BIOSYSTEMATIC STUDIES ON SPERGULARIA MEDIA AND S. MARINA IN THE NETHERLANDS II.

THE MORPHOLOGICAL ¡VARIATION OF S. MARINA*[1]

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SUMMARY

In this second paper on the biosystematics of the Dutch halophilous *Spergularia* species, the results are reported of a study of the morphological variation of *S. marina* by means of population samples from all parts of the Dutch area. This study was supplemented by the rearing of plants from seed samples in the experimental garden.

The seeds of *S. marina* are usually unwinged, but some plants also produce a few broadly winged seeds and in one population plants occur whose proximal capsules contain mainly broadly winged seeds. The differences between the populations persist in cultivation and are chiefly attributable to genetic differences. Winged seeds are upon the average larger and heavier than unwinged ones and also produce larger seedlings than the latter. The relative lengths of fruiting calyx and capsule do not provide a reliable diagnostic character in respect of *S. media*. The number of stamens per flower varies from 0 to 10 and there are great individual differences in numbers, but in certain plants the average number is always high and in other ones always low. These differences are partly caused by heriditary factors. The growth habit and some other vegetative characters vary too widely to be of appreciable taxonomic significance.

1. THE SEED

1.1. Variation in individual plants

The degree of development of the seed wing has up to now been considered to be a very reliable differential character of our halophilous species of *Spergularia*. According to HEUKELS-VAN OOSTSTROOM (1962) the seeds of *S. marina* are usually all unwinged but sometimes a few of the lowermost seeds of a capsule may be winged. As is the case in *S. media*, the seeds of *S. marina* show a considerable range of variation from unwinged to broadly winged. The seeds of *S. marina* resemble those of *S. media* rather closely in shape and size and therefore are classified in the present paper in the same way as those of *S. media* (compare STERK 1968, 1969). Some of the morphological types of seeds are shown in *fig. 1b, c, d* and *e*. In contradistinction to the situation in *S. media*, the nw-type of seed is usually of rare occurrence in *S. marina*, except in BVW-plants of the latter. In capsules containing only a few bvw-seeds the "transition" from the urw-seeds to the bvw-seeds is usually rather abrupt and there is no gradual change *via* a number of nw-seeds.

The capsules of *S. marina* are classified in the manner applied to those of *S.*

media in three groups, *viz.*, the BVW-, NW- and URW-types of fruits with over 70% of bvw-, nw- or urw-seeds, respectively.

The variation in the degree of development of the seed wing was accurately studied in 30 plants, chiefly in the proximal capsules but in a number of plants also in the most distal capsules. The percentages of bvw-, nw- and urw-seeds recorded for the individual capsules were estimated by means of the same scale with 11 grades as previously used for classifying seeds of S. media (STERK 1968, 1969).
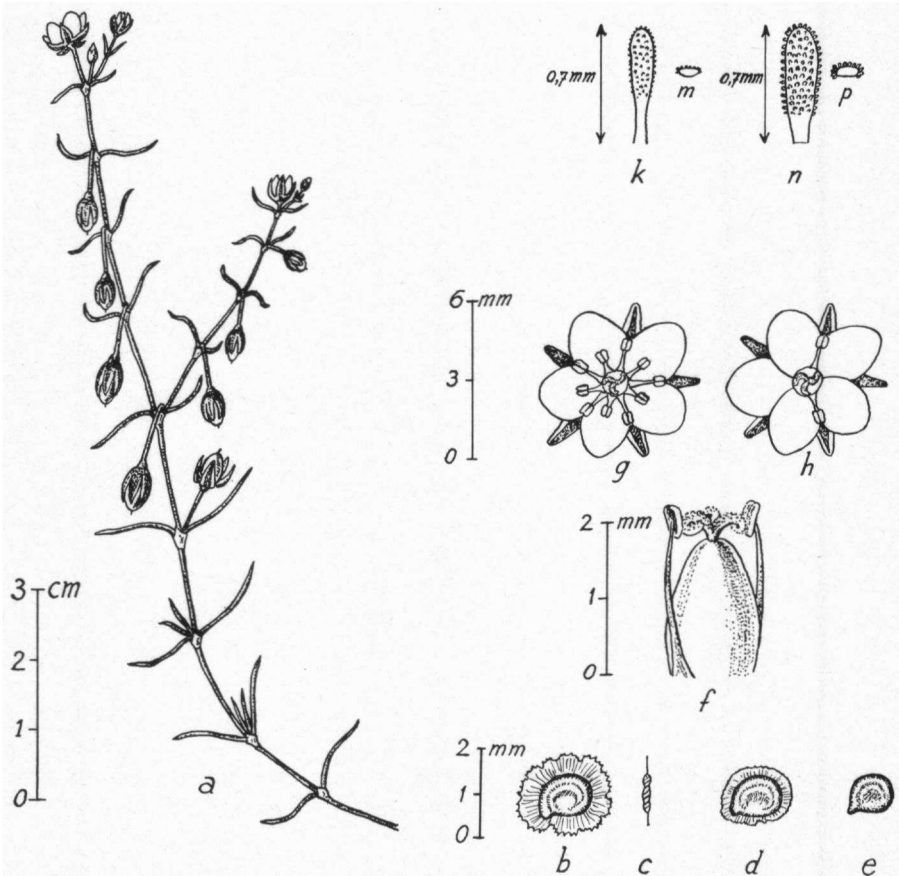

Fig. 1. *S. marina.* a. habit; b. and c. broadly winged seed; d. narrowly winged seed; e. unwinged seed; f. pistil with strongly recurved and twisted stigmas; g. flower with 10 fertile stamens; h. flower with 2 fertile stamens; k. and m. stigma of *S. media;* n. and p. stigma of *S. marina.*

The variation showing a consistent pattern in many individual plants, only a few characteristic examples are enumerated:

Plant S 3, prox.: 30 (urw 10)

    „   dist.:   27 (urw 10)

Plant S 1, prox.:   11 (urw 10); 10 (urw 9 bvw +); 1 (bvw 9 urw +)
    ,,   dist.:   37 (urw 10); 3 (urw 9 bvw +)
Plant S 226, prox.: 7 (bvw 10); 4 (bvw 9 nw + urw +); 2 (bvw 9 nw +);
                    2 (bvw 9 urw +)
    ,,   dist.:   2 (bvw 10); 1 (bvw 9 nw +); 1 (bvw 8 nw 1)
                    1 (bvw 8 nw + urw 1); 1 (bvw 6 nw 2 urw 1);
                    1 (bvw 5 nw + urw 3); 1 (bvw 3 nw 3 urw 3);
                    1 (bvw 2 nw 7 urw +); 1 (bvw 2 nw 3 urw 5);
                    1 (nw 8 urw 1); 1 (nw 7 urw 2);
                    1 (nw 2 urw 7).

Plants of *S. marina* can be classified in two groups of which the first includes all specimens exclusively producing urw-type of seeds, or predominantly urw-seeds with a small admixture of bvw-seeds, and the second all plants predominantly producing bvw-seeds in their proximal capsules. Representative specimens of the first group are the plants S 1 and S 3, and a representative example of the second is the plant S 226.

Plant S 1 produces in one of its proximal capsules chiefly bvw-seeds. This particular capsule contained only 19 seeds of which 18 were of the bvw-type and 1 was an urw-seed; this number of seeds lies so far below the mean number of seeds per capsule (73) found for this plant, that this particular capsule with only 19 seeds must have been an underdeveloped one in which the uppermost seeds were all abortive.

A comparison between the proximal capsules and the distal ones of the same individual plant revealed that all URW-plants contain fewer bvw-seeds in their distal capsules, and BVW-plants produce seeds with usually narrower wings in their distal capsules apart from a fairly large number of unwinged seeds.

In all plants examined the average number of seeds is lower in the distal capsules, which are upon the average also shorter than the proximal ones. All these phenomena, as in *S. media*, are suggestive of less favourable developmental conditions in the more terminal portions of the inflorescence than in the more basal ones, so that the capsules tend to be shorter and the seed wings to be narrower. On the basis of the main seed type present in their first formed capsules, the plants can be classified as "URW-plants" or "BVW-plants". "NW-plants", though theoretically to be expected, were not encountered during the present study.

1.2 Variation within populations

In the S.W. part of the Netherlands 19 populations were studied; another 19 populations were investigated in the Northern part and one in the centre (near Lelystad, Eastern Flevoland). For the exact localities see STERK (1968, 1969). The populations were sampled in 1959, 1963, 1964 and 1965.

On the basis of the results of the study of individual plants the capsules were classified as the BVW-type or URW-type with over 70% of bvw-seeds or urw-seeds, respectively.

The representative samples of the populations could be placed in one or two groups, of each of which a characteristic example is shown in *table 1*.

Table 1. *S. marina*. The relative frequency distributions of the capsule types of 2 representative population samples.

Locality	Percentage of capsules		Number of capsules
	Capsule type		
	URW	BVW	
Zwin, Zeeuws-Vlaanderen	100		100
De Grie, Terschelling	27	73	169

The population sample from De Grie is the only one in which a high percentage (73 %) of BVW-capsules was recorded and will be referred to as the "BVW-sample"; all other populations studied (*i.e.*, 38 out of 39) bear URW-capsules only. The "BVW-population" occurring at De Grie excepted, there are apparently no differences between populations in the northern and south-western parts of the country.

In the samples of the URW-type capsules occur with exclusively urw-type of seeds and also capsules containing, apart from the urw-seeds, bvw-seeds (of course in frequencies not exceeding 70 %). In order to obtain a better insight into the relative frequency of occurrence of bvw-seeds in the URW-capsules, the contents of 1837 capsules of 16 populations from various localities throughout the country were numerically analysed. The analysis revealed that URW-capsules with bvw-seeds are relatively infrequent; they were recorded in 11 % of the capsules examined. The representation of the bvw-seeds in these capsules is, barring a few exceptions, always less than 10 %. Capsules with about equal amounts of bvw- and urw-seeds are extremely rare. In URW-capsules containing a fairly high percentage of bvw-seeds the total number of seeds per capsule is always considerably lower than the average number of seeds of the population sample.

In the sample of the BVW-population of De Grie the percentage of URW-capsules is also rather high. This suggests that the sample consists of two different groups of plants. That these two groups occur sympatrically is strongly suggestive of genetic differences between them.

In order to assess the influence of the genetic predisposition and the environment on the degree of development of the seed wing, progeny was reared of seed samples of URW-populations and of the plants of the BVW-population of De Grie in the experimental garden under approximately the same environmental conditions.

Descendants of urw-seeds all proved to be URW-plants, those of bvw-seeds turned out to be BVW-plants. This uniformity shows convincingly that the degree of development of the seed wing is in the first place genetically determined. The uniformity of the progeny of the BVW-plants is the more striking considering that such plants occur sympatrically in the same site. The uniformity can be explained by assuming that fertilisation in *S. marina* takes place autogamously,

so that populations with homozygous biotypes originate which maintain them-selves genetically in their progeny.

The studies of individual variation had already shown that the first capsules to be formed contain a larger number of seeds with, upon the average, broader wings than the last capsules produced on the same plants; in addition, it ap-peared that the seed wing is more strongly developed in the seeds inserted on the lowermost part of the central placenta than in the more distally inserted ones. It thus becomes quite clear that the environmental factors have some effect on the development of the seed wing. It appeared, furthermore, that when less favourable conditions prevail (e.g., in the more shaded parts of the experimental garden) the percentage of winged seeds in the capsules of URW-plants tends to be lower than in plants growing in more favourable places (in the full sun) in the same garden. The results can be summarised in the conclusion that both the external conditions and the genetic predisposition have a marked influence on the formation of the seed wing.

1.3. Size of seeds and seedlings

The relation between the width of the wing and the body size of the seeds was studied in lots of urw-seeds and of bvw-seeds obtained by representative sampling of populations. The dimensions of the seed body "*a*" and "*b*" were determined in the same way as described for *S. media* and grouped according to the same "size classes" (compare STERK 1968, 1969).

Fig. 2 shows the "size" distribution of the urw-seeds and the bvw-seeds. It follows that the bvw-seeds are, upon the average, larger than the seeds of the urw-type. The weight of the bvw-seeds is, generally speaking, also higher than
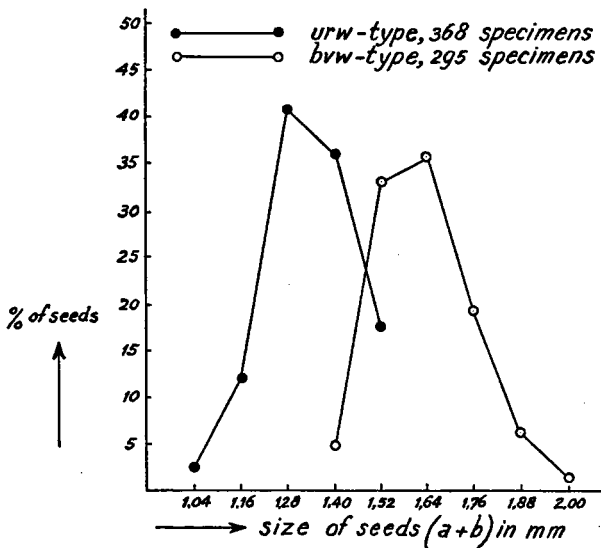

Fig. 2. *S. marina*. Rela-tion between the "size" of the seed body and the width of the seed wing.

that of the urw-seeds: the weight of 1,000 bvw-seeds and of 1,000 urw-seeds was determined and amounted to 0.070 g and 0.059 g, respectively.

It may be concluded that seeds of the bvw-type are upon the average larger and heavier than seeds of the urw-type. As was earlier shown in the case of *S. media*, seedlings raised from urw-seeds are, statistically speaking, of a smaller stature than those raised from bvw-seeds. The size relations are very much the same as in *S. media* (compare STERK 1968, 1969).

2. LENGTH OF FRUIT AND CALYX AND THE NUMBER OF SEEDS PER CAPSULE

Fruit length and calyx length, and the ratio between the two, were determined in 9 representative population samples including the BVW-sample from De Grie.

Table 2 gives a survey of the lengths of capsules and calyces of the URW- and BVW-types of capsules examined.

Table 2. *S. marina*. The length of fruit and the length of calyx in BVW- and URW-capsules.

Organ	Type of capsule	Number of organs examined	Percentage					
			Length in mm					
			2	3	4	5	6	7
fruit	BVW	121		0.8	3.4	76.0	19.8	
	URW	1029		2.4	33.1	55.2	9.2	
calyx	BVW	121		71.9	26.5	1.6		
	URW	1029	1.5	58.8	37.0	2.7		

The relative frequency distributions indicate that BVW-capsules are, generally speaking, longer than URW-capsules, the average length of capsules of the BVW-type being significantly different from that of URW-type (STERK 1968). Their mean fruiting calyx lengths do not differ significantly, so that BVW-capsules are somewhat more exserted from their fruiting calyces than the URW-capsules. In *S. marina* capsules that are not much longer than the calyx are of frequent occurrence. The ratio fruit length/calyx length does not qualify as a differential diagnostic character to distinguish *S. marina* from *S. media* owing to an overlap of their range of variation. In contradiction of the statement in *Flora Europaea* (Vol. 1, 1964, p. 154), the absolute length of the sepals does not qualify as a reliable differential character between the two species.

The number of seeds contained in a capsule was determined in 11 representative samples taken from populations in the field including the BVW-sample from De Grie. The mean number of seeds per capsule of 968 URW-capsules examined was 62, and that of 121 capsules of the BVW-sample, 49. The difference between the mean numbers of seeds per capsule of the fruits of the BVW-type and that of fruits of the URW-type appears to persist when plants of both types are cultivated in the experimental garden (STERK 1968).

3. THE NUMBER OF STAMENS PER FLOWER

3.1. Variation in individual plants

In many floras, the number of stamens per flower is reported as providing an important differential character to distinguish *S. marina* from *S. media*. According to HEUKELS-VAN OOSTSTROOM (1962), for instance, *S. marina* has 3–5 (–8) stamens per flower and *S. media* 10.

After a rather extensive preliminary study, the variation in *S. marina* was very accurately studied in 15 individual plants. The variation of three characteristic examples is shown in *table 3*.

Table 3. *S. marina*. The number of stamens per flower of 3 characteristic plants. n. = number, st. = stamens

Plant	Situation	Numbers of flowers											Mean n. of st.	Total number of flowers
		Number of stamens per flower												
		0	1	2	3	4	5	6	7	8	9	10		
S 111	proximal							2	11	12	5	5	8.0	35
S 111	distal					4	6	3	12	9	6		6.9	40
S 104	proximal			5	6	12	3	4					4.8	30
S 104	distal		1	23	19	2							3.5	45
S 231	proximal	2	26	5	1								2.1	34
S 231	distal	1	31	6	2								2.2	40

It appears that:

1. there are considerable differences in the variation of the androecium between the individual plants;
2. in a single plant the number of stamens is not the same in the proximal and the distal flowers of the inflorescence, but shows at the same time a broad variation, the frequency distribution suggesting the influence of a number of incidental factors; and
3. a shift occurs in the frequency distributions in the direction of the lower numbers of stamens when the androecia of the distal flowers are compared with those of the proximal ones; this shift is not apparent in plants in which the number of stamens of the proximal flowers is already low.

The shift in the frequency distributions can be explained by the less favourable conditions (a more scanty supply of nutrients) in the more distal parts of the inflorescence as compared to its proximal part, resulting in the development of a lower number of androecial elements per flower. The three plants that provided the flowers recorded in *table 3* were all reared in the experimental garden under approximately the same conditions, and the differences in the number of androecial elements is, up to a point, genetically determined. Plants grown in the garden from seed of these three plants showed the same differences as the mother plants, which confirms that the androecial differences are genetically predetermined (STERK 1968). Additional cultivation experiments in the garden

showed that plants grown in rich soil mixtures produce flowers with a significantly higher mean number of stamens than plants reared on a poor soil (STERK 1968).

3.2. Variation within populations

In the S.W. part of the country 11 populations of *S. marina* were studied, along the river Scheldt in Belgium one population, and in the N. part of the Netherlands 9 populations. The localities are shown by STERK 1968, 1969. Of each population about 100 flowers were examined, the representative samples having been gathered in the years 1959 up to and including 1965. *Table 4* shows two relative frequency distributions which are representative of the populations sampled.

Table 4. *S. marina*. Relative frequency distributions of the number of stamens per flower of two representative population samples. Ter. = Terschelling.

Locality	Percentage of flowers											Number of flowers
	Number of stamens per flower											
	0	1	2	3	4	5	6	7	8	9	10	
Ellewoutsdijk, Z-Beveland	1.7	7.4	50.8	27.7	9.6	1.1	0.6	1.1				150
de Grie, Horrekooi, Ter.	2.7	6.5	38.4	14.4	11.0	6.8	9.5	4.2	4.2	1.9	0.4	150

It appears that the number of stamens per flower varies from 0 to 10. Flowers containing 9 or 10 stamens were recorded in 8 of the 20 samples in low frequencies. In all samples the flowers with 2, 3 or 4 stamens are always the most frequent. Plants of the S 111 type are of very rare occurrence in the Netherlands, whereas plants of the S 104 and especially of the S 231 type are quite commonly encountered (compare *table 3*).

No differences could be found between the population samples from the northern and south western parts of the country and there are no ecological correlations either, so that the differences between the populations must be ascribed to incidental causes. All frequency distributions of the numbers of stamens in the populations are more or less asymmetrical and the distribution is not altogether caused by random factors: in *S. marina* the androecial reduction does not proceed beyond the presence of only two stamens per flower. Apparently a continued reduction has an unfavourable effect upon survival. The asymmetric frequency distribution is the result of the reduction of the androecium which has already progressed rather far in the majority of the populations but has not yet attained the ultimate state of reduction.

The above-mentioned data refer to fertile stamens, but sometimes also staminodes may occur. In 1209 flowers examined, 78.8 % contained fertile stamens only, 15.2 % had one staminode per flower, 4.9 % had 2 staminodes and 1.1 % had 3. Flowers with 1 fertile stamen contain the highest number of staminodia.

. Flowers with an under-developed (pistillodial) gynoecium are very rare and

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no special study was devoted to them. It is noteworthy that the mean number of stamens per flower in British populations of *S. marina* (recorded by SALISBURY 1958) differs from the number found in Dutch populations.

4. GROWTH HABIT AND LENGTH OF LEAVES AND INTERNODES

The habit form of *S. marina* is very variable, and so are its mode of branching and the length of its leaves and of its internodes. The natural habitat of *S. marina* consists of sites with sparse ("open") stands of vegetation. As a rule the plants are prostrate to ascending and much-branched, the principal ramifications originating in the lowermost internodes. In such plants the branches radiate outwards from one centre of ramification, and the internodes and leaves are relatively short. After repeated inundation of the plants, or after they have become buried under blown sand, a different kind of ramification develops and the growth habit rather closely agrees with that of plants growing in the shade (in the garden!). When plants grow interspersed among taller plants of a different species in stands which are not too crowded, they become lanky, are not much branched, and form long leaves and internodes. The amount of incident light is apparently the deciding factor. In dense stands of vegetation *S. marina* is not or hardly ever encountered and when occurring at all the plants are very lanky. The species seems to be intolerant of interspecific competition. In dried-up pools and in places where sods have been cut, on the other hand, populations of *S. marina* with a very high stand density may develop. In such dense stands the individual plants are usually dwarfed and consist only of an unbranched stem of a few cm tall bearing a single flower. In this case the intraspecific competition is presumably the cause of this nanism. When the prostrate, much-branched specimens with relatively short leaves and internodes, the lanky plants and the oneflowered nanistic forms were transplanted and grown in the experimental garden under the same conditions, the differences disappeared. The phenotypic differences of this kind are clearly attributable to a considerable degree of plasticity of the species. However, the progenies of different parent plants reared from seed in the same experimental garden sometimes exhibit small but apparently constant differences in habit form. Some progenies are of a more compact habit and other ones have much taller branches. Such differences must be genetically determined.

   S. marina is annual or biennial. The hibernating specimens form a corky periderm under the epidermal layer of the basal portions of the stems which turn brown and twig-like. Survival of the plants during the cold season only occurs in the ecologically most stable habitats and must be a rare phenomenon in the field. In periodically flooded sites the plants are always annual. Plants that apparently had survived more than one winter were never encountered among all specimens studied, the stratification of the periderm also suggesting only one period of activity of the phellogen. As is also the case in *S. media*, the covering of stem parts by sediments incites periderm formation and the buried stems sometimes root at the nodes.

A biometrical analysis of URW-plants and BVW-plants reared under the same conditions did not reveal any significant differences between the two groups in the size of their stems and leaves.

The great variability of the shape and the dimensions of stems and leaves render them practically useless for classificatory purposes.

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