CYTOGENETIC STUDIES IN SPERGULARIA: VIII

Barriers to the production of viable interspecific hybrids

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ABSTRACT. The results of a programme of interspecific hybridization in *Spergularia* are summarized. The most important barrier to the production of viable interspecific hybrids was seed incompatibility which caused production of only abortive seeds in 44 out of the 99 interspecific combinations attempted. Other barriers to production of viable hybrids were lethal chlorosis of hybrid seedlings in combinations involving *S. rubra* and *S. capillacea*, and failure of fruit development in some other crosses.

Thousands of controlled interspecific cross-pollinations were made during the course of a cytogenetic study in *Spergularia*. Hybrids synthesized as a result of these pollinations have been reported in a series of papers (Ratter 1965a, b, 1969a, b, 1972) but as yet data on barriers to successful hybridization have not been published. This paper attempts to present such data in summarized form.

The species studied and their chromosome numbers are listed below. Descriptions of all species, apart from *S. macrotheca*, are given in Flora Europaea vol. 1. *S. macrotheca* is from the SW coastal region of North America and is fully described in Rossbach's monograph of American *Spergularia* (1940).

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S. bocconii (Scheele) Aschers. & Graebn.	36
S. capillacea (Kindb. & Lange) Willk.	18
S. diandra (Guss.) Boiss.	18
S. fimbriata Boiss.	18
S. heldreichii (Fouc.) Simon & Monnier	36
S. macrotheca (Hornem.) Heynh.	36
S. macrotheca Guadalupe race	72
S. marina (L.) Griseb.	36
S. media (L.) C. Presl	18
S. nicaeensis Sarato ex Burnat	36
S. purpurea (Pers.) G. Don	18, 36
S. rupicola Lebel ex Le Jol.	36
S. rubra (L.) J. & C. Presl	36, 54

The techniques used for culture, emasculation and cross-pollination were described in Ratter 1965a.

RESULTS AND DISCUSSION

Results of the individual cross combinations are summarized in Table 1. Details of the origin of stocks used, number of attempted hybridizations, seed output, etc., have been omitted to save space, but such information is lodged at Edinburgh and can be supplied to anyone interested.

The commonest cause of failure to obtain viable hybrids was seed incompatibility. In 44 out of the 99 attempted interspecific hybridizations crossing

TABLE 1

Results of interspecific cross pollinations in *Spergularia*:

H=viable hybrid produced; I=total seed incompatibility; J=a proportion of incompatible seeds produced; K=fruits fail to develop; L=hybrids die of lethal effects; N=fruits rarely developed; — = hybridization not attempted; *macro.* (Guad.)=the stock of *S. macrotheca* from Guadalupe Island.

♂ ♀	*bocconii*	*capillacea*	*diandra*	*fimbriata*	*heldreichii*	*macrotheca*	*macro.* (Guad.)	*marina*	*media*	*nicaeensis*	*purpurea* (2x)	*purpurea* (4x)	*rupicola*	*rubra* (4x)	*rubra* (6x)
bocconii		K	I	HJ	H	—	—	H	K	H	HJ	I	HJN	IN	H
capillacea	I		K	I	—	—	—	I	I	I	—	—	L	—	—
diandra	K	I		I	—	—	—	K	—	—	—	—	—	—	—
fimbriata	—	—	—		—	—	—	—	—	—	—	—	—	—	—
heldreichii	—	—	—	H		—	—	HJ	—	H	—	I	I	—	—
macrotheca	—	—	—	—	—		—	—	IN	—	—	—	—	—	—
macro. (Guad.)	—	—	—	—	—	—		—	—	—	—	—	—	—	—
marina	H	I	I	I	HJ	I	I		I	HJ	—	HJ	H	HLJ	I
media	K	HLJ	K	I	—	I	HJ	I		I	—	HJ	HJ	IN	I
nicaeensis	H	—	—	H	H	—	—	HJ	I		H	HJ	HJ	I	LJ
purpurea (2x)	—	—	—	—	—	—	—	—	—	—		—	—	—	—
purpurea (4x)	I	—	—	HJ	I	—	—	IN	K	I	—		I	I	—
rupicola	K	—	—	HJ	I	—	—	HJ	IN	I	—	HJ		LJ	LJ
rubra (4x)	I	H	IN	I	K	—	—	HLJ	LJ	I	—	K	LJ		I
rubra (6x)	—	—	—	—	—	—	—	LJ	LJ	LJ	HJ	I	I	I	

was completely blocked from this cause, and in others a proportion of the seeds, varying from less than 1% to over 90%, was good, whilst the rest showed abortion due to incompatibility. Incompatible seeds vary greatly in size and appearance according to the stage at which abortion occurs. They range from small, flat, yellow seeds, little bigger than unfertilized ovules and lacking any detectable embryo, to darkly-pigmented seeds of normal size with torpedo-embryos filling three-quarters of the embryo sac and well-developed perisperm. In general, it is rare to see 'flat' unpigmented seeds with larger than a cotyledon-primordium (heart-shaped) embryo but the larger, pigmented seeds may have anything from no detectable embryo to late torpedos. The embryo-sacs of aborted seeds generally contain air-bubbles in their unfilled parts and the testa is often 'caved-in' over them. Rarely a type of inviable seed is produced with a fully-sized embryo but

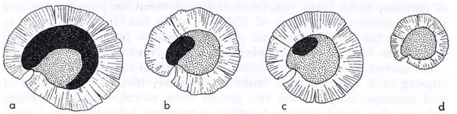

FIG. 1. Normal and aborted seeds of *Spergularia* × 16: a, normal winged seed of *S. media*; b & c, seeds of the cross *S. media* × *marina* showing embryos aborted after partial development; d, a smaller aborted seed of the same cross without embryo. Embryo marked as black, the rest of the body of the seed stippled.

little development of perisperm; such seeds are usually small and little pigmented. Abortive seeds are shown in fig. 1.

Seed incompatibility involving abortion of the developing hybrid embryo is well known in many plant families. In the Caryophyllaceae it has been described previously in *Dianthus* (Buell, 1953). Brink & Cooper (1947) reviewed the subject and showed that in many cases embryo abortion was caused by the dysfunction of the endosperm, and this seems a possible explanation of the phenomenon in *Spergularia*, since examination of ripe incompatible seeds showed breakdown in the endosperm layer lining the embryo sac.*

A number of workers have shown in crosses involving different ploidy levels that seed incompatibility is more common where the lower ploidy level is used as female parent. The results obtained in crosses of diploid and tetraploid *Spergularia* species conform to this pattern: with diploids as female parents there was one combination which yielded viable hybrids whilst seven showed total seed incompatibility; with the tetraploids as females, eight combinations yielded hybrids and ten showed complete seed incompatibility. In crosses at the homoploid level, total seed incompatibility was more common amongst diploids than tetraploids: one combination yielding viable hybrids to five with total seed incompatibility in the diploids as compared to twenty giving viable hybrids and sixteen showing complete incompatibility in the tetraploids.

Seedling lethality occurs in various crosses involving *S. rubra* (both tetraploid and hexaploid races) and also the closely related *S. capillacea* (see table 1). In this condition normal germination occurs and the seedling is at first healthy, but yellow spotting on the leaves develops at the time of the opening of the first or second pairs of true foliage leaves and soon develops into a lethal chlorosis. In all the hybrids in which this condition occurred, apart from *S. media* x *capillacea* and a single combination of *S. marina* x *rubra* (4x) and the reciprocal cross, the whole of the hybrid family died as a result of chlorosis. In the exceptions a few seedlings remained healthy and grew to maturity, whilst the remainder died at the usual early stage.

Occurrence of lethal chlorosis of seedlings similar to that taking place in *Spergularia* has been reported in a variety of interspecific hybrids in a number

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* The subject of seed incompatibility in *Spergularia* is treated in more detail in Ratter 1959.

of families; Smith (1943, 54), for instance, observed the phenomenon in a series of interspecific hybrids of *Melilotus*, whilst Sax (1945) reported it in lilacs. In the Caryophyllaceae, plastid anomalies producing variegated plants have been reported in hybrids of *Silene* (Newton, 1931).

An interesting aspect of the hybridizations is that they demonstrate that crossing of *S. marina* and *S. media* is completely blocked by a barrier of seed incompatibility. These two species show morphological similarities and are often found growing together in maritime habitats in the United Kingdom and many other parts of their range. A number of workers have failed to appreciate the range of morphological variation in each species and therefore have postulated the occurrence of hybrids between them. A large number of stocks of each species was used in the attempted hybridizations which totalled 269 with *S. marina* as female parent and 176 with *S. media*. With *S. marina* as female parent abortion always took place at an early stage so that all seeds produced were small, yellow and flat, but in the reciprocal cross development usually proceeded further and the seeds were well-pigmented and often contained torpedo embryos.

As shown in table 1, production of viable hybrids was completely blocked by seed incompatibility, failure of fruit development or lethal chlorosis of seedling in 65 out of the 99 attempted interspecific crosses. In addition, in many of the combinations where hybrids were obtained they represented only a small percentage of the potential output, the rest having been lost by partial operation of these barriers to hybridization. Barriers operative later in development also occur as well as those preventing production of viable hybrids, since the great majority of the viable interspecific hybrids showed complete sterility (Ratter 1965 a, b, 1969 a, b). As a result of these various barriers, gene exchange is impossible between all but a few of the *Spergularia* species studied.

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