

MISCELLANEOUS NOTES ON
SCIRPUS LACUSTRIS L. SENSU LAT. IN THE
NETHERLANDS

BY

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(*Ens, Northeasternpolder*)

With Plates 24—26

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This paper chiefly deals with the problem whether or not *Scirpus lacustris* L. and *S. tabernaemontani* Gmel. should be considered as separate species. As to this question, quite different opinions have been developed in literature. On the strength of an examination of the specimens occurring in the Netherlands, in this paper they are regarded as ecotypes (subspecies) of the ecospecies *S. lacustris* L. *sensu lat.*, which will be explained below. In addition data are given on the polymorphy, the distribution and the hybrids with *S. triqueter* L. in the Netherlands.

The examinations were made on living plants and herbarium specimens. During my endeavours I had the opportunity of consulting the collection preserved in the Rijksherbarium at Leyden, in which among others are inserted the herbaria Jansen and Wachter, Kern and Reichgelt, Kloos, Van Ooststroom, Van Soest, Vervoort and De Bruyn. Moreover, I was able to study the herbaria of the Royal Botanical Society of the Netherlands at Leyden, the Botanical Museum and Herbarium at Utrecht, the Hugo de Vries Laboratory at Amsterdam, the Botanical Laboratory at Groningen, the Plant Taxonomical and Geobotanical Institute at Wageningen, the Museum of Natural History at Maastricht and the Department of Botany of the Northeasternpolderworks at Kampen.

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DIFFERENT OPINIONS ON THE SYSTEMATICAL STATUS OF *S. lacustris* L. *sensu lat.*

In 1753 LINNAEUS described *S. lacustris*, that is in this paper the ssp. *lacustris*. GMELIN (1805) made the description of *S. tabernaemontani* (syn. *S. glaucus* Smith, 1812). C. HARTMAN (1848) classified *S. tabernaemontani* for the first time as a subspecies of *S. lacustris*, which he called ssp. *glaucus* (Smith) Hartman. However, ROTH already described in 1788 the var. β *minor* of *S. lacustris* L., which is obviously identical with the ssp. *glaucus* (ROTH, 1802; NEILREICH, 1859).

In the nineteenth century, especially MERTENS and KOCH (1823), CUSTOR (1830), KUNTH (1837) and KOCH (1837, 1844) considered these subspecies as separate species. On the other hand, FRIES (1828), DÖLL (1843), ANDERSSON (1849), C. J. HARTMAN (1849), MEYER (1849), PARLATORE (1852), GRENIER and GODRON (1855-'56), NEILREICH (1859), BÖCKELER (1870) etc. united these entities into one species in view of the strong resemblance, the unstable characteristics, the merging into one another under the influence of the environment or the occurrence of intermediate forms.

FRIES, ANDERSSON, C. J. HARTMAN and BÖCKELER considered the ssp. *glaucus* as the var. β *glaucus* of *S. lacustris*.

DÖLL' divided *S. lacustris sensu lat.* (as *S. lacustris* Döll) into the following four varieties:

- a. *vulgaris*, identical with *S. lacustris* L.
- b. *minor*, smaller than a, stems bluntly triangular above, glumes somewhat asperous and in some spikelets scattered flowers with 2 stigmas.
- c. *trigonus*, stems bluntly triangular above, at the tip bearded connectiva and mostly 2 stigmas, further as b.
- d. *tabernaemontani*, with glaucous and at the apex faintly triangular stems, connectiva at the tip practically not bearded and 2 stigmas.

In the wet year of 1838 DÖLL made the observation that from the var. d. *tabernaemontani* the stems had turned greener, higher and rounder, whilst in every spikelet flowers with two and three stigmas occurred. It follows that under the influence of changing environmental conditions some characteristics of *tabernaemontani* had altered into those of *lacustris*. This is in agreement with the opinion of NEILREICH (1859), who considered the var. α *major* Roth (ssp. *lacustris*) as the aquatic form and the var. β *minor* Roth (ssp. *glaucus*) as the terrestrial. NEILREICH remarked: "Zwei vom Wasserstande bedingte und daher vielfach in einander übergehende Varietäten". From some statements of MEYER (1849) it seems likely that he considered the var. c. *tabernaemontani* (ssp. *glaucus*) to be a modification owing to a saline habitat. Probably also GRENIER and GODRON (1855-'56) had thought of these subspecies as modifications. They distinguished the following varieties:

- α . *genuinus* Gren. et Godr. (ssp. *lacustris*), with 3 stigmas, trigonous fruits; dark-green robust plant; growing in water.

β. *digynus* Godr. (ssp. *glaucus*), with 2 stigmas, fruits compressed and smaller than in α; more slender than α, glaucous, growing on in winter flooded areas and in the mountains. Their following remark regarding *S. tabernaemontani* is worth quoting: "Aucun des caractères par lesquels on a voulu le distinguer du *S. lacustris* n'est constant".

PARLATORE (1852) pointed out that these plants are forms of one species which do not even have the status of varieties in view of the unstable characteristics, e.g. the number of stigmas, the asperity of the glumes and the length of the bearded points of the connectiva.

However, ASCHERSON and GRAEBNER (1902-'04) made a statement regarding the uniting into the same species as a consequence of the intermediates and the unstable characteristics: "Wir haben uns jedoch bisher davon nicht überzeugen können". They maintained the species *S. lacustris* L. and *S. tabernaemontani* Gmel., which had been accepted by most of the later botanists.

According to LOUSLEY (1931) the hybrid of *S. lacustris* L. and *S. tabernaemontani* Gmel. has been known in Germany and Denmark for a considerable number of years in localities where it grows with the parents. However, the authors BUCHENAU (1877), FOCKE (1881) and BRÜGGER (1882), cited by LOUSLEY, have recorded this hybrid only from Bremen in Germany. Undoubtedly FOCKE and BRÜGGER quoted BUCHENAU. BUCHENAU described the hybrid as follows: „hochwüchsig, grasgrün: Deckspelzen rotbraun, nicht rauh punktiert; Narben 3. Fr. sehr spärlich entwickelt, zwischen denen beider Arten die Mitte haltend; an der Innenseite des Hollerdeiches bei Kattrepel".

Although the affinity of the parents is close and they occur together in several localities, it is noteworthy that the hybrid was found only in one place. On the other hand the hybrid between the ssp. *lacustris* and *S. triqueter* L., which differ from each other considerably in morphological characteristics, is recorded from several localities. This may be the result of the fact that the hybrid mentioned first is not easily recognizable.

The scarce fruit formation is the only characteristic in the description of BUCHENAU that should be regarded as an argument in favour of the hybrid nature. But as nothing is known on the germinative power of the seeds and the viability of the plants developing from these seeds, the scarce fruit formation is no proof for the hybrid origin. The more so as the present writer now and then observed a scarce fruit formation in the ssp. *lacustris* and *glaucus*, although in other respects these plants did not differ from fertile ones.

Besides the hybrid, intermediates were recorded from several localities (DÖLL, 1843; MEYER, 1849; NEILREICH, 1859). In this connection the following statement was made by FOCKE (1881): "*S. lacustris* L. × *S. Tabernaemontani* Gm. ist ein wenig fruchtbare Mittelform, bei Bremen beobachtet. An andern Orten hat man Uebergänge gesehen, die nicht als Bastarde gedeutet werden".

From this review of the literature, it becomes quite clear that the opinions with regard to the systematical status of the ssp. *lacustris* and *glaucus* are quite different. However, it is open to question

whether or not the specimens studied by DÖLL, NEILREICH and others might be compared with the Dutch material. As appears from the literature, the characteristics of the ssp. *glaucus* are much more unstable in Central Europe than in the Netherlands. Moreover, in our country this subspecies reaches its optimal development in a brackish habitat with a range of 0.1–10⁰/_∞ chlorine or in an environment that was recently brackish, e.g. the coast of the Yssellake. On the contrary, in Central Europe the ssp. *glaucus* seems to grow in a fresh habitat under drier conditions than the ssp. *lacustris*. It is not known, however, if this contrast between the Dutch and Central European specimens is the result of environmental or genotypical differences. In no case, however, in the Netherlands these subspecies are modifications. In spite of the plasticity of *S. lacustris* L. *sensu lat.* (GLÜCK, 1923; SEIDEL, 1952a) it must in this connection not be overlooked that the modifiable varieties, described by DÖLL, NEILREICH, GRENIER and GODRON and others, might be in fact cross-breeds of the ssp. *lacustris* and *glaucus* or hybrids between *S. lacustris* L. *sensu lat.* and *S. triqueter* L. (LOUSLEY, 1931).

It follows that it is desirable to discuss the arguments which must be advanced in order to prove whether the two subspecies belong to the same or two different species.

In the opinion of DANSER (1950) the essence of the large species is an intermixing community or commiscuum. By this he understands a collection of forms which are mutually connected by the capacity of intermixing. Intermixing is the phenomenon that two forms which are crossed yield in the first generation more or less intermediate forms, which on selfing or fertilization by sister specimens, and also on back-crossing with one of the stem-forms, assume a great polymorphy, so that after a few generations the boundaries between the originally crossed forms are obliterated. In the same commiscuum all coinciding forms, both in wild growth and cultivated, are connected by series of intermediate forms. In addition, forms belonging to one commiscuum will, as a rule, yield fertile cross-breeds, whereas forms belonging to different commiscua will not. Thus the criteria of the systematists for distinguishing species coincide in the concept commiscuum.

However, it is rather extreme to look upon the absence of gradation, or the failure to breed together and to produce fertile offspring, as the only criteria of specific distinction. On that ground, besides the commiscuum-concept, also the morphological resemblance, the number of chromosomes and the distribution will be considered in discussing the species-concept of *S. lacustris* L. *sensu lat.*

In this connection, it is important that from the coast of the Yssellake in the Netherlands, an intermediate form with undiminished fertility and the same chromosome number as the ssp. *lacustris* and *glaucus* has been recorded of late years (tables 1, 2 and 3). Moreover, the characteristics of this intermediate proved to be of a stable nature. Seeing that the plants grown from the seeds of this intermediate are morphologically identical with the plants of the preceding generations,

the intermediate should not be regarded as the F 1 from the crossing of the subspecies. Furthermore, the possibility exists that artificially cross-breeds of the subspecies are achieved (Miss Dr K. Seidel, in a letter, 13 October 1953). Evidences for such cross-breeding in wild growth is provided by the observation that in the Netherlands highly fertile plants with overlapping characteristics are mainly found in areas where the subspecies grow together. It follows that in all probability the intermediate, which has obliterated the boundaries between the two subspecies, may be regarded as the result of "introgressive hybridization" *sensu* ANDERSON and HUBRICHT (1938) (HEISER, 1949), which means the gradual infiltration of the germplasm of one subspecies into that of the other through the repeated back-crossing of the cross-breed to one or both parents. According to the principle of DANSER, it is evident now that the ssp. *lacustris* and *glaucus* belong to the same commiscuum. Furthermore, in table 1 the great morphological resemblance is shown, whilst also a gradation occurs as has been pointed out above. Moreover, it is a matter of fact that these subspecies reach their optimal development in different habitats, which means they are ecotypes *sensu* TURESSON (1922). It follows that the ssp. *lacustris* and *glaucus* may be united into the same ecospecies, viz. *S. lacustris* L. *sensu lat.* An ample discussion of these data will be given below.

In spite of intermixing they usually remain distinct entities; in all probability owing to the fact that the chances of cross-breeds and back-crossings holding their own in competition with the parents are poor (HEISER, 1949). But as a consequence of the stable characteristics and the fertility, the intermediate from the coast of the Ysselake will be described in this paper as the ssp. *flevoensis* of *S. lacustris* L. *sensu lat.*, which only by the intervention of man continues existence in the habitat of the ssp. *lacustris*.

It must also be pointed out that in the Netherlands the hybrids between *S. lacustris* L. *sensu lat.* and *S. triqueter* L. are recorded from several localities. Although, this hybrid swarm shows a considerable lack of uniformity in morphological characteristics as well as in fertility, they usually are of low fertility; this means *S. lacustris* L. *sensu lat.* and *S. triqueter* L. belong to separate commiscua. The morphological characteristics, too, are entirely different, whilst they partly reach their optimal development in the same habitat, viz. in the *Scirpetum maritimi* Tüxen of the faintly brackish to fresh tidal estuaries in the S.W. of the Netherlands. Hence they are regarded as separate species.

SOME DATA ON *S. lacustris* L. *sensu lat.* IN THE NETHERLANDS

In the Netherlands the following three subspecies are distinguished:

1. ***Scirpus lacustris*** L. ssp. ***lacustris***; Linnaeus, Sp. Pl., 48-49, 1753.

Although it appears that some characteristics of the ssp. *lacustris* may overlap with the other, these plants usually are determined

TABLE 1
Comparative summary of the characteristics of the three subspecies of *S. lacustris* L. *sensu lat.*

ssp. <i>lacustris</i>	ssp. <i>fluvensis</i>	ssp. <i>glaucus</i>
Rhizomes hard and brittle; young white, later red-brown or dark red-brown; cells small (Plate 24)	Rhizomes fairly hard and tough; young white, later yellow- or red-brown; cells intermediate (Plate 24)	Rhizomes weak and tough; young white, later yellow or yellow-brown; cells large (Plate 24)
Stems round, $\frac{3}{4}$ - $3\frac{1}{2}$ m high; light-, yellow- or dark-green or glaucous; not club-shaped below; diameter $\frac{3}{4}$ -4 cm below	Stems round, $\frac{3}{4}$ -1 $\frac{1}{2}$ m high; glaucous; not club-shaped below; diameter $\frac{3}{4}$ -1 $\frac{1}{2}$ cm below	Stems round, sometimes faintly angular above, $\frac{3}{4}$ -2 $\frac{1}{4}$ m high; glaucous; robust plants club-shaped below; diameter $\frac{3}{4}$ -6 cm below
If stems are cut off during or shortly after flowering they dry up yellow-green	As in the ssp. <i>lacustris</i>	If stems are cut off during or shortly after flowering they dry up yellow
Before and during flowering mostly 2-12 leaves with distinct leaf-blades (Plate 25); in the end the leaf-sheaths frayed	Before and during flowering 1-2 leaves with distinct leaf-blades (Plate 25); in the end the leaf-sheaths frayed	Before and during flowering only 1 leaf with a leaf-blade or leaf-blades wanting (Plate 25); the leaf-sheaths slightly frayed or not at all
Spikelets elongated or elongated-ovoid	As in the ssp. <i>lacustris</i>	Spikelets ovoid, elongated-ovoid or elongated
Glumes glabrous or only on the midrib asperous, usually brown	Glumes asperous on the midrib, especially the outer glumes also asperous near the midrib, brown	Usually all the outer glumes asperous, red-brown
Number of stigmas 3	Number of stigmas 2 and 3, resp. about 60 and 40 % in every spikelet; flowers with 3 stigmas especially at the tip of the spikelet	Usually number of stigmas 2, but rather much some flowers with 3
Connectiva bearded at the tip	Connectiva bearded at the tip, but usually shorter than in the ssp. <i>lacustris</i>	Connectiva usually very shortly bearded at the tip
Fruits bluntly trigonous, 2 $\frac{1}{2}$ -3 mm long	Fruits faintly trigonous or compressed, about 2 $\frac{1}{2}$ mm long	Fruits compressed, about 2 $\frac{1}{2}$ mm long
Chromosome number 2 n = 42 (in Europe)	Chromosome number 2 n = 42	Chromosome number 2 n = 42

without much difficulty (table 1). It is a matter of fact that Netherlands specimens of the ssp. *lacustris* with aberrant characteristics have been rarely found, e.g. near Sleeuwijk along the Merwede, flowers mainly with 3 stigmas, glumes somewhat asperous, stems glaucous, leaf-sheaths frayed and distinct leaf-blades (herb. Kern and Reichgelt). But there is a difference in opinion with regard to the classification of the specimens from the Haringvliet and Hollands Diep in the S.W. of the Netherlands, as SEIDEL (1952*b*) placed the rushes from these brackish areas under *S. lacustris* L. (= ssp. *lacustris*). About this she states on page 304: "Die Variabilität ist aber gross" and eight lines further on: "Es steht fest, dasz ihre Formen und Bastarde die Salinität, den Tidenhub und die Strömung prächtig vertragen". But SEIDEL does not point out what should be understood by the forms and hybrids of *S. lacustris* L. Any Dutch florist, however, would place the specimens from the Haringvliet and a part of the plants from the Hollands Diep under the ssp. *glaucus*. Upon inquiry Miss Dr K. Seidel declared that she is fully aware of the plasticity of *S. lacustris* L. *sensu lat.* This plasticity means that this taxon is easily affected by environmental conditions, e.g. in a dry habitat the leaf-blades of the ssp. *lacustris* are very short or completely wanting, the length of the stem is dependent upon the depth of the water (GLÜCK, 1923; SEIDEL, 1952*a*). Beside it, undoubtedly, fertile cross-breeds of the ssp. *lacustris* and *glaucus*, which are anemophiles, occur where they grow together, by which the overlapping characteristics in these subspecies may be explained, e.g. in the specimens of Kern and Reichgelt above-mentioned.

In spite of this, it is not clear to me on what grounds SEIDEL arranged these plants under *S. lacustris* L., as they have at the most the typical characteristics of the ssp. *glaucus*, which does not exclude sometimes the presence of any influence of the ssp. *lacustris* (table 1).

The plants discussed above have yellow, tough and weak rhizomes, with large cells (Plate 24). In the summer no new adventitious roots are developed, as has been described by SEIDEL (1952*a*) for the ssp. *glaucus*. The leaf-blades are short or wanting; the leaf-sheaths are somewhat frayed or not at all. The colour of the usually round stems is glaucous; at the base the stems are mostly club-shaped. If the stems are cut off during or shortly after flowering they dry up with a yellow colour; they die off late in autumn. During flowering nearly all the glumes are asperous. The number of stigmas is 2, but spikelets with scattered flowers with 3 stigmas are rather much found. At the tip the connectiva are short or very short-bearded. The fruits are compressed. According to table 1 these are characteristics of the ssp. *glaucus*.

The ssp. *lacustris* is a characteristic subspecies of the *Phragmition eurosibiricum* Tüxen, *em.* Braun-Blanquet et Sissingh. In the *Scirpeto-Phragmitetum medio-europaeum* Tüxen, which especially dominates in the "haf- en fluviatiel-district" *sensu* VAN SOEST (1923, 1924), and the *Scirpetum maritimi* Tüxen, from the nearly fresh to somewhat brackish tidal estuaries and the coast of the Yssellake between the

Ketel and the Zwarte Water, the *ssp. lacustris* reaches its optimal development. The *Scirpeto-Phragmitetum* is a soil-building association of fresh and stagnant water, rich in nutritive substances, till a depth of 1 m. The habitat of the *ssp. lacustris* in the tidal estuaries may be saline during high floods, which mostly happens in winter when the overground parts of the bulrushes have died, owing to which it is only of slight influence.



Fig. 1. Distribution of *Scirpus lacustris* L. *ssp. lacustris* in the Netherlands. The data on this map are due to the herbaria mentioned in this paper, the "Nederlandsch Kruidkundig Archief" and the observations of the writer

As appears from the distribution map (Fig. 1) the ssp. *lacustris* is wanting in the North of the provinces of Noord-Holland, with the exception of Wieringen, Friesland and Groningen, in the Wadden Islands, in Goeree and Flakkee and in several islands of the province of Zeeland; doubtlessly this is the result of the brackish environment in these areas. But it is possible that this subspecies will be recorded from some localities in the areas mentioned above. On the contrary this plant grows frequently along rivers, in peat-lakes, in the Kamperisland and in the lakes of the province of Friesland (Fig. 1). Especially in the Kamperisland and in the fresh tidal estuaries, bulrushes have been planted out for more than a century. On account of its domination in a fresh environment, the ssp. *lacustris* is considered in this paper as the ecotype of a fresh habitat. In a brackish environment several stages of the life-cycle are hampered, e.g. the growth of seedlings and flowering.

With regard to the factor "water" the ssp. *lacustris* is an amphiphyte *sensu* IVERSEN (1936), characterized by being able to thrive and flower both submersed and terrestrially, without reduction of vegetative parts.

In the Netherlands the following varieties and forms are distinguished:

var. **capitatus** Hausskn., Mitt. Geogr. Ges. Thür., 31, 6, 1888.

The inflorescences are capitate crowded (Plate 26 A). It is open to question, however, if this variety has any systematical value, as on the same rhizomes I observed stems with normal as well as with capitate inflorescences. Was found in the Netherlands in some localities, e.g. in the Kamperisland.

var. **foliosus** Rouy, Fl. Fr., 13, 374, 1912.

The leaf-blades are erect, rigid and composed of spongy tissue similar to that of the flowering-stems. Probably, this variety may be considered as a modification, engendered by external circumstances.

In the herbarium of the Plant Taxonomical and Geobotanical Institute, Wageningen, a specimen is preserved, that might be placed under this name. This plant was collected in July 1919, in a brooklet near De Steeg (leg. E. de Vries).

var. **glaucopsis** Bakker, nov. var.

Caules glauci.

(Type: Herb. Bot. Dep. N.E. polder nr. 1709; 1954, mouth of the Zwarte Water).

This variety has the same stem-colour, which is in all probability genotypically fixed, as the ssp. *glaucus*. Found along the mouth of the Zwarte Water, where glaucous clones grow mixed with green ones, and in a pool along the Overijsselse Vecht near Dalfsen. Seeing that also the stem-colour of the ssp. *lacustris* may vary in face of changing environmental conditions, no other colour-varieties are distinguished.

var. **pendulus** Bakker, nov. var.

Caules tenues et graciles, ad basin diametro 1-2 cm, sub inflorescentiis 2-3 mm. Inflorescentiae plerumque magnae, post anthesin

nutantes. Hic varietas per multas formas intermedias in plantas erectas transgrediens.

(Type: Herb. Bot. Dep. N.E. polder nr. 1147; 1953, coastal area Kamperisland). See Plate 26 A.

This variety has been planted out in the coastal area of the Kamperisland (Yssellake), besides there are records of these plants from the Beulakker- and Belterwijde, Paterswolde, Vollenhove and the lake near Zuidlaren.

fo. **fluitans** (Coss. et Germ.) Glück, Beih. Bot. Clb., 39, 313–314, 1923.

Sheaths prolonged in leaf-blades ("Bandblätter" *sensu* GLÜCK, 1923). On every shoot 6–12 leaf-blades, which are 30–150 cm long and narrow lanceolate (Plate 26 A). Stems often compressed, with or without inflorescences; sometimes the stems are wanting. This plant is a modification of rather deep running water. In the Netherlands only found in the Zwarte Water near Genemuiden.

fo. **terrestris** Glück, Beih. Bot. Clb., 39, 313, 1923.

The leaf-blades are short or completely wanting. This modification has been found several times on the newly reclaimed soils in the Northeasternpolder.

2. **Scirpus lacustris** L. ssp. **flevensis** Bakker, nov. ssp.¹

Differt a ssp. lacustre rhizomatibus sublentis, longitudine caulum vulgo minore, glumis nonnullis verrucosis, connectivis vulgo brevius pilosis, spiculis flores 2 et 3 stigmatibus praeditos gerentibus, achaeniis planioribus, in sectione transversa plano-convexis vel obscure triquetris. Differt a ssp. tabernaemontano rhizomatibus subduris, caulibus ad basin nunquam clavatis, glumis minus verrucosis, connectivis vulgo longius pilosis, spiculis flores 2 et 3 stigmatibus praeditos gerentibus, achaeniis nonnullis in sectione transversa obscure triquetris.

(Type: Herb. Bot. Dep. N.E. polder nr. 1153; 1952, Ketelveld, coastal area Yssellake).

The intermediate characteristics are further shown in a convincing way in the tables 1 and 2 and Plates 24 and 25. No varieties are distinguished, as the specimens are rather homogeneous.

This subspecies occurs in the shallow water of the coastal area of the Yssellake between the Ketel (the mouth of the Yssel) and the Ganzendiep.

In Genemuiden, the centre of rush manufacture in the Netherlands, the ssp. *flevensis* has been known as "fransje" for at least sixty years owing to its usefulness in the making of rush-bottomed chairs, for the stems are thin, uniform in thickness and tough. That is why this rush is regularly planted out in the coastal area between the Ketel and the Ganzendiep; so here these plants are propagated by means of the vegetative underground rhizomes.

¹ The name "flevensis" has been derived from the Lake Flevo, which was situated in the area of the present Yssellake between 300 B.C. and 1200 A.D. This name has been proposed by Dr V. Westhoff.

As has been pointed out above, this rush has no hybrid nature, in spite of the intermediate characteristics. It will be explained below on what observations this conclusion is based.

In the first place, a comparative study has been made of the number of filled and unfilled fruits and pollen grains from the three subspecies involved. The relative number of good and bad fruits furnishes an indication of female fertility (HEISER, 1949). For this purpose thirty spikelets of each subspecies, grown on the coast of the Yssellake, were collected. The spikelets had been taken from the first stems of the rhizomes, as only stems and inflorescences of the same series should be compared (SEIDEL, 1952a). The average numbers per spikelet for filled and unfilled fruits in the ssp. *lacustris* as well as in the ssp. *flevensis* proved to be respectively 9 and 14; in the ssp. *glaucus* these numbers were 12 and 14. So in this connection the subspecies are well matched. Moreover, in table 2 it is shown that the total number of filled and unfilled fruits in the ssp. *flevensis* is about as great as in the other. Furthermore, in each of the subspecies about 94–98 % pollen grains proved to be filled and of a normal size, which shows the high male fertility.

TABLE 2

Some data on the fruits of the three subspecies of *S. lacustris* L. *sensu lat.*

Subspecies and locality	Average thousand- kernelweight in gr. (air dry)	From thousand fruits are (average):		
		unfilled	filled	
			trigonus	com- pressed
ssp. <i>glaucus</i> , Vollenhovense Meer . .	1.43	196	—	804
ssp. <i>glaucus</i> fo. <i>maior</i> , Biesbos . . .	1.81	182	14	804
ssp. <i>flevensis</i> , Ramsveld	1.85	213	394	393
ssp. <i>flevensis</i> , Ketelveld	1.85	158	443	399
ssp. <i>lacustris</i> , Ramsveld	2.65	119	876	5
ssp. <i>lacustris</i> var. <i>pendulus</i> , Ramsveld	2.82	181	816	3

Secondly, the germinative power of the ssp. *lacustris* proved to be nearly equal to the germinative power of the trigonous and compressed fruits of the ssp. *flevensis*; in the ssp. *glaucus* it reached a somewhat higher level. On the other hand, the ssp. *flevensis* was intermediate between the other subspecies as to the rapidity of germination (table 3). Before germination the fruits were kept in moist soil, at first six months at -2° C and after that six months at 2° C. The germination tests were made between moist filter-paper in petri-dishes, which were placed in day-light.

Thirdly it appeared that the plants grown from the seeds of the ssp. *flevensis* were morphologically identical with the plants of the preceding generations, which does not occur in hybrids.

It does not call for further comment that these properties never

TABLE 3

Germinative power of the subspecies of *S. lacustris* L. *sensu lat.*

Subspecies	Average % germinated seeds after:				
	6 days	12 days	18 days	24 days	30 days
ssp. <i>glaucus</i>	0	85	90	91	91
ssp. <i>flevensis</i>					
a. trigonous fruits	0	44	63	76	78
b. compressed fruits	0	43	61	72	80
ssp. <i>lacustris</i>	0	7	62	78	82

are to be found together in hybrids or in the F 1 of crossings between lower taxa of the same species.

The diploid chromosome number proved to be 42 (counts made by Miss H. D. Schotsman), which is in accord with the number counted in the Scandinavian (HÅKANSSON, 1928) and Dutch (SCHOTSMAN) material of the other subspecies. In Japanese specimens of the ssp. *lacustris*, TANAKA counted respectively $2n = 38, 40$ and 42 . The first number refers to fertile plants, whereas the other were counted in variegated varieties with total or partial pollen sterility. As an examination of Japanese herbarium specimens has shown, it is not likely that the plants studied by TANAKA might lend themselves to a comparison with Dutch material.

Experience has proved that this subspecies cannot compete with the ssp. *lacustris*; at least for the present, as by the enclosure of the Zuydersea (now called Yssellake) the environment has been turned into permanent fresh water and the tidal effect has disappeared. If this rush had not been planted out regularly in consequence of its importance for the making of rush bottomed-chairs, it would probably have perished long ago. The fact that this subspecies only has been found between the Ketel and the Ganzendiep, where planting out occurred till recently, is in favour of this hypothesis. In accordance with this view the ssp. *flevensis* might be compared with the races of our cultivated plants, which cannot continue existence without the intervention of man.

The classification as a subspecies is an obvious fact. On account of the intermediate characteristics it is impossible to consider this plant as a variety of one of the other subspecies, whereas the classification as a separate species does not agree with the close affinity of the ssp. *lacustris* and *glaucus*, of which the ssp. *flevensis* is the intermediate. Nevertheless, as this rush grows in an environment where the ssp. *lacustris* reaches its optimal development, it is difficult to regard this plant as an ecotype. This does not exclude, however, the possibility that this subspecies may be adapted to an unknown habitat and it is open to question whether this habitat still occurs in this area. In this connection it is worth mentioning that after the environment in the Yssellake has turned into permanent fresh water, the ssp. *glaucus* has been almost crowded out by the ssp. *lacustris* in the coastal area between the Ketel and the Ganzendiep.

For three years I observed a transplant experiment with the three subspecies in a shallow and fresh pool near Blokzijl, where they grow without competition. As appears from this trial the ssp. *flevensis* does not seem to have the character of a modification, as the characteristics summarized in table 1, did not change at all.

Finally, it is still possible that the ssp. *flevensis* should be in fact a hybrid, which became apomictic. However, apomixis is not known of *S. lacustris*. As has been pointed out above, it is thought that the ssp. *flevensis* originated from crossing between the ssp. *lacustris* and *glaucus*, followed by back-crossings with the parents, which involved "introgressive hybridization".

The ssp. *flevensis* differs from the var. *β. bodamicus* Gaudin and *b. minor* Döll of *S. lacustris* by the round stems and the presence of about sixty percent flowers with 2 stigmas. In these varieties the stems are bluntly triangular above, whilst in the spikelets flowers with 2 stigmas have only sporadically been found. In the var. *c. trigonus* Döll on the contrary, nearly all the flowers have 2 stigmas. Probably these varieties are hybrids with *S. triquetus* L. (NEILREICH, 1859; LOUSLEY, 1931). Also *S. kalmussii* Ascherson, Abromeit et Graebner, as recorded from some parts of Germany, differs from the ssp. *flevensis* by the very thin, low and bluntly triangular stems above, the hypogynous bristles twice as long as the fruits and the nearly glabrous glumes, whilst all the flowers have 2 stigmas; in all probability this species belongs in fact also to *S. lacustris* L. *sensu lat.*

3. **Scirpus lacustris** L. ssp. **glaucus** (Smith) Hartman; Smith, Engl. Bot., 33, t. 2321, 1812; C. Hartman, Fl. Gev., 36, 1848; *S. tabernaemontani* Gmelin, Fl. Bad., 101-102, 1, 1805.

The ssp. *glaucus* is not always easy to distinguish from the ssp. *lacustris*, because several characteristics may overlap, as has already been pointed out above (table 1). Hence, the possibility does seem to exist that the highly fertile specimens with frayed leaf-sheaths, rather long leaf-blades, elongated spikelets, flowers with 3 stigmas scattered in the spikelets, glabrous or nearly glabrous glumes or long bearded connectiva at the tip are the result of crossings with the ssp. *lacustris* in one of the preceding generations. In the Herb. Bot. Dep. N.E. polder, for instance, specimens from Koedood, Oude Maas, are preserved with in each spikelet some flowers with 3 stigmas and a specimen from the Kamperisland with during flowering nearly glabrous glumes and at the tip rather long bearded connectiva. It must be kept in mind, however, that as a consequence of the plasticity the ssp. *glaucus* might vary according to the environmental conditions, e.g. the length and the diameter of the stems.

In the Netherlands the ssp. *glaucus* is a characteristic subspecies of the *Scirpetum maritimi* Tüxen, an association occurring sometimes in fresh but usually brackish water. According to IVERSEN (1936) this subspecies is "halophil", "oligo-mesohalob" and "polyhygroob", which means that it reaches its optimal development in a wet and brackish environment with a range of 0.1-10 ‰ Cl, which is the

habitat of the *Scirpetum maritimi*. In this connection it must not be overlooked that in the tidal estuaries the chlorine concentration may increase to a much higher level during high floods. Although this subspecies is the ecotype of brackish habitats, it also grows, usually with a lower vitality and competition power, in a fresh environment. But I can fully agree with the statement of IVERSEN, as it might explain why the ssp. *glaucus* is only frequently recorded from the

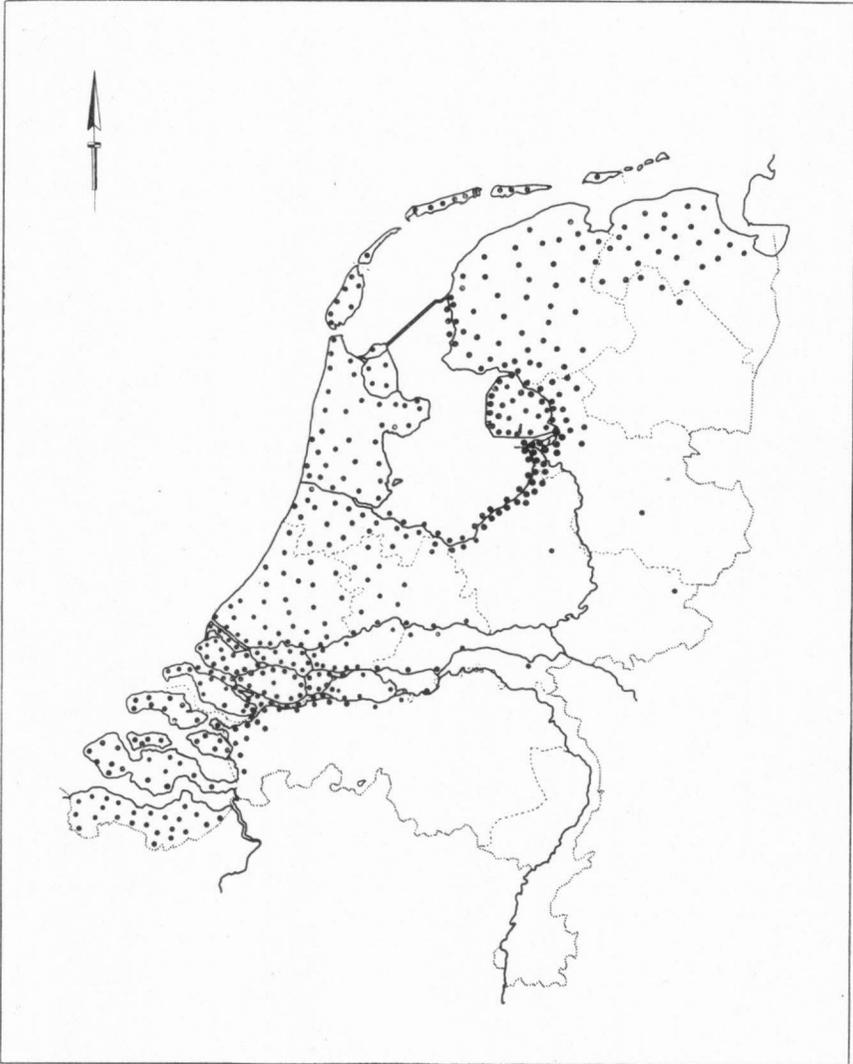


Fig. 2. Distribution of *Scirpus lacustris* L. ssp. *glaucus* (Smith) Hartman in the Netherlands. The data on this map are due to the herbaria mentioned in this paper, the "Nederlandsch Kruidkundig Archief" and the observations of the writer

Western part of the Netherlands, where the environment is often more or less brackish (Fig. 2).

With regard to the factor "water", this plant may be considered as a telmatophyte *sensu* IVERSEN, as it is able to grow in anaerobic and wet soils owing to the presence of aerenchymatic tissue. In contrast with the ssp. *lacustris*, this subspecies does not develop submersed "Bandblätter" (GLÜCK, 1923).

In the Netherlands the following variety and forms can be distinguished:

var. **compactus** Bakker, nov. nom.; var. *capitatus* Hausskn., Mitt. Geogr. Ges. Thür., 31, 6, 1888.

The inflorescences are capitate crowded (Plate 26). Seeing that on the same rhizomes stems with normal as well as with capitate inflorescences were observed, it is open to question whether this variety is of any systematical significance. It has been found in the Netherlands in the Kamperisland and Texel, and near Amsterdam, Blokzijl, Markelo, Rotterdam and Spakenburg.

fo. **maior** (Custor) Bakker, comb. nov., Gaud. Fl. Helv., 6, 337, 1830.

This form is characterized by the measurements of the stems and the inflorescences. The length of the stems is as much as 2.75 m and the diameter below 6 cm, whilst the inflorescences are large and strongly ramified (Plate 26). According to CUSTOR the colour of the stems is glaucous or green; the Dutch specimens, however, usually are glaucous, sometimes nearly green. But for the rest our specimens are in accordance with CUSTOR's description. LOUSLEY (1931), on the contrary, supposes that this plant should be considered as a hybrid between *lacustris* and *glaucus*. As a result of my observations the specimens in the Netherlands had better be called a modification, which comes into being when the ssp. *glaucus* grows as a pioneer in fresh, or slightly brackish, current water, rich in nutritive substances. In the Netherlands the fo. *maior* has only been found in the fresh or slightly brackish tidal estuaries in the S.W. and on the coast of the Yssellake.

fo. **tenuis** Bakker, nov. fo.

Caules tenues, ad basin diametro 3–6 mm.

(Type: Herb. Bot. Dep. N.E. polder nr. 1288; 1953, between Kampervnieuwstad and Oosterwolde).

From ditches near the coast of the Yssellake and brackish and wet dune valleys specimens are recorded with low (40–80 cm) and thin stems (3–6 mm below), sometimes even faintly angular above. As appears from a transplant experiment those plants must be regarded as a modification owing to poor environmental conditions.

In gardens the var. *zebrinus* André from Japan with variegated stems is cultivated on a moderate scale. Only a profound study may prove if this variety in fact belongs to the ssp. *glaucus*.

THE HYBRIDS OF *S. lacustris* L. *sensu lat.* AND *S. triqueter* L. IN THE NETHERLANDS

The determination of these hybrids is by no means simple. Besides the usual lack of uniformity which one expects in a simple Mendelian cross the situation is, in all probability, greatly complicated by numerous back-crosses with the parents (LOUSLEY, 1931). It follows that the hybrid swarm of *S. lacustris* × *S. triqueter* will show a great variability, ranging from one parent to the other. In consequence, it is difficult to form a description which will fit all specimens. Moreover, it is sometimes impossible to decide whether the ssp. *lacustris* or the ssp. *glauca* is one of the parents. Beside it, the fertility is often manifestly less than in the species, but rather fertile specimens may be found. In the Netherlands these hybrids are only recorded from the fresh tidal estuaries in the S.W., where *S. triqueter* occurs.

The following hybrids are distinguished:

S. × *carinatus* Smith, Engl. Bot., 27, t. 1983, 1808 (pro sp.);
S. × *duvalii* Hoppe, Sturm D. Fl., 1(9), 3(1), 1814 (pro sp.);
S. lacustri-triqueter Neilreich, Fl. N. Oesterr., 126–127, 1859.

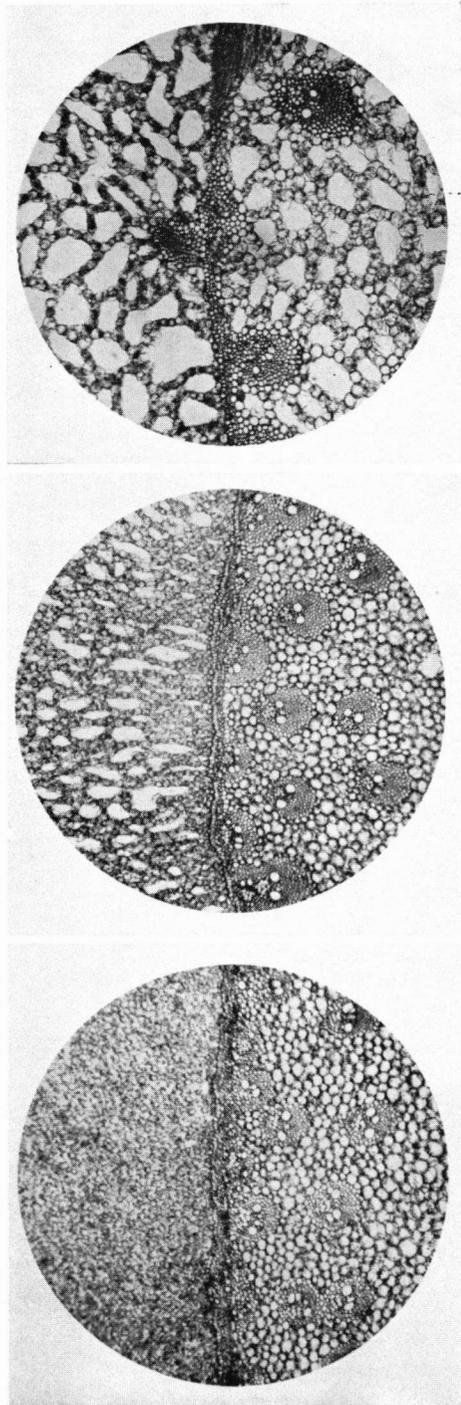
S. × *carinatus* was recognized as the hybrid of *S. lacustris* L. ssp. *lacustris* and *S. triqueter* by NEILREICH (1859). All the Dutch specimens I have seen may be classed under the var. *sub-lacustris* Lousley (1931). The description of this variety runs as follows: "Stem triangular above. Panicle large, exceeding the bract and resembling that of *lacustris*. Stigmas 2 or 3. Anthers bearded, in some plants. A tall stout plant". In this connection, it is worth mentioning that the plants described by SMITH and HOPPE have only 2 stigmas. In the following a short description of the Dutch material is given.

a. Herb. Bot. Dep. N.E. polder: near Malta in the Biesbos, about 1 m above mean low tide, with the putative parents, nr. 1353, leg. Bakker, Boer and Zonneveld, 1953.

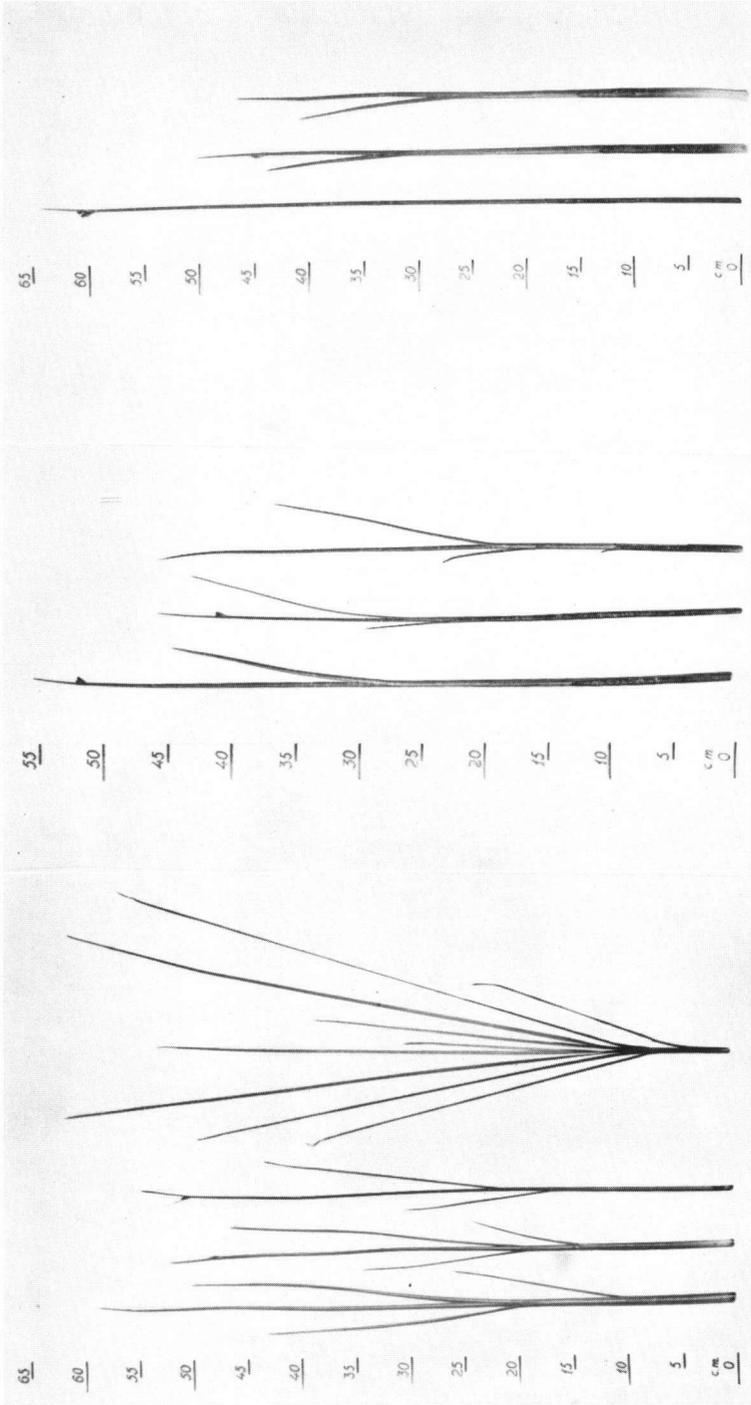
In general habit, the hard, brittle and red-brown rhizomes, the round base, the fresh green colour and the length of the stems (as much as 2 m), on each stem the leaves with at least two distinct leaf-blades and the large panicles, mostly as long as or overtopping the lower bracts, it agrees with *S. lacustris* ssp. *lacustris*. It approaches to *S. triqueter* by the bluntly triangular upper part of the stems and the triangular and rigid lower bracts. With the exception of the midrib the glumes are glabrous. In every spikelet flowers with 2 and 3 stigmas occur (table 4). The connectiva are pointed at the tip, short bearded. Furthermore this plant is characterized by the production of about 90 % filled pollen grains and a small number of ripened fruits (about 5 %). These fruits are compressed, brown and able to germinate.

In 1952 I made a transplant experiment with this hybrid in a shallow and fresh pool near Blokzijl. As appears from this trial the characteristics summarized above did not change at all.

b. Rijksherbarium Leyden: Dordrecht along the Merwede, leg. Kloos, 1914; Dordrecht, Nieuwe Biesbospolder, leg. Kloos,



Cross sections in the corresponding rhizome-regions of the ssp. *lacustris* (left), *flevensis* (centre) and *glaucus* (right) of *Scirpus lacustris* L. sensu lat. (47 ×)



The growth of leaf-blades of *Scirpus lacustris* L. *sensu lat.* To the left the sp. *lacustris* with 2-8 leaf-blades (the specimen with 8 leaf-blades belongs to the fo. *fitzingeri*), in the centre the sp. *sevensis* with 1-2 leaf-blade(s) and to the right the sp. *glauca* with 1 leaf-blade or leaf-blades wanting



A Inflorescences of the var. *pendulus* (left), a normal specimen (centre) and the var. *capitatus* (right) of *Scirpus lacustris* L. ssp. *lacustris*



B Inflorescences of the fo. *maior* (left), a normal specimen (centre) and the var. *compactus* (right) of *Scirpus lacustris* L. ssp. *glaucus* (Smith) Hartman

Van Dijk and Prins, 1934 (Ned. Kruidk. Arch., 129, 45, 1935) and Rijswijk along the Maas, with the putative parents, leg. Kern and Reichgelt, 1943 and 1946.

In general habit, the length of the stems (as much as 2 m), the round base of the stems and the leaves with often two distinct leaf-blades on each stem, these specimens resemble *S. lacustris* ssp. *lacustris*. The material approaches to *S. triqueter* by the bluntly triangular upper part of the stems and the triangular lower bracts. The panicles are as long as or overtopped by the lower bracts. The spikelets are elongate and the glumes glabrous. In the spikelets nearly all the flowers have 3 stigmas, but in all the spikelets scattered flowers with 2 stigmas occur. The connectiva are short bearded. A rather large number of filled pollen grains has been counted. In all probability ripened fruits are formed, mostly trigonous.

c. Herb. Bot. Dep. N.E. polder: along the Oude Maas near Koedood, about 1 m above mean low tide, with the putative parents, nrs. 1767–1770, leg. Bakker and Boer, 1954.

In general habit, the red-brown rhizomes, the length of the stems (as much as 1.75 m) and the round base of the stems, it agrees with *S. lacustris* ssp. *lacustris*. It resembles *S. triqueter* by the rather weak and thin rhizomes (diameter about 0.5 cm), the weak stems, the bluntly triangular upper part of the stems, the colour of the stems, the leaves with not more than 1 leaf-blade on each stem and the panicles strongly overtopped by the triangular lower bracts. At one side the stems are often channelled for 5–20 cm below the panicles. With the exception of the midrib the glumes are glabrous. In each spikelet flowers with 2 and 3 stigmas occur (table 4). The connectiva are somewhat pointed at the tip, very short bearded. About 10–30 % filled pollen grains has been counted. Fruits are rarely ripened.

d. Herb. Bot. Dep. N.E. polder: on a coffer-dam in the Zuid-Maartensgat, Biesbos, about 1.50 m above mean low tide, with the putative parents, nrs. 1771–1772, leg. Bakker and Boer, 1954.

In general habit, the red-brown and rather hard rhizomes (diameter about 0.8 cm) and the fresh green colour and the length of the stems (as much as 1.75 m), it approaches to *S. lacustris* ssp. *lacustris*. It agrees with *S. triqueter* by the stems, distinctly triangular for a considerable distance below the panicles, the leaves with only one leaf-blade on each stem and the rather small panicles, strongly overtopped by the triangular lower bracts. With the exception of the midrib the glumes are glabrous. Mostly some flowers with 3 stigmas occur (table 4). The connectiva are pointed at the tip, scarcely bearded. About 40–50 % filled pollen grains has been counted. Some fruits are ripened.

By the stems, triangular for a considerable distance below the panicles, the scarcely bearded connectiva and the small panicles, this material approaches to the var. *sub-triqueter* Lousley. Owing to the length of the stems and the well developed reproductive organs I have still classed this hybrid under the var. *sub-lacustris*.

TABLE 4

Average and extreme numbers of flowers per spikelet with 2 and 3 stigmas in hybrids of *S. lacustris* L. *sensu lat.* and *S. triqueter* L.

Name and locality	2 stigmas	3 stigmas	Number of panicles studied
<i>S.</i> × <i>carinatus</i> , Malta	13(16–11)	4(7–2)	20
<i>S.</i> × <i>carinatus</i> , Oude Maas	8(11–4)	7(11–5)	15
<i>S.</i> × <i>carinatus</i> , Z. Maartensgat	15(19–10)	1(2–0)	18
<i>S.</i> × <i>scheuchzeri</i> , Jonge Deen	15(19–8)	2(4–0)	20
<i>S.</i> × <i>scheuchzeri</i> , Oude Maas	15(18–12)	3(7–1)	20

S.* × *scheuchzeri Brügger, Jahresber. Naturf. Ges. Graubünden, 108–111, 25, 1882; *S.* × *kukenthalianus* Junge, Mitt. Bot. Staatsinst. Hamburg, 73, 12, 1904; *S.* × *arunensis* Druce, Bot. Soc. Exch. Cl. Br., 68, 7, 1923.

The hybrid *S. lacustris* L. ssp. *glaucus* (Smith) Hartman × *S. triqueter* L. (*S.* × *scheuchzeri*) was for the first time described by BRÜGGER (1882). It is a curious fact, however, that BRÜGGER collected this hybrid in an area, where the putative parents did not occur. Moreover, it will be noticed that in BRÜGGER's description there is no reference to the male and female sterility.

Owing to BRÜGGER, JUNGE (1904) and LOUSLEY (1931) this hybrid has glaucous stems, bluntly triangular above, more or less asperous glumes and 2 stigmas. Furthermore an ill fruit formation is recorded by JUNGE. The Dutch specimens are usually characterized by dark- or grey-green stems, bluntly triangular above, more or less asperous glumes and often in the spikelets scattered flowers with 3 stigmas. The fertility is usually manifestly less than in the species. With regard to the scattered flowers with 3 stigmas it must be kept in mind, that in the ssp. *glaucus* scattered flowers with 3 stigmas are rather much found. In the following a short description of the Dutch material is given.

Herb. Bot. Dep. N.E. polder: Boerenplaat, nrs. 1351 and 1373, N. Jonge Deen, nr. 1353, and Rode Vaart, nrs. 74–75, in the Biesbos and along the Oude Maas near Koedood, nrs. 1774–1775, about 60–80 cm below mean low tide, with the putative parents, leg. Bakker and Boer, 1953 and 1954.

The rhizomes are thin (diameter 4–5 mm), weak, tough and yellow-white. The stems are weak, grey-green, bluntly triangular above and sometimes compressed or channelled for some distance below the panicles. The length of the stems is as much as 1.50 m, they have nearly all not more than 1 leaf with a distinct leaf-blade. The lower bracts are triangular and of different length, in the specimens of the Biesbos as long as or overtopped by the panicles. The glumes are more or less asperous, dull red-brown. Flowers with 2 stigmas predominate (table 4). The connectiva are slightly bearded or not at all. Many empty pollen grains are formed. A rather large

number of fruits is ripened; the fruits are compressed and yellow-brown. This hybrid flowers in August.

In so far as may be judged of the herbarium material, the following specimens also belong to this hybrid:

Rijksherbarium Leyden: Dordrecht along the Maas, leg. Van Hoven; Rotterdam along the Nieuwe Maas, nrs. 2195–2196, leg. Danser and nrs. 4737–4742, leg. Jansen and Wachter, 1908 (in Prodr. Fl. Bat. ed. alt. as *S. lacustris* × *triquetrus* and in Fl. Bat. as *S. duvalii*; JANSEN and WACHTER, 1917); Rotterdam near the Schwaardijk, leg. Danser, 1909; fore-lands along the Nieuwe Maas near Vlaardingen, nrs. 22616–22619, leg. Jansen and Wachter, 1918; Schiedam near the Sterrebos, leg. Kern, 1938; Rozenburg, leg. Vervoort and De Bruyn, 1944.

In each spikelet of rushes, collected on the fore-lands along the Nieuwe Maas near Vlaardingen in 1917 by Jansen and Wachter (nrs. 14923–14934), flowers with 2 and 3 stigmas occur in a ratio of about 5 to 2, whilst the outer glumes are asperous to some extent. The thin stems are bluntly triangular for a considerable distance below the panicles. The production of many empty and misshapen pollen grains and the bluntly triangular stems suggest, that this homogeneous material, in contrast with the ssp. *flevensis*, should be considered as a hybrid with *S. triqueter* L. In spite of the large number of flowers with 3 stigmas I consider this hybrid on account of the general habit and the asperous glumes as *S.* × *scheuchzeri* (JANSEN and WACHTER, 1917).

S. × *schmidtianus* Junge (*S. lacustris* L. ssp. *lacustris* × *S. americanus* Pers.), which is almost or completely sterile, has not been recorded in the Netherlands.

SUMMARY

In literature quite different opinions have been developed with regard to the species-concept of *S. lacustris* L. and *S. tabernaemontani* Gmel. In the nineteenth century several authors considered these species as modifications of *S. lacustris* L., owing to the resemblance, the unstable characteristics, the merging into one another under the influence of changing environmental conditions or the occurrence of intermediates. This does not exclude, however, the possibility that the unstable characteristics, the occurrence of intermediates and probably even the merging into one another should be ascribed to the growth of hybrids between the species mentioned above; from one locality this hybrid is on record. Consequently, in the twentieth century they are usually considered as separate species.

An examination of the specimens occurring in the Netherlands showed, that in one locality in our country a highly fertile intermediate grows, with the same chromosome number as the other two forms, whilst the plants developing from the seeds of the intermediate are equal in morphological characteristics to those of the preceding generations. It follows that on no account the intermediate can be a hybrid. It is thought that the intermediate has been originated by

"introgressive hybridization" *sensu* ANDERSON and HUBRICHT (1938), which means in this case by crossing of *S. lacustris* L. and *S. tabernaemontani* Gmel. followed by back-crossings with the parents. Moreover, in some instances the possibility does seem to exist that between these species cross-breeds with undiminished fertility are yielded. It follows that in some localities in the Netherlands the boundaries between these species have been obliterated. According to these data the above-mentioned species are considered to belong to the same commiscuum *sensu* DANSER (1950). On the strength of the fertility of the cross-breeds, the occurrence of gradation, the same chromosome numbers, the morphological resemblance and the fact that they reach their optimal development in different habitats, they are in this paper united into the same species. This means they are ecotypes (sub-species), respectively the ssp. *lacustris* and the ssp. *glaucus* (Smith) Hartman, of the ecospecies *S. lacustris* L. *sensu lat.* The intermediate has been described as the ssp. *stevensis* of *S. lacustris* L. *sensu lat.*, which, in all probability, continues existence in the habitat of the ssp. *lacustris* as a consequence of the planting out by man.

In the course of this examination data on the polymorphy, the distribution and the hybrids of *S. lacustris* L. *sensu lat.* × *S. triquetra* L. in the Netherlands have been obtained.

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