REDUCTION OF THE ANDROECIUM IN SPERGULARIA MARINA (CARYOPHYLLACEAE)

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SUMMARY

A study of the variation in the number of fertile stamens in flowers of *Spergularia marina* revealed that this number fluctuates between 0 and 10 but is usually 2 to 5. A statistical analysis showed that reduction did not take place at random, because certain stamens tend to disappear more often than other ones, the progressive reduction also proceeding according to certain rules. Although the causal explanation for these phenomana can only be a tentative one for the time being, the statistical data are put on record in order to draw the attention to the occurrence of such singular processes.

A study of androecial variability in *Spergularia marina* (L.) Griseb. showed that the number of fertile stamens per flower fluctuates between 0 and 10. Flowers with an optimum development of the androecium (with two whorls of 5 fertile stamens) are very rare. The majority of the flowers have 2 to 5 fertile androecial elements and evidently the reduction of the androecium has progressed rather far in this species (STERK 1968, 1969).

It is a question whether the reduction proceeds according to a certain pattern or at random. In the first case certain androecial configurations may be expected to occur in relatively high frequencies, but in the second no such preference of occurrence of special configurations may be anticipated.

The possibility to study the reduction is provided by the circumstance that, at least in the populations studied, all phases of a progressive reduction are represented, i.e., all intermediate stages between flowers without fertile stamens and flowers with 10 fertile stamens occur. The pentamerous calyx has a quincuncial aestivation which can be either dextrorse or sinistrorse, as shown in *fig. 1* in the two diagrams of flowers with 10 fertile stamens. The petals which alternate with the sepals are not shown in the diagrams.

It appeared that there are no differences in the relative positions of the stamens between flowers with a dextrorsely and those with a sinistrorsely quincuncial calyx, so that there was no need to take the difference in aestivation into account in the inquiry into androecial reduction in the species under discussion.

The fixation of the position of the stamens in the floral diagrams is appreci-

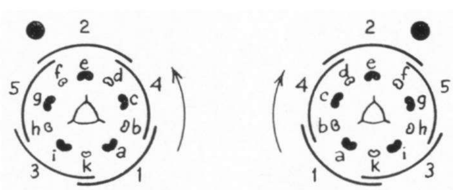

Fig. 1.
Spergularia marina. Diagrams of flowers with fully fertile androecia showing anti-clockwise and clockwise spiral aestivation of the calyx.

ably facilitated by the inequality of the sepals, the two outer sepals, nos. 1 and 2, having a very narrow membranous margin, the two innermost ones, nos. 4 and 5, a broad membranous margin, and the intermediate sepal, no. 3, partly covered and partly free, one narrow and one broad margin.

In all, 750 flowers were examined. The flowers were classified in 10 categories according to the number of fertile stamens present. In *table 1*, the actual androecial configurations are compared with the configuration to be expected statistically if the reduction would take place at random.

Table 1. *S. marina.* Comparison of the androecial configuration with the mathematically possible configurations to be expected if the reduction proceeds at random.

Flower category	Number of flowers examined	Number of configurations found	Number of possible configurations	Percentage of configurations found in respect of all possible ones
10		0	1	0
9	92	9	10	90,0
8	82	23	45	51,5
7	78	23	120	19,1
6	99	30	210	14,2
5	84	22	252	8,7
4	109	19	210	9,1
3	104	7	120	5,8
2	102	5	45	11,1
1		0	10	0
0		0	1	0

The results shown in this *table 1* clearly indicate that the reduction does not occur completely by chance. The considerable differences between the recorded percentages of each of the possible androecial configurations in the respective flower classes are striking. In flowers with 2–5 fertile stamens these percentages are relatively low. This means that, on the one hand, the reduction is not altogether a chance phenomenon, and, on the other, chance (*i.e.*, the statistical probability) plays a certain part. In the groups with 6–9 fertile stamens the percentage of recorded androecial patterns increases with a higher place in this sequence, especially the flowers with 8 or 9 fertile stamens showing a high percentage of representation of the various possible patterns. This may be taken as an indication of a gradually increasing significance of random reduction according as the number of fertile stamens is higher. The picture becomes even clearer when the relative frequencies per flower class are considered. *Table 2* shows the androecial patterns actually recorded in a relative frequency exceeding 3%.

It appears that certain configurations occur per class in very high frequencies. In flowers with 2 fertile stamens 5 androecial patterns were observed, one of which with a frequency of 96%. Furthermore, the relative frequencies of the most common pattern tends to be lower according as the number of fertile stamens per flower is higher.

Table 2. *S. marina.* Staminal configuration in 750 flowers examined. For the position of the stamens see fig. 1.

Flower category	Number of flowers	Configuration of stamens	Percentage of flowers
2	102	cg	96,0
3	104	cgi	64,4
		cgk	26,9
		cgd	3,8
4	109	cgik	56,9
		cgkd	12,8
		cgid	5,5
5	84	cgikd	40,5
		cgika	16,7
		cgike	10,7
		cgikb	7,1
6	99	cgikda, cgikae	13,1
		cgikde	8,1
		cgikdb, cgikaf	7,1
		cgidae, cgikab	5,1
		cgikbh, cgkdab	4,0
		cgkdae, cgidab, cgkdbe	3,0
7	78	cgikdab	21,8
		cgikabe, cgikdae	11,5
		cgikdbe	7,8
		cgikaef, cgikdaf	6,4
		gikdbef, cgkdabe, cgikdbf	3,8
8	82	cgikdbfh	19,5
		cgikdabf	15,9
		cgikdabe	13,4
		cgikdaef	10,9
		cgikdaeh, cgikdafh, cgikabef	4,9
9	92	cgikdabef	40,2
		cgikdabfh	21,7
		cgikdbefh	14,1
		cgikdabeh	7,6
		cgikabefh	6,5
		cikdabefh	4,3

Table 3 shows the frequencies of the various patterns per flower class for the total number of flowers examined.

From these data an insight into the course of reduction can be gleaned. A sequential arrangement of the androecial patterns of all flowers examined from the highest to the lowest frequency of occurrence yields the following reduction series of the individual stamens (compare *fig. 1*):

c-g-i-k-d-a-b-e-f-h

The reduction of androecial elements apparently commences with the elimination of stamen h and proceeds in the abovementioned sequence from right to left.

Table 3. *S. marina.* Staminal configurations in 750 flowers examined. The position of the sepals is indicated by means of the figures at the top of the table, the position of the stamens by letters; compare fig. 1.

Flower category	Number of stamens per position Position of sepals and stamens										Number of flowers
	1		4		2		5		3		
	a	b	c	d	e	f	g	h	i	k	
9	79	90	91	86	72	85	88	55	90	92	92
8	61	61	80	74	43	65	77	40	77	78	82
7	57	50	73	59	45	25	77	12	72	66	78
6	61	38	98	58	42	18	95	13	80	91	99
5	26	12	83	45	15	7	82	2	73	75	84
4	11	7	105	24	7	1	107	5	81	89	109
3	2	–	104	4	1	1	104	1	67	28	104
2	–	1	100	–	1	–	100	–	1	1	102
Total	297	259	734	350	226	202	730	128	541	520	750

A comparison of the overall sequence with the corresponding sequences of the individual flower classes shows that there is, broadly speaking, a good agreement between them. When the overall sequence is related to the recorded androecial patterns tabulated in *table 2*, it appears that the serial arrangement represents a general trend and must not be taken too precisely. Among flowers with 3 fertile stamens the configuration that may be expected according to the general reduction series, *viz.* c-g-i, is also the most commonly recorded one (representation 64.4%), but the combination c-g-k is also not rare either (representation 26.9%). In addition, with the exception of one pattern, all other possible combinations of stamens c and g with a third androecial element were found, albeit in frequencies lower than 3%. That the pattern c-g-b was not encountered may be ascribed to the relatively small number of flowers of this category (with three fertile stamens) included in the investigation.

There appears to be a marked tendency towards the reduction of stamens according to a certain standard sequence of disappearance, but there are certain deviations from this general trend. Flowers with more than 5 fertile stamens seem to have a greater plasticity in this respect than those with fewer than 5 fertile stamens; of the flowers with 5 such androecial elements 40.5% have the pattern to be expected from the overall sequence of reduction, whereas this percentage is only 21.8% in flowers with 7 of such elements. It should be noted that in 58.9% of the flowers with 7 elements 5 of the 7 stamens have the androecial configuration c-g-i-k-d, and in 42.2% of these flowers 6 stamens occur in the pattern c-g-i-k-d-a. Both these high percentages of representation may be anticipated on account of the above-mentioned rule of thumb. The plasticity is especially noticeable in the patterns towards the end of the sequence but far less so in those at the other side.

It has already been mentioned that, judging from the percentages of actually recorded patterns in respect to the mathematically possible number, chance distribution plays a greater part in flowers with 6–9 fertile stamens than in flowers with 2–5 such elements. A consideration of the occurrence of the various configurations per flower category confirms this conclusion.

If staminodial androecial elements are taken into account, stamen development seems in most cases to be inhibited in those positions in the flower that may be predicted on the basis of the above-mentioned "reduction sequence". The reduction of the androecial elements clearly follows a certain pattern within the morphological structure of the flower. *Fig. 2* shows the most frequently recorded stamen configurations in flowers with 2 to 9 stamens, respectively, with two exceptions, *viz.* the configuration in flowers with 8 fertile stamens (which is more often c-g-i-k-d-b-f-h than the figured c-g-i-k-d-a-b-e), and in flowers with 6 stamens (in which category two different configurations occur in equal frequencies, only one of which is shown).

A comparison of the diagrams shows that the reduction proceeds very irregularly. The stamen in position h is the first to disappear and subsequently the one in position f. Both these stamens occupy an epipetalous position. The next to disappear is the episepalous stamen e, and, successively, the epipetalous b, the episepalous a, the epipetalous d, the epipetalous k and, ultimately, the episepalous stamens i, g, and c.

In connection with the findings concerning androecial reduction in *S. marina* a preliminary study was made of the situation in *S. rubra.* The results of this study will be discussed by comparing them with those obtained in a similar

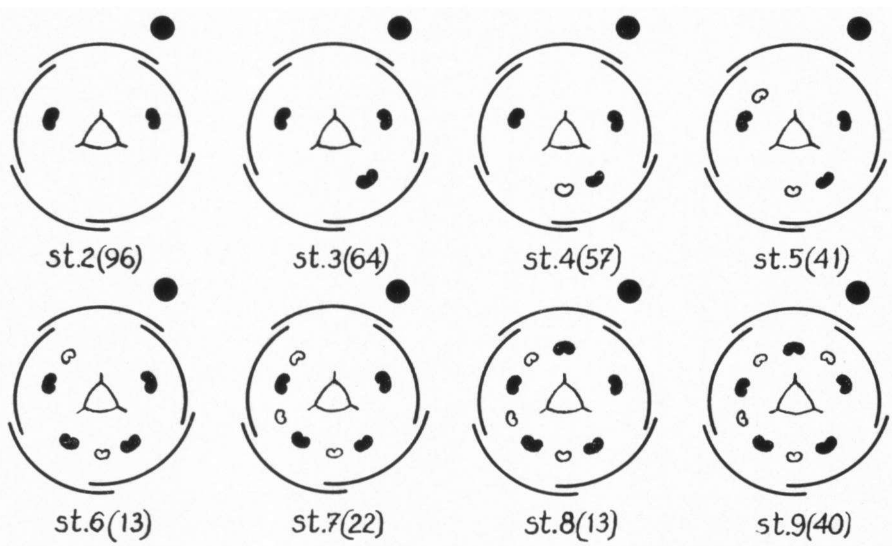

Fig. 2. *Spergularia marina.* Floral diagrams of flowers with 2–9 fertile stamens with the most commonly occurring stamen configurations. The figures in brackets represent the percentage of representation of each particular pattern among the flower category in question. Episepalous stamens are drawn in black.

Table 4. Comparison of the 'reduction sequence' of the stamens in flowers of *Spergularia marina*, *Sp. rubra* and *Stellaria media*. (For the position of the stamens, see fig. 1). The data relating to *St. media* borrowed from MATZKE (1932).

Species	Position of stamen									
Sp. marina	h	f	e	b	a	d	k	i	c	g
Sp. rubra	h	f	b	d	k	e	a	i	c	g
St. media	f	h	b	d	k	a	e	i	c	g

investigation of *Stellaria media* ssp. *neglecta* var. *typica* Beguinot by MATZKE (1932). The progressive reduction sequences of *Spergularia marina, Sp. rubra* and *Stellaria media* are shown in *table 4.*

There is a striking similarity between the sequences of *Spergularia rubra* and *Stellaria media*, whereas that of *Spergularia marina* deviates. Another interesting difference is that in *Sp. rubra* and *St. media* the whorl of epipetalous stamens becomes reduced first and only afterwards the episepalous one, whereas in *Sp. marina* the reduction does not occur in such a regular pattern, as discussed above. On the basis of his conception of the "genetic succession" of floral elements and of the numbering of the stamens according to this principle, Matzke stated that in *Stellaria media* the episepalous stamens disappear in an ascending direction along the "genetic spiral" and the epipetalous ones in a descending direction. This interpretation could, in my opinion, also apply to the stamens in *Spergularia rubra*, but the reduction sequence in *Sp. marina* is not conformable to this pattern of reduction.

It is noteworthy that at either end of the reduction sequence all three species show good agreement: the epipetalous stamens 8 and 10 (and also 9, if in *Sp. marina* the positions 2 and 9, with frequencies of representation of 226 and 259, respectively, are interchanged) are the first to disappear in all three species, whereas the episepalous stamens 3, 4, and 5 persist the longest. The differences are in the intermediate parts of the respective reduction sequences.

It is not easy to explain why in *Sp. marina* the sequence of reduction proceeds to the episepalous elements e and a before the small epipetalous stamens in the positions d and k have disappeared. In order to obtain a better insight into this complicated sequence of reduction a study of the floral ontogeny and the pattern of vascularisation in the flower (and pedicel) is required. During a discussion of the problem with Dr. W. A. van Heel, he suggested that to explain the general tendency of progressive reduction as shown in *fig. 2* one might postulate that the androecial reduction is a matter of restriction of the available space on the floral apex, which would be more pronounced in positions facing the angles of the triangular pistil and be less noticeable in positions opposite the three faces of the pistil. If this is indeed the case, the spaces remaining opposite the more distally situated developing fourth and fifth sepals would be more favourable from a developmental point of view.

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