SOME REMARKS ON THE VARIABILITY OF SPERGULARIA MARGINATA AND SPERGULARIA SALINA IN THE NETHERLANDS

BY

A. A. STERK

(Communicated by Prof. J. Lanjouw at the meeting of November 27, 1965)

1. Introduction

In the literature Spergularia marginata (DC.) Kittel and S. salina J. & C. Presl are described as polymorphic species of the coasts of W. Europe which are morphologically very close to each other. This polymorphism has led to the description of a large number of nomenclaturally very confusing infraspecific entities. The morphological similarity, on the other hand, has led to very diverse opinions on the taxonomic distinctness of the two species.

In the Dutch literature Holkema (1870) expressed the opinion that Spergularia marginata and S. salina represent not two but one species which he called S. halophila Marss., following Marsson (1869). In the flora of Heimans, Heinsius and Thijsse (1960) three Dutch species are distinguished, S. marginata Kittel, S. salina Presl and S. media Fr. Heukels van Ooststroom's flora (1962) recognizes two species: S. marginata (DC.) Kittel and S. salina J. & C. Presl. Most recent authors distinguish two species in this connection e.g. Clapham c.s. (1962), Hegi (1935), Lawalrée (1952), Monnier (1953, 1962), Ratter (1959), Salisbury (1958) and Tutin c.s. (1964).

CLAPHAM c.s. (1962), Hegi (1935) and Lawalrée (1952) suggest the possibility of hybrid origin of the so-called intermediates between S. marginata and S. salina.

Nomenclaturally there is no accordance in literature. In Flora Europaea (Tutin c.s. 1964, p. 155) S. marginata Kittel and S. salina J. et C. Presl are used as synonyms of resp. S. media (L.) C. Presl and S. marina (L.) Grisebach. For the present Heukels-van Ooststroom (1962) will be followed.

The present investigation tries to shed some light on this confusing species problem. To this end the variability of the populations in the Netherlands of the halophilous species of Spergularia was studied.

This population analysis formed the basis of further biosystematic research. A more extensive publication is in preparation. The present article deals with the variability of the principal diagnostic characters reported in Heukels-Van Ooststroom for S. marginata and S. salina. The method employed for sampling the populations is not described here.

2. The number of stamens per flower

The number of stamens in each flower is regarded as an important character for distinguishing S. marginata and S. salina. According to Heukels-Van Ooststroom (1962), S. marginata has 10 stamens and S. salina 3-5(-8). The character was studied in 20 populations of S. marginata and in 14 of S. salina.

On the basis of the number of stamens the flowers are grouped in 10 classes. The following table shows the relative frequency of these classes in some population samples. It gives an impression of the internal variability of the populations and of the differences in variability between the Dutch populations.

TABLE 1

Relative frequency of flowers with different numbers of stamens in some representative population samples of S. marginata and S. salina.

	locality	percentage of flowers									number of		
Species		number of stamens per flower											
		0	1	2	3	4	5	6	7	. 8	9	10	flowers
S.m.	Goudplaat						0.4		1.1	2.6	9.1	86.8	265
8.m.	Boschplaat	2.5	0.4	0.8	0.4			1.3	0.4	2.5	6.6	85.1	242
S.s.	Ellewoutsdijk	1.7	7.4	50.8	27.7	9.6	1.1	0.6	1.1				177
S.s.	De Grie	2.7	6.5	38.4	14.4	11.0	6.8	9.5	4.2	4.2	1.9	0.4	263

The variability in the number of stamens per flower in the sample from the Goudplaat (Noord-Beveland) is typical for most of the populations of S. marginata. The population from the Boschplaat (island of Terschelling) shows a striking, although low, percentage of flowers without any stamens. Such flowers were found in 4 out of 20 samples.

The fluctuations in the sample from Ellewoutsdijk (Zuid-Beveland) are typical for most of the populations of S. salina studied by the author. The population from De Grie (island of Terschelling) includes a small number of flowers with 8, 9, or 10 stamens. These were found in 2 out of 14 samples. A comparison of the data for S. marginata and S. salina shows that in both species flowers with from 0-10 stamens may occur. However, the distribution of frequencies is different. S. marginata rarely has fewer than 9 stamens, S. salina rarely has more than 5 or fewer than 2. The overlapping is, therefore, slight.

These data show that the number of stamens per flower cannot be regarded as an absolutely dependable character to distinguish S. marginata from S. salina. The variation in the populations studied by the author disagrees with that in Heukels-Van Ooststroom (1962); the fluctuations

are much wider. As a result of a detailed investigation this was only to be expected. More strikingly, however, the most common form of S. salina with two stamens was not reported.

Both species show a reduction of the androeceum resulting in a number of stamens below 10. This reduction is of a different kind in the two species.

Where in S. marginata the number of fertile stamens per flower is lower than 10, there always are some staminodes present that bring the total to 10.

In the extreme case of a flower without any fertile stamens there are always two whorls of 5 staminodes each. However, flowers with an androeceum of 9 parts, fertile stamens and/or staminodes, are occasionally found.

In S. salina there may also be staminodes, namely, in 20 % of the flowers studied. The number per flower is usually 1, less often 2, and rarely 3. Most flowers lack staminodes and a total of 10 androeceal members is only found in flowers with 7 or more fertile stamens. This difference in the degree of reduction of the androeceum characterizes the two species very well. Flowers with a reduced androeceum have a well-developed pistil.

3. The diameter of the flower and the shape of the stigmas

In fully open flowers of S. marginata the diameter fluctuates between 7 and 13 mm. Flowers with 8-10 stamens are 10-13 mm. across; those with only 1-8 stamens are often smaller, 9-10 mm. in diameter. Flowers without any fertile stamens are distinctly smaller; they are 7-9 mm. in diameter. This shows that there is a correlation between the reduction of the androeceum and the size of the flower.

In S. salina the floral diameter is from 4 to 8 mm. A diameter of 7-8 mm. occurs therefore in both species. In S. marginata flowers of this size always have 10 staminodes. The diameter of the flower together with the reduction of the androeceum is a good criterium for distinguishing the two species.

In the Flora Europaea (Tutin c.s. 1964, p. 154) the length of the sepals is cited as a diagnostic character: S. media (L.) Presl (=S. marginata Kittel) has usually sepals of more than 4 mm. and S. marina (L.) Grisebach (=S. salina J. et C. Presl) has usually sepals of less than 4 mm.

In the investigated population samples 39 % of the flowers of S marginata has sepals of more than 4 mm. and 51 % has sepals of 4 mm. whereas 5 % of the flowers of S. salina has sepals with more than 4 mm. and 37 % has sepals of 4 mm. length.

Because of the overlapping in length of the sepals, this character is for the Dutch populations not a reliable criterium for distinguishing both species.

Another diagnostic character is found in the shape of the stigmas. In S. marginata, when the flower first opens they are erect or gradually divergent and slightly reflexed at the apex.

The papillose part is directed to the inside, away from the anthers. Later during anthesis (under favorable conditions the flowers are mostly open for 3 days) the stigmas sometimes return to a vertical position.

In S. salina the stigmas are usually reflexed at anthesis and occupy a horizontal position. Their stigmatose parts face the anthers; very often the two organs adhere to each other when the flower opens. Under favorable conditions the flower is open for one day.

The differences in the position of the stigmas in the two species are connected with the way of pollination.

4. The seed margin

The degree of development of the seed wing is usually regarded as one of the principal diagnostic characters of S. marginata and S. salina. According to Heukels-Van Ooststroom (1962) all the seeds of S. marginata are broadly winged, or the uppermost ones in the fruit may be unwinged. The seeds of S. salina are all unwinged or occasionally the lower seeds in the fruit are winged. A similar distinction is found in Heimans, Heinsius & Thijsse (1960).

Careful observation at a magnification of \times 40 shows that in S. marginata all transitions from very broadly winged to quite wingless seeds are present. In the following table the seeds are classed according to the width of the wing.

 ${\bf TABLE~2} \\ {\bf Classification~of~the~seeds~of~S.~marginata~according~to~the~width~of~the~seedwing.}$

symbol of class	degree of development of the seed wing	width of wing in mm.
urw nw	unwinged to rudimentary winged narrowly winged	0-0.15 0.16-0.30
\mathbf{bvw}	broadly to very broadly winged	> 0.30

Most capsules contain seeds mainly or exclusively from 1 class (i.e., over 60 % of the seeds belong to one class). On the basis of their seeds the capsules are arranged in classes in table 3.

TABLE 3 Classification of the capsules of S. marginata according to the degree of development of the wing of their seeds.

symbol of class	seeds in the capsule						
URW NW	seeds r			kclusive	oly urw		
BVW	seeds	"	"	"	bvw		

In the Delta region (s.w. Netherlands) capsules were taken from 11 populations and in the "Wadden" region (West Frisian islands and coasts of Groningen and Friesland) from 14 populations.

As a whole 3443 capsules were studied. The following table shows the frequency distribution of the types of capsules in some representative population samples and gives an impression of the variability of this character.

TABLE 4
Relative frequency of capsules in some population samples of S. marginata.

locality	percen	tage of c	total number		
	URW	NW	BVW	of capsules	
Noord-Beveland, Goudplast	0	0	100	150	
Zeeuws-Vlaanderen, Zwin	o	2.2	97.8	150	
Goeree, Kwade Hoek	0	15.7	84.3	. 197	
Oostvoorne, Groene Strand	5.1	7.3	87.6	144	
Terschelling, de Grie	0	2.0	98.0	150	
Schiermonnikoog, Westerkwelder	7.7	18.5	73.9	408	
Terschelling, Boschplaat	30.0	15.5	54.5	150	
Texel, Slufter	88.3	9.7	2.0	196	

The table shows that the degree of development of the seed wing in S. marginata is very variable. The seeds in a single capsule may be from scarcely or not winged to broadly or very broadly winged. This variability is present in the Delta region (s.w. Netherlands) as well as in the "Wadden" region (n. Netherlands). In the Delta region 5 out of 11 samples contain capsules of the type URW; the frequency of this type is, however, low. The highest percentage was found at Oostvoorne, namely, 5.1%.

In the "Wadden" region 13 out of 14 samples contain capsules of the type URW. Only the sample from De Grie, isl. Terschelling, lacks URW-capsules. Among the other populations, 6 samples contain over 20 % URW-capsules, 3 have 10–20 % URW-capsules and in 4 there are 10 % or less than 10 % URW-capsules. In this respect the "Wadden" population differ from those of the Delta region.

The distribution of frequencies fluctuates more in the "Wadden" than in the Delta region. This can be correlated with differences in the milieu. The samples with the highest percentages of the URW-type capsules are from sandy soil, those with the lowest from clayey soil. In the Delta region this correlation is less clear. Presumably the habitats of S. marginata in the Delta region are less divergent than those in the "Wadden" region.

S. salina also has winged and unwinged seeds. Both types resemble those of S. marginata very closely. The seeds of S. salina have been classed in the same way as those of S. marginata (see table 2). Narrowly and rudimentary winged seeds, nw and rw, prove to be rare.

Capsules with exclusively or predominantly narrowly or rudimentary winged seeds were not present in our samples. When unwinged and winged seeds occurred together in one capsule, the latter were virtually always broadly or very broadly winged. The transition between seeds of the type uw, unwinged, and the type bvw, broadly to very broadly winged, is nearly always abrupt.

The capsules were arranged in two groups: UW, with only or mainly uw seeds, and BVW, with only or mainly by seeds. In the Delta region samples were taken from 8 populations, in the "Wadden" region from 16, and in the polder "Oostelijk Flevoland" from 1.

Altogether 2166 capsules were studied. In 24 out of 25 samples all capsules belonged to the group UW. Only in the sample from de Grie, Terschelling, 27.7 % from a total of 169 capsules belonged to the group UW and 72,7 % to group BVW. Therefore in this sample there are capsules with 100 % broadly or very broadly winged seeds. In the literature no indication was found that certain plants of S. salina may have exclusively broadly winged seeds. Further study of the nature of these plants is in progress.

Summing up, we may state that in S. marginata capsules occur with exclusively or mainly winged seeds beside capsules with exclusively or mainly unwinged seeds. In S. salina, disregarding the still insufficiently known population from De Grie, there are capsules with exclusively or mainly unwinged seeds. The degree of development of a wing on the seed is, therefore, not a reliable diagnostic character. Its variability proves to be much greater than the descriptions in the Dutch floras would lead us to believe (see above).

5. Discussion

An investigation into the most important diagnostic characters of S. marginata and S. salina by means of an analysis of population samples provided an impression of the internal variability of individual populations and of the differences in variability of different populations.

It is a significant question whether the variability as it was found may be ascribed to two species, *S. marginata* and *S. salina*. Do the plants with unwinged seeds growing in the populations of *S. marginata* really belong to that species?

The same question holds, mutatis mutandis, for the plants with broadly winged seeds in the populations of S. salina.

Extensive morphological, cytological, and ecological investigations have shown that with regard to S. marginata the answer is in the affirmative. The studies of the plants with broadly winged seeds in the populations of S. salina have not yet been concluded; the chromosome number is still unknown. With the exception of the seed character these plants do not differ morphologically from the other, they grow in the characteristic habitat of S. salina among plants with unwinged seeds. It seems very likely that they represent a winged form of S. salina. So far they have only been found on Terschelling, and there they seem to be confined to

parts of De Grie and De Groede. Breeding experiments have shown that winged and unwinged forms of S. marginata and S. salina are genetically determined (STERK, 1963). Thus the differences between the populations with regard to the seed character seem to be primarily genetically founded. In S. marginata they are correlated with differences in the milieu.

Outside of the Netherlands unwinged forms of S. marginata have been found in Britain, Ireland, and France (Tutin c.s., 1964); (Ratter, 1959), Spain, Portugal, and North Africa (Monnier, 1953, 1962). No literature references to winged forms of S. salina have come to the author's attention.

A last note, not quite within the scope of the present article, pertains to the differentiation of the halophilous *Spergularia* species in the flora by Heimans, Heinsius & Thijsse (1960). Three species are listed: *S. marginata* Kittel, *S. salina* Presl, and *S. media* Fr. The difference between *S. salina* and *S. media* is stated to be in the leaves. Those of *S. salina* are said to be biconvex, those of *S. media* convex only below and flat above.

According to the present author's observations this character fluctuates much in a single plant, is strongly influenced by the habitat, and has therefore no diagnostic value. The species S. media Fr., as distinguished in this flora, is identical with S. salina Presl.

Summary

The variability of the principal differentiating characters of Spergularia marginata and S. salina was studied by means of analyses of population samples. Both species proved to be sharply definable in the Netherlands; no intermediates were found. In certain habitats a form of S. marginata occurs with exclusively unwinged seeds. It seems that S. salina, on the other hand, has a form with broadly winged seeds only. So far it was found in but a single Dutch station.

Acknowledgements

This investigation was supervised by Prof. Dr. J. Lanjouw, Utrecht. It was carried out at the Botanical Museum & Herbarium, Utrecht (director: Prof. Dr. J. Lanjouw) and at the Botanical Laboratory, Department of Plant Taxonomy, of the Free University, Amsterdam (director: Prof. Dr. L. Algeba).

The investigation was partly made possible by a grant from the Netherlands Organization for Pure Scientific Research (Z.W.O.), for which the author wishes to express his gratitude.

The author is much indebted to Prof. Dr. J. Lanjouw for his continuous interest and stimulating discussions.

He also thanks drs. M. Vroman, Head of the Department of Plant Taxonomy of the Free University for all the facilities he has given, mr. J. Beelen (Amsterdam), mr. J. H. Ietswaart (Amsterdam) and

mr. P. Ketner (Utrecht) for their assistance in the investigation, miss H. Schaake for her technical assistance and dr. K. U. Kramer (Utrecht), for translating the Dutch text.

(Botanical Museum and Herbarium, Utrecht, Botanical Laboratory, Free University, Amsterdam.) Present address: Hugo de Vries-laboratorium Plantage Middenlaan 2a Amsterdam-C.

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