

SENECIO CONGESTUS (R.Br.) DC. IN THE LAKE YSSEL POLDERS

D. BAKKER

(*Biology Department, Wieringermeer Authority, Kampen, The Netherlands*)

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1. INTRODUCTION

An arctic paramorph of the species was treated as *Senecio congestus* (R.Br.) DC. in 1837 and this appeared to be the correct name (FERNALD, 1945). Therefore the name *Senecio tubicaulis* Mansf., proposed in 1940, must be rejected. The binominal *Senecio palustris* (L.) Hook. (1834), frequently used for this species, is excluded by *Senecio palustris* Velloso, published for a S. American taxon in 1827.

As to the polymorphy of the European material no exact data are available. RUPRECHT (1846) separated the plants from the arctic part of Europe under the name *S. arcticus*, but it is questionable whether this material merits specific rank. According to FERNALD (1945), who distinguished three varieties of *S. congestus* in N. America, the var. *palustris* (L.) Fern. might be identical with the Eurasian material; this paramorph being treated in some Floras as var. *palustris* (L.) Hyl. But with regard to this question a closer examination is desirable.

This treatise refers to a very small part of its area of distribution, where the species shows a slight variability in morphological characteristics only and so *S. congestus* is not subdivided.

S. congestus is a boreal species, which occurs on both sides of the Atlantic. According to HEGI (1929) its area of distribution comprises: N. Russia, S. Sweden, Esthonia, Latvia, Lithuania, Denmark, Poland, Czechoslovakia, Hungary, Germany, the Netherlands, Belgium (very rare; GOFFART, 1945), N. France (probably extinct; FOURNIER, 1946), British Isles (extinct; CLAPHAM, TUTIN and WARBURG, 1952) and Siberia. Fernald (1950) records the species from the Northern part of N. America.

VAN OOSTSTROOM (1956) states that the species is locally common in the Netherlands, especially to the North of the line Zuid-Beveland, Dordrecht, Nijmegen; not being known from Zuid-Limburg.

After the enclosure of the Zuiderzee (since 1932 called Lake Yssel), soon followed by desalinization, *S. congestus* established itself on the bare and muddy shores, which came into being as a result of the disappearance of the tidal movement (FEEKES, 1936, 1941). In all probability, its diaspores were wind-borne from the adjacent peaty habitats, e.g. the Twiskeland (WESTHOFF, 1943), Noordwest-Overijssel (DE LEEUW, 1929; VAN SOEST, 1937; FEEKES and BAKKER, 1954) and the vicinity of Kampen (VAN SOEST, 1933) (Fig. 1).

In the saline Wieringermeer, after the emergence of the land from

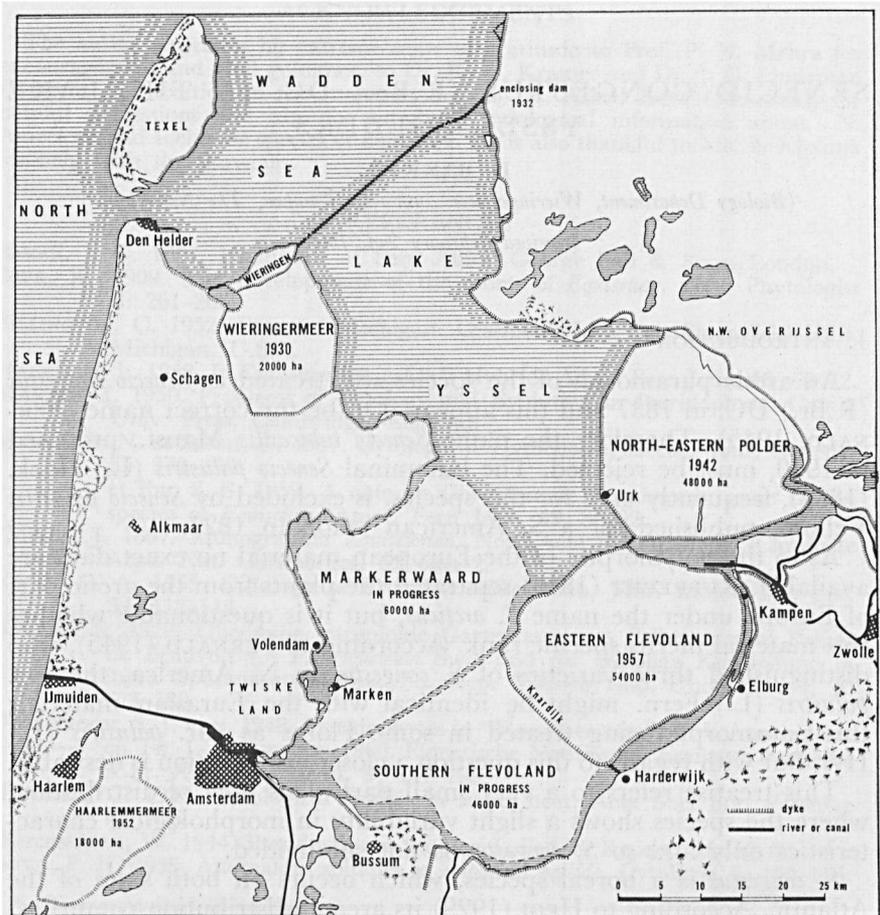


Fig. 1. Reclamations in the Lake Yssel with adjacent areas.

the water in 1930, a *S. congestus* aspect occurred only locally, viz. in fresh seepage regions (FEEKES, 1936). On the other hand, in the two polders (North-Easternpolder and Eastern Flevoland), which had been drained dry after the enclosure of the Zuiderzee in 1942 and 1957 respectively, the species established itself temporarily on a large scale. In the fresh or faintly brackish North-Easternpolder a *S. congestus* aspect occupied about 1200–1400 ha during the 1943–1944 season (FEEKES and BAKKER, 1954). In the nearly fresh Eastern Flevoland this aspect was found on at least 10.000 ha from August 1958 till July 1959. The first establishments in those polders mainly arose from seed, disseminated from small sources along the coast of the Lake Yssel.

After the optimum years 1943–1944 and 1958–1959, in the North-Easternpolder and Eastern Flevoland respectively, *S. congestus* decreased rapidly. At present the species occurs only sporadically and

with a low vitality in the North-Easternpolder, whereas it covers 1000 ha at most in Eastern Flevoland. Probably the species will decrease still more in the latter polder during the following years.

This phenomenon was also observed shortly after the reclamation of lakes in the Netherlands during preceding centuries. In this connection it may be of interest to quote GEVERS VAN ENDEGEEST (1861) after the reclamation of the Haarlemmermeer in 1852: 'From the mud millions of plants grew up after recession of the water, rushes and reed and a large number of willows, and in the muddiest soils the Marsh fleawort, the well-known waterplant of our reclamations, which disappears without trace after one or two years. From afar this plant with its yellow flowers gave an impression as if the drained soils had turned into rape fields; the wind-borne seeds were disseminated as far as the surrounding towns'.

Consequently, in two of the three polders in the Lake Yssel and in the Haarlemmermeer the establishment of *S. congestus* took place rapidly on a large scale, but was followed by a strong decline after some years. In addition, in Eastern Flevoland it was observed that species with vegetative propagation often started to take possession of the open spaces immediately after the *S. congestus* vegetations had died off, especially *Phragmites communis*, but also *Scirpus maritimus* and *Typha latifolia*. Thus, in some months a *S. congestus* aspect changed into an aspect of *Phragmites*, *Scirpus maritimus*, *Typha latifolia* or into a mixture.

In some instances, however, species with vegetative propagation did not occur and after *S. congestus* had died off, development of a thin vegetation took place during the first years only. Locally, on the other hand, the perished vegetation of *S. congestus* was succeeded by a new generation of the same species, which became equally vigorous.

In order to find an explanation of these phenomena several ecological characteristics of the species were studied. The majority of the field trials have been made in Eastern Flevoland. The results will be dealt with in this paper.

2. LIFE FORMS

S. congestus is a hapaxanthous species. In the Netherlands the majority of the population are winter annuals. The seed of the winter annuals germinates in the June-August period; the plants survive the winter with leaf-rosettes (mainly one rosette per plant), which are lost before flowering in May and June. The dissemination chiefly takes place in June, whereas the plants die in July. The dead stems may largely cover the soil surface during several months.

In the Lake Yssel polders only the winter annuals play an important part in the vegetation. Hence this study refers mainly to this life-form.

Moreover, in June and July flowering summer annuals may arise from seed that has survived the winter. Their vitality is considerably smaller than that of the first winter annual generation, as had been

observed by VALLIN (1925) in S. Sweden. Besides, in autumn flowering summer annuals occur, viz. a small part of the plants grown from seeds, which have germinated immediately after dissemination in June, may flower in September and October. Their first generation usually shows the same vitality as the first generation of the winter annual life-form.

According to HEGI (1929) perennial plants of *S. congestus* are found too, but in the Lake Yssel region they have never been observed. In this connection, it should be noted that sometimes plants with more than one leaf-rosette may occur. In this case, stems and flower-stalks arise exceptionally from rosettes before the winter, whereas other rosettes of the same plants do not produce them before the next spring.

It seems possible that these differences in life-form are connected with phenomena of vernalization and photoperiodism, but this has not been studied.

As to the structure of the root system, *S. congestus* belongs to the type with adventitious roots. The primary root and the lateral roots are slightly developed and they are lost in the juvenile stage. Some weeks after germination adventitious roots, arising from the base of the rosettes, start growth and they increase considerably in length and number before the winter.

With regard to the factor water, the plant should be considered as a telmatophyt (IVERSEN, 1936), as it prefers unaerated, wet and muddy soils, where the species is capable of taking root by means of a strongly developed system of air-canals in leaves, stems and roots. The adventitious roots are surrounded by a thick layer of aerenchyma tissue (Fig. 2).

Pollination may be achieved in different ways. The heads have about 21 female ray-florets and 80–140 hermaphrodite disc-florets, rich in honey and pollen. Hence they are much visited by insects (Coleoptera, Diptera, Hymenoptera and Lepidoptera). But pollination is also achieved in the absence of insects. For the tips of the style-arms of the disc-florets bear small brushes, collecting pollen shed into the anther-tubes during emergence of the styles. After the style-arms have curled downwards the stigmatic surfaces come into contact with pollen on the brushes.

In Eastern Flevoland, where on the Knardijk (Fig. 1) about 800 bee-hives had been placed along the *S. congestus* vegetations in May 1959, some information was obtained about the fruit-setting of entomophilous and automophilous pollinated heads. It appeared that the bees visited the flower-heads mainly within a distance of 500–600 m from the Knardijk. At a distance of 1000 m the author sporadically observed bees, and other pollinating insects as well.

In this area thirty heads with mature fruits (in this paper generally called seed) have been collected at random at a distance of respectively 50, 1000 and 2000 m from the bee-hives on the Knardijk. Of each sample the germination was determined, as is shown in Table 1. In view of the fact that the non-germinating seed did not exhibit red

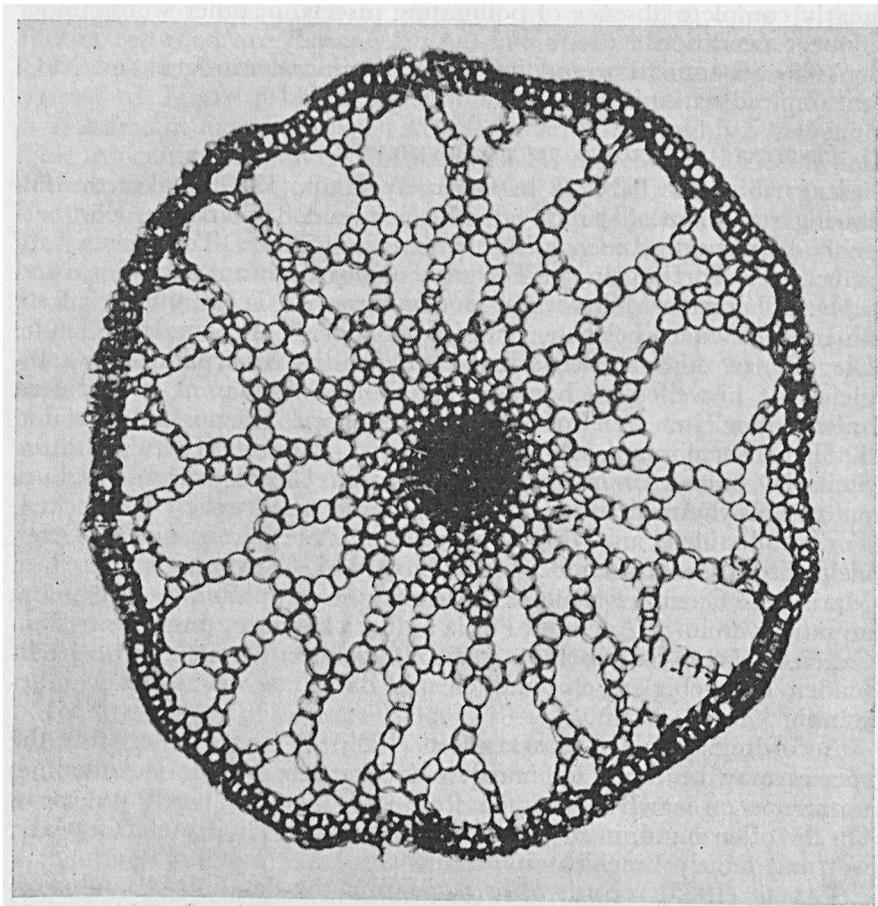


Fig. 2. Adventitious root of *S. congestus* in transverse section, showing the aerenchyma layer (75 ×).

colouring after treatment with sodiumbiselinite, the germination was taken as a measure of the fruit-setting.

It follows from Table I that the extent to which pollinating insects occurred and the degree of fruit-setting did not correlate. Although an explanation of this phenomenon cannot be given, it is clearly shown that fruit-setting may take place on rather a high level in a

TABLE I

Viability of *S. congestus* seed in, respectively, presence (50 m) and nearly complete absence (1000 and 2000 m) of pollinating insects. In brackets the limits of variation.

	Mean germination % at a distance from the Knardijk of:		
	50 m	1000 m	2000 m
Series 1	38 (11-80)	57 (25-85)	29 (6-63)
Series 2	67 (20-95)	77 (39-98)	77 (35-97)

nearly complete absence of pollinating insects, in other words under pioneer conditions.

As to dissemination and influence of mineral nitrogen and NaCl an ample discussion will follow under 6, 7 and 8.

3. HABITATS ACCORDING TO LITERATURE

Regarding the habitats in Germany HEGI (1929) makes the following statement: 'Trupp- oder herdenweise, vielfach nur vorübergehend (mitunter auch verschleppt), in frischen Torfstichen, auf unberasteten Torfhügeln, in Torfgräben, bisweilen auf sumpfigen und schwach berasteten Moorwiesen, Hochmooren, an Teich- und Seeufern, auf abgelassenen Teichen. Nur in der Ebene und im Hügellande. Die Pflanze zählt zu den sehr bezeichnenden Moorpflanzen, wenngleich sie bisweilen auch massenhaft auf Faulschlamm an Seeufern auftritt, begleitet von Equisetum, Heleocharis, Scirpus paluster und S. Tabernaemontani, Acorus Calamus, Rumex Hydrolapathum, Stellaria palustris, Nasturtium palustre, Cicutula virosa, Galium palustre usw. Am liebsten stellt sie sich aber auf frischen Torfstichen, Torfabfallhaufen, an Torfgräben usw. ein. Sie ist an solchen Orten vielfach mit Carex pseudocyperus, C. Oederi, C. cyperoides, Cladium Mariscus, Cirsium rivulare, Nasturtium amphibium, Oenanthe aquatica vereinigt. Auch mit Pirola uniflora kann sie zusammentreffen. Gegen stärkeren Rasenschluss ist sie infolge ihrer fast stets zu beobachtenden Kurzlebigkeit empfindlich und daher an vielen Orten unbeständig'.

According to VAN OOSTSTROOM (1956) in the Netherlands the species may be found in marshes and peat-bogs, but is sometimes numerous on newly reclaimed fresh soils and on newly cut peat. On the other hand, in the opinion of FEEKES (1941) it prefers a peaty, wet and faintly brackish environment.

VALLIN (1925) records *S. congestus* from the desalinated landwardsides of seaweed-banks, washed ashore on the island of Väderö in S. Sweden. Here a nitrophilous vegetation occurred, in which *Ranunculus sceleratus* showed the greatest frequency.

NORDHAGEN (1940) found that the vegetations of the desalinated landwardsides of the seaweed-banks along the Norwegian coast and on the island of Väderö were highly comparable, but *S. congestus* did not occur in the Norwegian localities. In the opinion of Nordhagen these vegetations belong to the nitrophilous *Bidentetum tripartiti* Koch. It is questionable, however, if *S. congestus* may be considered as a faithful species of this association as a result of inconstancy ('meteorische Pflanze').

On the other hand, in Germany ROLL (1939) regards *S. congestus* as a faithful species of the *Bidentetum tripartiti*, together with *Bidens tripartita*, *Ranunculus sceleratus*, *Polygonum hydropiper* and *Alopecurus geniculatus*. He points to the low competitive power and to the nitrophilous character of the association.

SISSINGH (WESTHOFF, DIJK, PASSCHIER and SISSINGH, 1946) classes *S. congestus* with the faithful species of the *Rumicetum maritimi*, a pioneer

association on embanked or dredged up soils. The other faithful species recorded are *Rumex maritimus* and *Ranunculus sceleratus*.

The name *Rumicetum maritimi* has been changed into *Ranunculetum scelerati* by TÜXEN (1950), with the following faithful species: *Ranunculus sceleratus*, *Rumex maritimus*, *R. palustris* and presumably *S. congestus*. This association is found: 'Auf feuchten bis nassen, an Stickstoff und Nährstoffen reichen offenen Böden am Rande von Viehtränken, Dorfteichen, auf der Sohle abgelassener Fischteiche und auf Abwasser Versickerungsflächen (Rieselfeldern), auch in Flachmoor-Torfstichen'.

From the literature mentioned above the conclusion may be drawn, that *S. congestus* is a pioneer of wet and bare soils. According to HEGI (1929) the rapid decline may be the result of the low competitive power, but this holds good as well for the species which usually grow together with *S. congestus*.

The species shows its optimum development on soils rich in mineral nitrogen, e.g. on seaweed-banks and dredged up soils, along ponds etc., where nitrophilous summer annuals frequently occur. Moreover, *S. congestus* is often found together with *Ranunculus sceleratus*, an extreme hydrophilous species.

Apparently there has been some controversy in literature as to the question whether *S. congestus* shows a NaCl-tolerance or not.

4. OBSERVATIONS ON THE VEGETATION-CYCLE OF *S. congestus* IN EASTERN FLEVOLAND

On five sample plots, each 100 m² (10 × 10 m) in extent, the vegetation-cycle was studied in Eastern Flevoland during the years 1957–1959 (Table II). The plants on these plots took root in silty clay loam, emerging from the water in the spring of 1957. During germination and seedling growth, which took place in the summer of 1957, the soil surface was wet and bare. Shallow pools even covered the plots 3 and 4 till the autumn of 1959.

On all the plots the aspect was formed by *S. congestus* rosettes during the autumn and winter of 1957. Nevertheless, plot 5 showed a much thinner cover than plots 1–4. And so on plots 1–4 a very dense vegetation of flowering *S. congestus* occurred in June 1958, whereas at that time on plot 5 an open vegetation was met with, in which *S. congestus* and *Ranunculus sceleratus* predominated. This difference may be attributed to the fact that in the summer of 1957 plots 1–4 were 0.5–1.5 km remote from the nearest fruiting sources of *S. congestus*. But this distance amounted to 7 km for plot 5. It follows that the thin cover of the latter plot should be the result of the low accessibility (HEIMANS, 1940) to *S. congestus*. This was clearly shown in the summer of 1957 by means of a sowing experiment, performed at a distance of about 0.3 km from plot 5. Here a nearly continuous vegetation of rosette-plants was found in the autumn of the same year.

In June 1958 the total cover had increased on all plots in comparison with the situation in September 1957. On plots 1–4 the increase was mainly due to the growth of the *S. congestus* plants. However, the greatest increase took place on plot 5, but here vigorous *Ranunculus*

scleratus plants played an important part too. This might be the result of the rather open vegetation in the latter case, where competition was still of slight influence.

The total cover on all plots proved to have decreased in September 1958, but not in the same measure, whilst plants of the new *S. congestus* generation were either entirely absent or of low vitality. It was found that this decrease of the total cover depends on the degree in which species with vegetative propagation are present. The occurrence of the latter appeared to be connected with edaphic factors and accessibility, as will be discussed below.

Twenty nine seedlings of *Phragmites communis*, sown in May 1957, grew on plot 1 of Table II in September 1957. Furthermore six seedlings of *Scirpus maritimus* were found, arising from seed deposited at the bottom by the water of the Lake Yssel, prior to reclamation. In all probability they were disseminated from the *Scirpus* vegetations along the coast, about 1 km away. Owing to the heavy vegetation of the first *S. congestus* generation the vegetative propagation of *Phragmites* and *Scirpus maritimus* was hampered. But they could increase considerably by means of vegetative propagation after *S. congestus* had died off, because the soil surface was thinly overgrown and still wet at that time. It appeared that in September 1958 the *S. congestus* aspect of June 1958 had changed into a *Phragmites* aspect and the vegetation was nearly continuous in June 1959.

On plot 2, about 0.4 km away from plot 1, nearly the same edaphic factors prevailed as on plot 1. Nevertheless, on account of the scarce establishment of *Phragmites* (two plants), the vegetation on plot 2 remained thinner than on plot 1. This might be explained by the fact that the vegetative propagation of *Phragmites* takes place more rapidly than that of *Scirpus maritimus*. The sparse establishment of *Phragmites* might be the result of the chance occurrence that not much seed had been deposited on plot 2.

On plots 3 and 4 the total cover decreased considerably after the first *S. congestus* generation had died off, because species with vegetative propagation were sparse or did not occur at all. The absence of *Phragmites* was due to an environment unfavourable to the establishment from seed (seepage pools), sown in 1957. Meanwhile *Phragmites* penetrated into plot 3 by means of vegetative propagation from a source along the dyke. The small scale establishment of *Scirpus maritimus* may be connected with the sporadic supply of diaspores. For the seed sources of this species were about 15 km away from these plots.

In view of the fact that in the summer of 1958 diaspores of *S. congestus* were deposited in excess on the plots 3 and 4, while the soil surface was wet and thinly covered with vegetation, the scarce establishment of the second generation could not be the result of low accessibility, drought or competition. An ample discussion of this phenomenon will follow under 8.

On plot 5 the species with vegetative propagation increased too, but rather slowly owing to the small number.

TABLE II
Vegetation-cycle of *S. congestus* on five sample plots (10 × 10 m in extent) in Eastern Flevoland after its emergence from the water in the spring of 1957. The frequently occurring species are recorded only. Italicized figures = fruiting plants.

Nr.	Soil surface mostly wet, 3 and 4 usually with shallow pools												
	September '57	June '58	September '58	June '59	September '59	September '57	June '58	September '58	June '59	September '59	September '57	September '59	
1.	Total cover	85 %	95 %	80 %	95 %	Cover	Stem height	Cover	Stem height	Cover	Stem height	Cover	Stem height
	<i>Ranunculus sceleratus</i>	< 5 %	< 5	cm	< 5	%	34-56	< 5	cm	5	18-37	5	Brought under cultivation
	<i>Senecio congestus</i>	75 %	80	cm	122-153	—	—	—	—	—	—	—	—
	<i>Phragmites communis</i>	29 ×	10	cm	128-147	60	165-198	80	155-183	80	155-183	80	155-183
	<i>Scirpus maritimus</i>	6 ×	< 5	cm	39-61	10	82-103	10	47-66	10	47-66	10	47-66
2.	Total cover	70 %	85 %	60 %	85 %								
	<i>Ranunculus sceleratus</i>	< 5 %	5	cm	39-51	10	< 5	< 5	31-46	< 5	31-46	< 5	Brought under cultivation
	<i>Senecio congestus</i>	65 %	70	cm	119-161	5	< 13	10	41-84	10	41-84	10	41-84
	<i>Phragmites communis</i>	2 ×	< 5	cm	111-140	15	171-192	35	140-176	35	140-176	35	140-176
	<i>Scirpus maritimus</i>	13 ×	10	cm	41-73	25	61-97	35	53-83	35	53-83	35	53-83
3.	Total cover	90 %	95 %	< 5 %	35 %								
	<i>Ranunculus sceleratus</i>	< 5 %	< 5	cm	22-43	—	—	15	28-47	15	28-47	5	21-47
	<i>Senecio congestus</i>	85 %	90	cm	135-184	< 5	< 7	< 5	21-53	< 5	21-53	5	< 14
	<i>Phragmites communis</i>	—	—	—	—	—	—	—	22-46	—	22-46	20	58-77
	<i>Catabrosa aquatica</i>	< 5 %	< 5	cm	24-36	—	—	15	16-28	15	16-28	25	< 11
4.	Total cover	85 %	95 %	10 %	20 %								
	<i>Ranunculus sceleratus</i>	< 5 %	< 5	cm	18-41	—	—	5	16-43	5	16-43	5	16-39
	<i>Senecio congestus</i>	80 %	90	cm	116-173	< 5	< 8	< 5	29-66	< 5	29-66	15	< 12
	<i>Scirpus maritimus</i>	1 ×	< 5	cm	25-43	5	41-69	10	43-65	10	43-65	15	53-91
	<i>Catabrosa aquatica</i>	—	—	—	—	< 5	< 9	5	14	5	14	20	< 15
5.	Total cover	15 %	50 %	35 %	75 %								
	<i>Ranunculus sceleratus</i>	< 5 %	25	cm	27-96	< 5	< 5	25	38-57	< 5	38-57	< 5	< 8
	<i>Senecio congestus</i>	10 %	20	cm	118-166	< 5	< 9	< 5	87-121	< 5	87-121	30	143-191
	<i>Phragmites communis</i>	1 ×	< 5	cm	78-91	5	128-151	10	86-111	10	86-111	30	143-191
	<i>Scirpus maritimus</i>	5 ×	5	cm	31-64	20	62-91	35	41-83	35	41-83	55	88-106

In addition, a controversy with the data of Table II had been observed locally in the autumn of 1959. In some seepage pools in Eastern Flevoland vegetations of the second *S. congestus* generation appeared, with the same vitality as the first generation, at least in the rosette-stage. This phenomenon took place in pools which dried out during the extreme drought of June and July. Although the dry weather continued, the soil surface of the pools became wet again in August. In all probability the evaporation decreased at that time as a result of the shortening of the days, so that the seepage-water level rose. Under 8 an explanation of this phenomenon will be discussed.

5. VITALITY

It is by no means simple setting up criteria of vitality valid for species with different life-forms. For this reason the criteria discussed below should be considered only an approach to the problem. The criteria are: seed output, dry matter production, stem height and number of flower stalks at the stem base. The figures recorded only refer to the winter annuals.

In order to obtain information about the seed output, ten plants of the first and second generations had been collected at random in June 1959. In this material the number of heads per plant and seeds per head as well as the percentage viable seed per head were determined. Finally the number of plants per 100 m² was counted. On the basis of these figures it was possible to calculate the mean output of viable seed per 100 m² (Table III). It can be seen from Table III that the seed output of the second generation had decreased in a high degree compared with the first generation.

TABLE III
Seed output of the first and second *S. congestus* generations in Eastern Flevoland (June, 1959). In brackets the limits of variation.

	Mean number:		Mean % viable seed per head	Per 100 m ² mean number of:	
	heads per plant	seed per head ¹⁾		plants ²⁾	viable seed
1st generation	978 (517-1731)	120 (81-161)	55 (23-81)	263 (111-474)	16 976 124
2nd generation	115 (43-223)	111 (71-152)	61 (42-74)	97 (0-223)	758 540

¹⁾ seed of 10 heads per plant counted.

²⁾ plants of 10 × 100 m² counted.

Moreover, it was observed that plants of *S. congestus*, growing on bare and muddy soils without inter- and intraspecific competition, may produce 150.000-200.000 viable seeds. In other words, even after the establishment of a single plant a considerable increase might be achieved in the next year.

As to the dry matter production of *S. congestus* no data have been.

recorded in literature. In Eastern Flevoland the production of the second generation mostly remained considerably behind that of the first one. In Table IV these figures are compared with the dry matter production of vigorous *Phragmites*, Winter wheat and Lucerne, growing in Eastern Flevoland. It appeared that in this respect the first generation partly coincided with the reed and the two crops. So it is likely that the first generation reached a high vitality in Eastern Flevoland. That this should be true can be deduced from the data concerning the stem height and the number of flower stalks at the base of the stems, as will be explained below.

TABLE IV

Annual dry matter production of some natural vegetations and agricultural crops in Eastern Flevoland.

Species	Dry matter production of the aerial parts in kg per ha
<i>Senecio congestus</i> , 1st generation, 1959	9000-11.000
<i>Senecio congestus</i> , 2nd generation, 1959	2000- 3.000
<i>Phragmites communis</i> , 3rd year, 1959	8000-13.000
Winter wheat, 1959	8000-14.000
Lucerne, 3-4 cuts, 1959	8000-14.000

First, in the majority of the W. European Floras it is stated that the maximum stem height amounts to 1 m (FOURNIER, 1946; CLAPHAM, TUTIN and WARBURG, 1952; VAN OOSTSTROOM, 1956). HEGI (1929) records: 'bis über 100 cm hohe Pflanze'. In S. Sweden on seaweed-banks VALLIN (1925) observed plants up to a height of 1.50 m. On the other hand, according to FERNALD (1950) the species does not exceed 0.60 m in N. America. From Table II it follows that the first *S. congestus* generation on the five plots reached a height of more than 1.50 m. FEEKES and BAKKER (1954), too, described from the North-Easternpolder first vegetations up to a man's height. In addition, the mean height of fifty *S. congestus* plants of the first generation, collected at random in June 1959, amounted to 1.54 m, with a variation of 1.29-1.93 m, whereas the second generation had a mean height of 0.71 m, with a variation of 0.38-1.09 m.

Secondly, according to HEGI (1929) the stems of *S. congestus* are only branched in the upper parts. But in the Lake Yssel polders the first generation even bears flower stalks at the base of the stems, e.g. these fifty plants: meanly 7 with a variation of 0-13. In the second generation this figure was 1 with a variation of 0-3.

All the figures recorded refer to vegetations on heavy soils. Nevertheless on wet and muddy, sandy soils the first generation may also exhibit the high vitality described.

6. DISSEMINATION

From a morphological point of view the *S. congestus* diaspores, formed by achenes and pappi, are well 'adapted' to anemochorous dissemination (Fig. 3). The more so as their weight is low, viz. about

700 mg per 1000 diaspores. And the fall velocity in calm air proved to be about 16 cm per sec. It should be noted, however, that these diaspores might be disseminated by water and animals too.

S. congestus diaspores are beaten out of the heads by rain. And in this case they land on the earth around the mother plants, because as a result of the high humidity opening of the pappi is prevented.

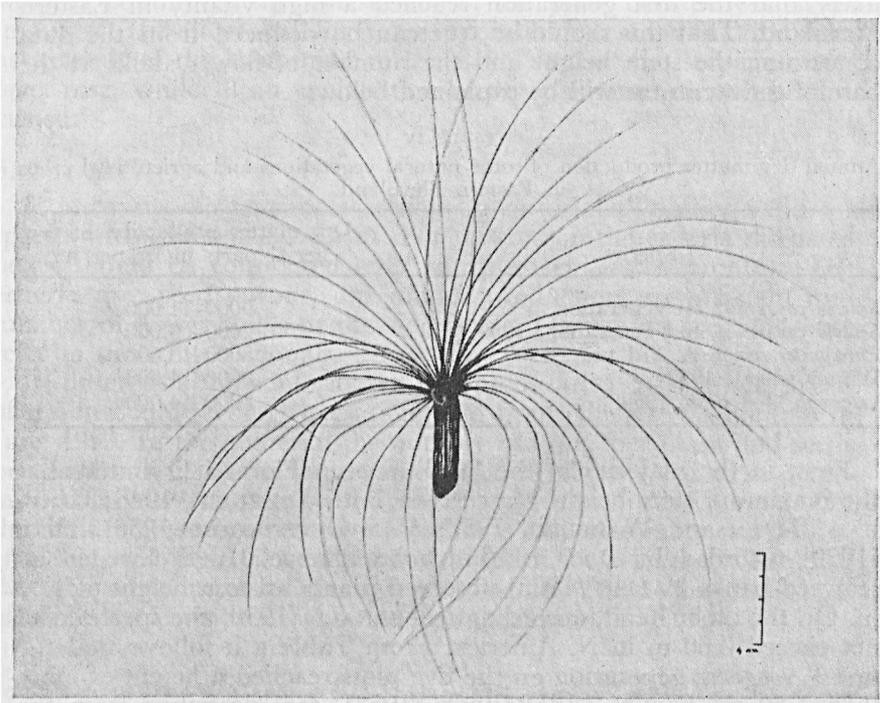


Fig. 3. Diaspore of *S. congestus*.

Dry weather favours air transport. Yet they are partly deposited in the neighbourhood of the mother plants too, especially in heavy vegetations on a large scale. But long-distance transport by wind and convection currents appears to be possible as well.

We possess very few exact data on the flying-distance of diaspores (MÜLLER, 1955). In this connection the most reliable observations have been made by FEEKES (1936) concerning the migration of *Aster tripolium* into the newly reclaimed Wieringermeer. From a source in the border area *Aster* migrated in three years and in three laps into the whole Wieringermeer area, 20.000 ha in extent, by way of anemochorous dissemination. This means that many diaspores must have covered a distance of 6–8 km. But according to BOUWMAN (1936) large numbers of diaspores were also observed in Schagen, a town 10 km from the Wieringermeer (Fig. 1).

In Eastern Flevoland in 1957 there was an opportunity to obtain

some information about the flying-distance of *S. congestus* diaspores. On a clay dump, 0.5 ha in extent and 0.3 km from the Eastern dyke of the new polder, a fruiting *S. congestus* field was found in June 1957. It appeared that this vegetation yielded 750 million viable seeds. At that time the wind blew from the East on several days, resulting in an intensive air transport of diaspores from the clay dump to the virgin soil in the new polder. Here, in the autumn of 1957, 2-7 km to the West of the source, the estimated number of plants amounted to 5 million. This estimate was based on countings of plants on fifty plots, each 100 m² in extent, which had been chosen at random. It follows that at least 0.65 % of the viable seed covered a flying-distance of 2-7 km. Still more to the West its establishment was prevented owing to the occurrence of rather deep water in June and July 1957.

More valuable data concerning the flying-distance of *S. congestus* diaspores were collected in 1959. As has been stated in the introduction a fruiting vegetation of the species covered at least 10.000 ha of Eastern Flevoland in June and July of that year. Doubtlessly this must be considered as an exceptionally extended source of dissemination. In that period dry winds blew nearly every day, mainly from the N.E., E, and S.W., while convection phenomena occurred frequently.

From this source countless numbers of diaspores were disseminated nearly all over the Netherlands and even over the German frontier (Fig. 4). Clouds of diaspores have been recorded as far as 90 km on days when the wind blew from the direction of Eastern Flevoland, e.g. in Amsterdam, The Hague, Rotterdam, Groningen, Nijmegen. As can be seen from Fig. 4 diaspores have even been collected at a distance of about 200 km, e.g. in Hanover and Cologne. It seems possible that they too originated from Eastern Flevoland, as will be pointed out below.

The present author followed a cloud of diaspores by car in a North-eastern direction over a distance of 90 km on June 27th. The density in which the diaspores had been deposited on the soil surface appeared to fluctuate considerably. Especially along obstacles, e.g. forests, houses and dams, the density proved to be relatively high, up to a maximum of 12 viable seeds per m². On level country the number mostly varied from 0-2 per m². But in many instances a correlation between the density of the deposited diaspores and the nature of the ground apparently did not exist. Yet, with growing distance from the source the ratio of viable and non-viable seed usually decreased, in all probability owing to the lower weight of the latter. But it proved impossible to make an estimate of the percentage of viable seed covering a certain distance, on account of the irregular distribution on the soil surface. For the same reason the percentage remaining behind in Eastern Flevoland could not be estimated.

Undoubtedly the clouds of diaspores have come from Eastern Flevoland. For in the remaining part of the Netherlands and in the adjacent countries *S. congestus* occurred only locally at that time and

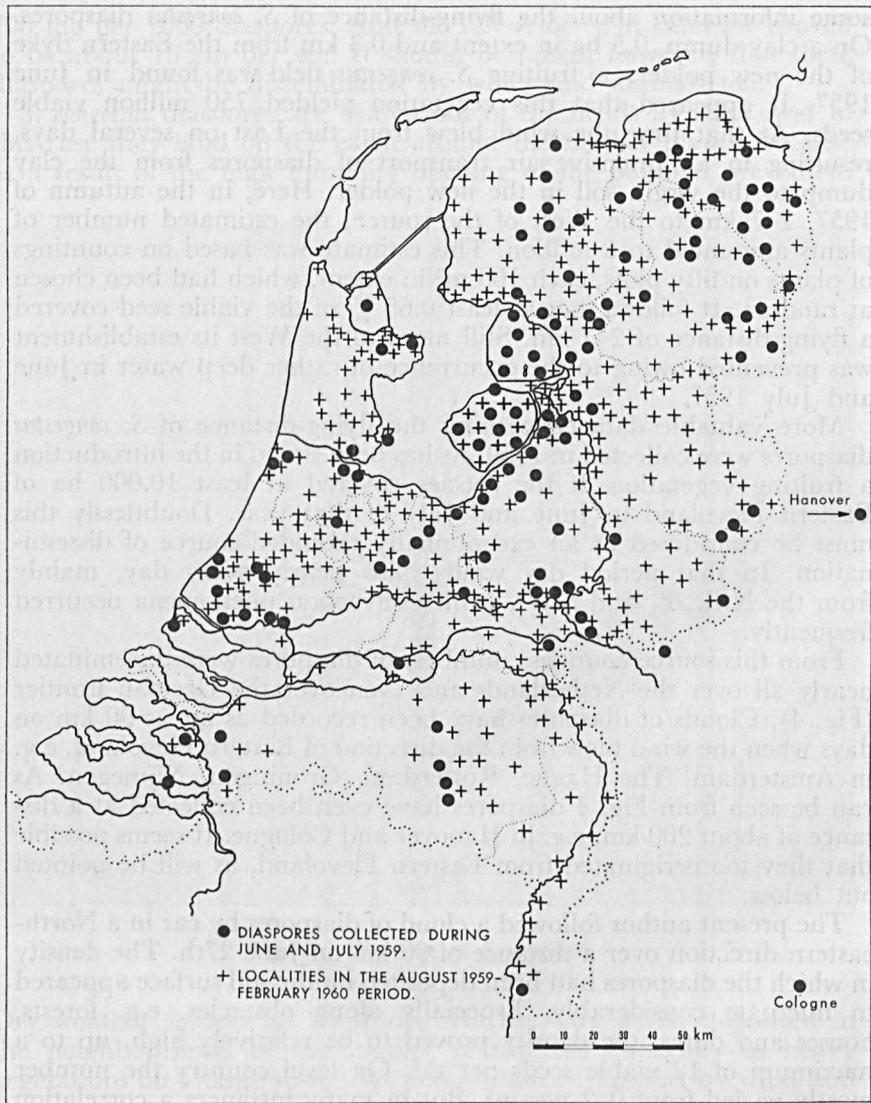


Fig. 4. Data on dissemination and establishment of *S. congestus* in the Netherlands.

in small sources, which would not have been capable of producing these large numbers of diaspores.

The dissemination from Eastern Flevoland in 1959 was followed by a large-scale establishment in the greater part of the Netherlands (Fig. 4). The local scarcity of the species, as recorded on the map of Fig. 4, may be caused by adverse conditions for its growth. But the direction of the wind during dissemination may have played a part as well. A study of this phenomenon is in progress.

In view of the fact that before August 1959 the plant grew sparsely or was wanting in the South and East of our country, occurrence in these regions should be paid special attention to. For on the basis of these data, it is likely that a part of the diaspores flew 90–160 km. It is due to this that the supposed origin of the diaspores collected in Hanover and Cologne gains in probability.

It is noteworthy that not only the large-scale anemochorous dissemination, but also the dry weather conditions must be responsible for the establishment all over the country. As a result of the drought, the water level of ditches, ponds, pools, rivers etc. fell during the summer of 1959, by which favourable habitats came into being nearly everywhere (see 7 and 8).

The question arises whether or not hydatochorous dissemination may be important for the species concerned. Laboratory tests on water with smooth and faintly waving surfaces showed that *S. congestus* diaspores remained floating for five days at most. In view of the fact that dissemination mainly takes place in June and July, the majority of the floating seed germinates within some days, on account of the high water temperature (see 7). If the seedlings are not washed ashore in an environment favourable to growth, they are lost after 1–2 weeks. It is evident now that at this time of the year hydatochorous dissemination over short distances can only play a part.

After landing on the water surface, seed of plants flowering in autumn does not, as a rule, germinate the same season owing to the low temperature. But partly, it is still capable of germination the next spring (see 7). Hence only the small seed output of the autumn plants (see 2) can be considered with regard to hydatochorous dissemination over long-distances and so hydatochorous dissemination cannot be as effective as anemochorous. All the more so as wind transport may follow the shortest way to a certain point, whereas in many instances well suited habitats cannot be reached by way of water unless by devious ways.

Now we shall have to discuss epizoöchorous dissemination. For the weak and short living achenes of the species endozoöchorous dissemination can be left out of consideration. Although not observed, epizoöchorous dissemination might be expected for *S. congestus*, in view of the fact that thousands of migrating ducks, geese and waders feed on the new soils.

In my opinion, however, epizoöchorous dissemination over long-distances is not likely to have been significant with pioneers in the Lake Yssel region. *Limosella aquatica* and *Cyperus fuscus*, which in the border area occur exclusively at the mouth of the river Yssel, have only been found in the North-Easternpolder and in Eastern Flevoland at a distance of at most 10 km from this source. In addition, *Scirpus americanus*, *Leersia oryzoides*, *Juncus obtusiflorus*, *Scirpus acicularis*, *Glyceria declinata* a.o. grew rather commonly in the border area along Eastern Flevoland. But they established themselves in the new polder at a distance of at most 3 km from the nearest sources. Between these areas and the polder many waterfowl flew to and fro. If long-distance

dissemination by birds were of significance in this case, the species should occur in the other parts of the polder as well. The more so as it was learned from sowing experiments that the absence of these species could not be attributed to edaphical factors. In all probability the species above mentioned were mainly disseminated by the water of the Lake Yssel before the dykes had been closed.

On the other hand, in the North-Easternpolder typical anemochorous species had been found, viz. *Hieracium caespitosum*, *Gnaphalium luteo-album* and *Epilobium lanceolatum*. Here they grew 20, 50 and 100 km respectively, from the nearest habitats outside the polders (BAKKER and VAN DER ZWEEP, 1956). This may emphasise the significance of anemochorous dissemination over long-distances. Originally it was thought that *Carex extensa* had penetrated into the North-Easternpolder by means of endozoöchorous seed supply, e.g. from the Wadden Islands (BAKKER and VAN DER ZWEEP, 1956). But a closer examination of the herbaria has shown that the species must formerly have been overlooked in the Zuiderzee region.

7. INFLUENCE OF THE ENVIRONMENT ON GERMINATION AND SEEDLING DEVELOPMENT

In this part, only the environmental factors which proved to be of major importance for germination and seedling development, will be discussed.

As to the ripening of the seed, it appeared that in the flower-head the seed is already capable of germinating to a maximum at the time the involucre is coloured brown; it does not exhibit any form of dormancy. This means that in an environment favourable to germination all the viable seed is able to germinate within a week. In this case, the embryos of the non-germinating seed do not show any red colouring after treatment with sodiumbiselinite. In other words, it is non-viable.

On the strength of field experience, it was thought that under natural conditions all the seed of the winter annual loses viability within three months. But in wet places it germinates immediately, even under adverse conditions for further growth, e.g. under heavy vegetation. On the contrary, it looked as if the seed of the summer annual, flowering in autumn, maintains its viability till the next spring.

In order to obtain information about this problem germination tests in the laboratory have been made. It appeared that viability decreased considerably after two months storage at about 21° C in combination with a high (59 %) or a rather high (23 %) moisture content of the seed. In the latter case, viability was nearly lost after 7 months' storage, whereas in the first case viable seed did not occur at all (nrs. 4 and 6 in Table v). On the other hand, at low temperature (8° C) the rate of germination proved to be independent of the moisture content of the seed for at least 7 months (nrs. 1, 3 and 5 in Table v). At about 21° C and a low moisture content (10 %) viability did

TABLE V

Influence of different modes of storage on the viability of *S. congestus* seed. In brackets the limits of variation.

Nr.	Mean germination % immediately after harvest	Modes of storage		Mean germination % after:		
		tempera- ture	moisture content in %	2 months	7 months	14 months
1.	96 (94-100)	8° C	10	89 (80-97)	89 (84-95)	92 (90-95)
2.	96 (94-100)	± 21° C	10	84 (77-92)	78 (66-83)	81 (83-98)
3.	96 (94-100)	8° C	23	76 (71-81)	79 (72-81)	75 (60-86)
4.	96 (94-100)	± 21° C	23	63 (53-73)	7 (3-10)	0
5.	96 (94-100)	8° C	59	88 (72-89)	95 (90-98)	66 (59-79)
6.	96 (94-100)	± 21° C	59	20 (13-38)	0	0
7.	75 (73-76)	8-12° C	in soil, under water	—	14 (2-24)	0
8.	75 (73-76)	± 21° C	in soil, under water	—	30 (8-68)	8 (0-34)

not change after 14 months storage (nr. 2 in Table v). Storage took place in bottles hermetically closed with paraffin wax.

From the results of the laboratory tests the conclusion may be drawn that under conditions unfavourable to germination the seed loses viability in the summer in consequence of high temperature and moisture content. The moisture content of the disseminated seed amounts to at least 40 %. Independent of the moisture content seed of *S. congestus* may maintain viability at a high level during the winter as a result of low temperature.

Besides, the seed was kept under water (at a depth of 50 cm). It was learned that at 8-12° C and at about 21° C viable seed may still occur after 7-14 months' storage (Table v, nrs. 7 and 8). In this connection it seems possible that viable seed is to be found at the bottom of the Lake Yssel polders during recession of the water. This phenomenon was sporadically observed in Eastern Flevoland. Early flowering summer annuals with a low vitality arose from this seed.

With regard to the influence of 'depth of sowing', germination was also examined in laboratory tests. Aerated soil (vegetable mould) and unaerated mud from Eastern Flevoland were compared as germination substrata. The rate of germination was determined by counting the emerged seedlings. Table vi clearly shows that in both tests the maximum seedling production took place after sowing on the soil surface. Unlike when in the mud, however, seedlings still emerged from a depth of 2 cm out of vegetable mould. Undoubtedly this was

due to the considerable difference in aeration of the soil. Moreover, in vegetable mould large-scale germination proved to be possible, but the majority did not emerge, in all probability as a result of the mechanical resistance of the soil. In the unaerated mud the seed germinated only to a very small extent.

TABLE VI
Influence of 'depth of sowing' on the seedling emergence of *S. congestus*. In brackets the limits of variation.

Germination substratum	Mean % emerged seedlings at a 'depth of sowing' of:						
	0	0.5 cm	1 cm	1.5 cm	2 cm	2.5 cm	3 cm
Aerated vegetable mould	97 (94-100)	32 (26-40)	12 (3-19)	4 (1-5)	6 (2-8)	0	0
Unaerated mud	82 (79-83)	4 (0-8)	0	0	0	0	0

Referring to the results of Table VI, it is to be noted that under natural conditions the mainly anemochorous disseminated diaspores are usually deposited on the soil surface.

Nevertheless, germination may only proceed on soil surfaces covered with a thin film of water, like the young marine sediments in the Lake Yssel polders. Seedling development must take place under wet conditions, but in water of more than 2 cm depth penetration of the roots into the bottom usually does not succeed.

It appeared from field studies that a vigorous seedling growth is exclusively found on muddy substrata, e.g. on clay and peat, on newly deposited sand etc. It is noteworthy that in some instances *S. congestus* rosettes were even observed in ditches on thick layers of perishing *Lemna minor* and *L. gibba* or *Azolla filiculoides* (among others recorded by Mr. C. G. van Leeuwen in a letter of September 1959). On the other hand, on compact substrata, even under wet conditions, the seedling growth proved to be inhibited or quite impossible, e.g. on boulder clay, sand banks, gravel, marl. This might be connected with the occurrence of adventitious roots, adapted to life in unaerated soils. The thick and weak layer of aerenchyma tissue around these roots shows only a slight resistance to mechanical pressure, but in this direction closer examination is desirable.

As to the influence of temperature and intensity of light, it was learned that in full daylight maximum germination takes place at temperatures of 25-30° C. The seed may even germinate in the dark on a limited scale, but at lower temperatures (18-20° C) higher intensity of light is required. In weak light the seedlings perish after some time, e.g. under heavy vegetation. It follows that bare soils are favourable to germination and seedling development, because especially on the soil surface temperature and the intensity of the light may rise to high values during the growing season.

It was also observed that germination and seedling growth may be achieved in the pH-range 3.5-8, but at pH 3.5-5 the vitality is low.

TABLE VII
 Influence of NaCl- and KNO₃-content of the substratum on germination of *S. congestus*. In brackets the limits of variation.

Mean germination %:	
Series 1	
Van der Crone's solution	40 (36-42)
Diluted sea-water, 1 g/l NaCl	18 (16-22)
Diluted sea-water, 3 g/l NaCl	15 (8-20)
Diluted sea-water, 5 g/l NaCl	12 (6-18)
Diluted sea-water, 10 g/l NaCl	12 (11-14)
Series 2	
Van der Crone's solution	40 (36-42)
Diluted sea-water, 1 g/l NaCl + 5 g/l KNO ₃	55 (48-62)
Diluted sea-water, 3 g/l NaCl + 5 g/l KNO ₃	31 (24-32)
Diluted sea-water, 5 g/l NaCl + 5 g/l KNO ₃	26 (12-36)
Diluted sea-water, 10 g/l NaCl + 5 g/l KNO ₃	7 (6-10)

The soils in the Lake Yssel polders, however, have mainly a pH within the suitable range (6.5–8).

Finally, the influence of NaCl on these life-stages has been studied in the laboratory, because in literature some controversy is met with respecting this question (see 3). Moreover, in Eastern Flevoland vigorous seedlings were found up to a NaCl-content of about 3 g per l soil moisture (C-figure), whereas in the brackish parts of the Netherlands *S. congestus* sporadically occurs, e.g. in the S.W. (Fig. 4).

Taking Van der Crone's solution as standard, the laboratory tests took place on diluted sea-water, artificially prepared and composed of two series, each containing solutions with 1, 3, 5 and 10 g NaCl per l respectively (ZIJLSTRA, 1946). To the solutions of the second series 5 g KNO₃ per l was added. Table VII shows that on the NaCl-solutions of the first series germination did not reach the level of the Van der Crone's solution. But apparently under the influence of KNO₃, on 1 g NaCl of the second series germination surpassed the standard. It increased to a large degree on 3 and 5 g NaCl, in comparison with the first series. However, KNO₃ did not favour germination on the 10 g NaCl-solution. With regard to the NaCl-tolerance of the seedlings no reliable data were obtained. But on the basis of this test it seems possible that KNO₃ increases the NaCl-tolerance of this life-stage as well.

In view of the laboratory tests it was thought that the NaCl-tolerance might depend on the mineral nitrogen content in the soil. In support of this thesis is the fact that the young marine sediments in Eastern Flevoland are at first rich in mineral nitrogen (Table VIII).

TABLE VIII

Some edaphical factors of three *S. congestus* habitats after the first generation had died off compared with those of three adjacent bare fields (Eastern Flevoland, October, 1959).

Depth	Nr.	Died off first generation					←Distance→ about 2 m	Bare fields				
		¹⁾ NH ₄ ⁺ in %	lutum in %	humus in %	NaCl ²⁾ in g/l	pH		¹⁾ NH ₄ ⁺ in %	lutum in %	humus in %	NaCl ²⁾ in g/l	pH
0–20 cm	1	1.4	26.1	3.0	1.0	7.0	67.3	25.5	2.9	1.2	7.7	
	2	1.6	7.5	1.8	0.9	7.2	20.0	9.8	1.8	1.1	7.6	
	3	1.8	30.4	3.0	3.0	7.0	6.4	28.6	3.0	3.0	7.2	
20–40 cm	1	1.8	41.2	3.2	1.9	7.3	92.4	35.2	3.4	2.2	7.7	
	2	1.3	26.2	2.7	1.6	7.4	78.7	29.8	2.9	1.9	8.0	
	3	6.9	33.7	3.6	3.3	7.3	66.2	28.6	3.1	3.0	7.5	
40–60 cm	1	9.5	31.3	3.7	3.0	7.5	94.3	30.5	3.5	3.0	7.7	
	2	8.4	26.4	3.2	2.4	7.4	82.1	27.6	3.3	2.4	8.0	
	3	57.0	31.1	3.7	3.2	7.5	112.4	32.1	4.1	3.1	7.7	
60–80 cm	1	88.4	33.4	4.6	3.6	7.5	132.6	33.7	4.7	3.7	7.5	
	2	59.7	31.9	4.1	2.8	7.4	91.2	30.3	4.3	2.9	7.7	
	3	118.9	34.5	4.8	3.6	7.5	124.3	31.5	5.2	3.7	7.6	

¹⁾ mg mineral nitrogen per kg dry matter.

²⁾ g NaCl per l soil moisture (C-figure).

8. VITALITY DECLINE

In this connection attention should be paid to the drying up of the soil surface. The first summer after recession of the water (1957) large areas of the heavy soils in Eastern Flevoland were covered with films of water necessary to germination of the species. But these films usually evaporated during dry periods in the second and third year. Yet dry periods did not prevent extensive germination in the summer of 1958, because as a result of rainfall the soil surface became wet again after some weeks of drought. In the very dry summer of 1959, however, the soil surface of large areas remained dry till the end of the growing season. For this reason, especially in the North-western part of Eastern Flevoland, the seed, deposited at the bottom, was not able to germinate after the first generation had died off in July 1959. On the other hand, germination and seedling growth took place in this area on four square metres, which were watered several times. In other words, with normal rainfall establishment might have been achieved.

It can be seen from Table II (nrs. 3 and 4) that also in permanently wet habitats a rapid vitality decline occurred. It seemed possible that the accumulation of dead stems of the first generation had caused a mulching effect. On this wet organic material, covering the soil surface to a maximum of 75 %, germination did not succeed, presumably owing to poisonous substances developed by anaerobic decomposition of the dead plants. In view of the fact that mostly the seedlings on the uncovered soils also showed a low vitality, even in case of immediate removal of the organic material after dying off, this phenomenon could not be the main cause of the vitality decline. Neither could seedling competition as a result of the high density be the general explanation, because in habitats thinly covered with seedlings of the second generation the vitality usually was low as well.

It is evident now that the rapid vitality decline should be attributed to changes in the edaphon, brought about under the influence of the first generation. As *S. congestus* mainly occurs together with nitrophilous pioneers (see 3 and 4), it was thought that this might be due to exhaustion of the mineral nitrogen by the first generation and by microbes and denitrification. It should be noted that the mineral nitrogen of unaerated and wet sediments in the Lake Yssel polders almost exclusively occurs as ammonium. Under these conditions ammonium supply by means of mineralization of organic matter takes place very slowly.

In order to obtain information about the nitrogen uptake by *S. congestus*, the ammonium contents of soils covered with dead stems of the first generation and of bare soils were compared, as is shown in Table VIII. The latter remained bare as a result of a permanent cover with seepage water to a depth of at least 2 cm. The sample plots 1, 2 and 3 on bare soils were about 2 m away from the dead vegetations 1, 2 and 3 respectively, while the bare and the originally overgrown plots of each number only differed to a small extent in lutum and

humus percentages (per 100 g dry matter), in g NaCl per l soil moisture and in pH.

On the three *S. congestus* habitats of Table VIII in the uppermost 60 cm, where the roots are found, the mineral nitrogen contents usually proved to be low in comparison with the bare fields. Nevertheless, it is questionable whether the figures of the bare soils might be considered as actual data for the three *S. congestus* habitats at the moment when the first generation started its development. In any case, Table VIII clearly shows that during the growth of these heavy vegetations the mineral nitrogen level of the uppermost 60 cm must have decreased considerably.

Meanwhile, by studying the nitrogen content of the species, it appeared that the uptake of mineral nitrogen by the first generation must take place on a large scale. From Table IV it can be seen that in Eastern Flevoland the aerial parts of the first generation produced meanly 10.000 kg (9.000–11.000 kg) dry organic matter per ha. Its mean nitrogen content amounted to 185 kg per ha. The adventitious roots contained about 2500 kg dry matter per ha, with 35 kg nitrogen. In other words the uptake of the first generation amounted to meanly 220 kg nitrogen per ha.

According to SMITS (1953), in the lutum-range 18–36 % the apparent density (dry volume-weight) of young marine sediments, as has been recorded in Table VIII, lies between 0.86 and 0.58. And so in this case the dry-weight per ha of the uppermost 60 cm varies from 6×10^6 (the soil volume in l per ha) \times 0.86 = 5.16×10^6 kg to $6 \times 10^6 \times 0.58 = 3.48 \times 10^6$ kg. In other words, in the lutum-range 18–36 % 1 mg mineral nitrogen per kg dry matter of the uppermost 60 cm corresponds with 5.16 to 3.48 kg mineral nitrogen per ha of the same layer. It follows now that in the lutum-range 18–36 % a vigorous growth of *S. congestus* may be achieved if the species could assimilate $220/5.16 = 42.6$ mg to $220/3.48 = 63.2$ mg mineral nitrogen per kg dry matter from the uppermost 60 cm of the soil. In view of the fact that the soil-layers of the plots from Table VIII are within this lutum-range, it appears that the required mineral nitrogen level did not occur on the plots with the died off vegetations. But on the bare soils it might even be exceeded.

In view of these results the conclusion may be drawn that the rapid vitality decline mainly depends on the strong decrease of the ammonium content in the rhizosphere. Apparently a considerable amount of this nitrogen may be embodied in the first generation of *S. congestus*.

The question arises now what might be the explanation of the high vitality of the second generation growing in some seepage pools during the autumn of 1959. These pools dried out for the first time in June and July and in the uppermost 20–30 cm of the soil aeration had taken place to some extent. But in August the soil surface became wet again (see 4) and so the seed was capable of germination. Although not analysed, it seems possible that mineral nitrogen was liberated from organic matter owing to temporary aeration. It is noteworthy in this connection that under laboratory conditions the soils in Eastern

Flevoland showed a considerable nitrogen mineralization after the first generation had died off.

9. CONCLUSION

The exceptional opportunity arose in 1959, when it was possible to collect data on the flying-distance of *S. congestus* diaspores. Usually long-distance dissemination will be overlooked owing to the small number of diaspores taking part in this phenomenon. However, on the basis of the observations in 1959 it is likely that anemochorous dissemination over long-distances must be the explanation of the rapid appearance on bare and wet soils, far remote from fruiting sources.

Besides it should be noted that the occurrence of large fruiting *S. congestus* sources in reclaimed areas of the Netherlands might have caused the temporary increase in the adjacent countries in the past, e.g. after the Haarlemmermeer had been drained dry in 1852. Therefore it might be desirable now to look at the species in W. Germany, Belgium, N. France and even in Great Britain.

It is true that the majority of the plants which established themselves in the summer of 1959 nearly everywhere in the Netherlands (Fig. 4), were killed before flowering in 1960, mainly owing to the cleaning of water courses by men and the rising of the water level of the habitats. But on account of the large-scale establishment, it is likely that flowering plants will still be found frequently in the spring of 1960.

It was found that growing as a pioneer on wet and bare soils a single established plant is capable of producing 150.000–200.000 germinative seeds, even in the nearly complete absence of pollinating insects. So a considerable increase might be expected in the next year. That this is true was observed in Eastern Flevoland, where the vast *S. congestus* vegetation arose from seed produced by small sources, which had established themselves in the border area before.

On the basis of this study the conclusion may be drawn that the high vitality of the first generation in the Lake Yssel polders should be attributed to the favourable conditions for germination, seedling growth and further development shortly after the soils had been drained dry. In other words *S. congestus* is a species well 'adapted' to the extreme pioneer conditions prevailing at that time. The ephemeric character is connected with changes in the edaphon under the influence of the vegetation.

SUMMARY

1. In order to find an explanation for the rapid establishment and the ephemeric occurrence of *S. congestus* vegetations in the Lake Yssel polders several ecological characteristics of the winter annual life-form of the species were studied. In this area only the winter annual plays an important part in the vegetation.
2. On five sample plots in Eastern Flevoland the vegetation-cycle of *S. congestus* was studied in the years 1957–1959. In view of these observations we may suppose that the decline in vitality should mainly be attributed to changes in the edaphon under the influence of the first *S. congestus* generation. Apart from *S. congestus* in Eastern Flevoland *Ranunculus sceleratus* showed the highest degree of presence in the vigorous vegetations of the first species.

3. Taking seed output, dry matter production, stem height and number of flower stalks at base of stems as criteria, the vitality of the first generation of *S. congestus* in Eastern Flevoland proved to be high. Usually, the second generation showed a considerable decline in vitality.
4. It was observed that the diaspores may be disseminated over long distances by wind and convection currents, viz. at least 90 km and in all probability as far as 200 km. This must be the explanation of the rapid appearance in new and well suited habitats, far remote from fruiting sources of the species, e.g. in 1959. As to dissemination over short distances, it was found that hydatorchorous transport of diaspores may be effective as well.
5. The seed of the winter annual life-form loses viability within three months after dissemination owing to high temperatures and moisture contents. On account of rather low temperatures, seed of the autumn flowering summer annuals may survive the winter.
Wet soil surfaces appeared to be favourable to germination. Moreover, these soils ought to be muddy and bare for a vigorous growth of seedlings. It seems possible that the NaCl-tolerance of the germination- and seedling-stage depends on the mineral nitrogen content of the soil.
6. Beside the wetness of the soil, the high vitality of the first generation should be attributed to the high mineral nitrogen content of the soil at the time of its emergence from the water. The rapid decline in vitality of the next generation is due to the decrease of the mineral nitrogen content of the soil under the influence of the first generation.

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