, compare suspicious plants with other individuals, especially with fertile plants of putative parents. For the identification of a specimen which may belong to either one of the three hybrids, the following key can be used:

1. Utricle beak with a white membrane at the apex (a character inherited from *C. hostiana*); glumes with a wide membranous margin: *C. hostiana* hybrids 2
1. Utricle beak without a white membrane at the apex; glumes with a narrow white membranous margin . . . . . *Carex demissa* × *C. oederi*
2. Stems 18–55 cm; utricles 3–4 mm long, beak 1–1.6 mm long . . . . . *Carex* ×*fulva*
2. Stems up to 25 cm; utricles less than 4 mm long, beak less than 1 mm . . . . . *Carex* ×*pauliana*

With its height of 18–55 cm, *Carex* ×*fulva* is the tallest of these three hybrids (Jermy et al. 2007). It forms more or less loose tufts, which resemble upright growing plants of *C. demissa*. *Carex* ×*pauliana* also grows upright, but its plants are is generally much shorter, being 12–25 cm tall. *Carex demissa* × *C. oederi* has the general appearance of its parents, i.e. more ascending than the upright growing *C. hostiana* hybrids. Besides, it misses the white membrane at the top of the utricle beak. Table 1 lists the characteristic features of the three hybrids, which are based on the examination of Frisian material.

FINAL REMARK

In contrast with the situation in the past, turf stripping of rough parts of degenerated Cirsio dissecti-Molinietum has taken place during the last 10 to 15 years as a vegetation management measure. Turf stripping and topsoil removal were also carried out in some agricultural parcels that were recently purchased by nature protection organisations, which creates favourable regeneration possibilities for the Cirsio dissecti-Molinietum. Especially on the slopes of stream valleys, this management measure, in combination with the improvement of the hydrological

Table 1. Average measurements for a few characters of the *Carex* hybrids *C.* ×*fulva* Gooden., *C.* ×*pauliana* F.W. Schultz, and *C. demissa* Hornem. × *C. oederi* Retz.

Character	*Carex* ×*fulva* (n=8)	*Carex* ×*pauliana* (n=5)	*Carex demissa* × *oederi* (n=3)
Stem length (cm)	27.9	14	10
Bract length (cm)	5.5	4.6	5.7
Leaf length (cm)	7.1	7.2	6
Leaf width (mm)	2.0	1.8	1.4
Male spike length (mm)	18.6	14.5	10.9
Female spike length (mm)	12.8	11.2	9.3

conditions, has had a positive influence on the quality of Cirsio dissecti-Molinietum vegetations. Characteristic species such as *Carex* pulicaris, *C. hostiana*, *C. demissa*, *C. oederi*, and the hybrids *C.* ×*pauliana* and *C. demissa* × *C. oederi* have taken advantage of these management measures.

The hybrids *Carex* ×*pauliana* and *C. demissa* × *C. oederi* were found for the first time in July / August 2017. This was very late in the season, because Cirsio dissecti-Molinietum vegetations are yearly mown, usually in August. It is likely that both hybrids may be found in more places in June / July 2019, so earlier in the season. Especially the older turf stripped parts in the Frisian stream valleys are suitable habitats for these two hybrids.

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Appendix

The records of the three *Carex* section *Ceratocystis* hybrids in the Province of Fryslân, the Netherlands, are listed below.

Abbreviations:

L: Herbarium of Naturalis at Leiden
obs.: Observation only, no herbarium material
pJK: Private herbarium of Jac. Koopman

RECORDS OF *CAREX ×FULVA*

Duurswoude Hooiweg, 11.36, vochtige heide [wet moorland], 7-6-1952, L.3117594
Eernewoude, Oksekoppen, tussen de ouders in een prachtig *Carex* landje met veel *C. hostiana* en iets minder *C. demissa* [between the parents in a wonderful *Carex* meadow with a lot of *C. hostiana* and a bit less *C. demissa*], D. Franke & D.T.E. van der Ploeg, 8-6-1954, L.3117596, L.3130032 & L.3117608
Oldeboorn-Veenhoop, Unlân fan Jelsma, 11.23, blauwgras [Cirsio dissecti-Molinietum], D.T.E. van der Ploeg, 13-5-1961, L.3117597
Akkrum-Sorremorre-Veenhoop, blauwgraslandreservaat, M. Baaijens & D.T.E. van der Ploeg, 6-6-1961, L.3117598
Wijnjeterp, Hooiweg, 11.36, vochtige hei in Staatsbos [wet moorland], D.T.E. van der Ploeg, 24-7-1962, L.3117616
Hooiweg Duurswoude, natte heide [wet moorland], 11.36, M. Baayens, D.T.E. van der Ploeg, L. Vermast & G. de Jong, 6-1963, L.3117614
Kootstertille, SBB-reservaat in Drogehamster Mieden, moeras [swamp], D.T.E. van der Ploeg, 3-7-1965, L.3117611
Akkrum, Lege Midden, Unlân fan Jelsma, 11.23, blauwgrasland [Cirsio dissecti-Molinietum], D.T.E. van der Ploeg, 20-7-1965, L.3117615
Aan de "Hooiweg" bij Wijnjeterp, vochtig hooiland, F. Rudolphy, 21-5-1966, L.3117612
Aan de "Hooiweg" bij Wijnjeterp, vochtig hooiland, F. Rudolphy, 27-7-1966, L.3117613
Jelsma's Unlân tussen Goëngahuizen en Veenhoop, 11.23, veel tussen de stamouders op blauwgraslandstripen [a lot between the parents in Cirsio dissecti-Molinietum], F. Rudolphy, 18-6-1973, L.3117618
"Stuttebos" bij Oldeberkoop, 11.56, blauwgraslandterrein, tussen de stamouders, steriel [Cirsio dissecti-Molinietum, between the parents, sterile], F. Rudolphy, 24-6-1973, L.3117617
Eernewoude, Oude Venen, 11.13, F. Rudolphy, 14-6-1980, L.3117587
Omgeving van de Veenhoop, H. Joustra, 6-1981, L.3118041
Unlân fan Jelsma, 11.23.41, Goëngahuizen, Junco-Molinion, Jac. Koopman, 27-5-1990; pJK
Stuttebos, E of Oldeberkoop, 11.56.53, Junco-Molinion, Jac. Koopman, 2-7-2003; pJK
Stuttebos, E of Oldeberkoop, 11.56.53, Junco-Molinion, H. Waltje & Jac. Koopman, 27-5-2011; pJK
W of Bakkeveen, 11.26.55, Junco-Molinion, H. Waltje, W. Poelstra & Jac. Koopman, 13-6-2012; pJK
Rotstergaaster Wallen, 16.13.32, Junco-Molinion (Koopman 1986), without *C. hostiana*), Jac. Koopman (obs.)
Oldelamer, 16.13.51, Junco-Molinion (in the nineties till around 2005), Jac. Koopman (obs.)
Twijzeler Mieden, 06.45.34 and 06.45.35, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Drogehamster Mieden, 06.45.44, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Polder Rohel, 06.46.22, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Hoannekrite, 11.13.52, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Hokke's Aldfean, 11.22.15 and 11.22.25, U.G. Hosper & A. Timmerman. Period 2015–2018 (obs.)
Unlân fan Jelsma, 11.23.41, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
't Oude Bosch, 11.26.55 and 11.27.51, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Rome, Beetsterzwaag, 11.34.35 U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Rome, Beetsterzwaag, 11.35.31, U.G. Hosper & A. Timmerman, period 2015–2018 (obs)
't Sker, 11.36.13, U.G. Hosper & A. Timmerman, period 2015-2018 (obs.)
Weinterper Skar, 11.36.22 and 11.36.23, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Stuttebos, 11.56.53, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Rotstergaaster Wallen, 16.13.32, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)
Brandemeer, 16.13.51, U.G. Hosper & A. Timmerman, period 2015–2018 (obs.)

RECORDS OF *CAREX ×PAULIANA*

't Oude Bosch, 11.27.51, U.G. Hosper & A. Timmerman, 2017; pJK
Weinterper Skar, 11.36.22, U.G. Hosper & A. Timmerman, 2017; pJK

RECORDS OF *CAREX DEMISSA × C. OEDERI*

Hoornsterzwaag, Miedweg, 11.46, langs slootje [along small ditch], J.F. Neve, 8-6-1963, L.3130035
Boornbergum Krite, 11.24, oever van slootje [shore of small ditch], D.T.E. van der Ploeg, 5-9-1985, L.3130029
Stuttebos, E of Oldeberkoop, 11.56.53, wet places in Junco-Molinion, where the top soil had been removed, H. Waltje & Jac. Koopman, 27-5-2011; pJK
Hurdegaryp, 06.43.53, path on loamy soil, H. Waltje, 1-6-2012; pJK
Weinterper Skar, 11.36.22: 2017, U.G. Hosper & A. Timmerman, 2017 (obs.)