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THE RELATION BETWEEN THE GENETIC DETERMINATION AND THE ECOLOGICAL SIGNIFICANCE OF THE SEED WING IN SPERGULARIA MEDIA AND S. MARINA

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SUMMARY

Plants with winged seeds and plants with unwinged seeds occur in *Spergularia media* and in *S. marina*. The degree of development of the seed wing is more differentiated in *S. media* than it is in *S. marina*, seeds with a narrow wing being of common occurrence in populations of *S. media* and absent in *S. marina*. In a stable environment the plants produce mainly winged seeds and in unstable habitats unwinged ones. Since *S. marina* occurs only in unstable types of environment, plants with winged seeds are very rarely encountered in this taxon. In *S. media* 'winged' is dominant over 'unwinged', but in *S. marina* 'unwinged' is dominant over 'winged'. The considerable difference in dominance is correlated with differences in selective pressure: in populations of *S. media* the predominating selection pressure acts in favour of the phenotype with winged seeds and the genetic factors for 'winged' are dominant, whereas in populations of *S. marina* the selective pressure favours the phenotype with unwinged seeds and the genetic factors for 'unwinged' are dominant over 'winged'. In *S. media* the phenotypic character 'winged' is most probably determined by two factors, one of which is epistatic, and in *S. marina* this characteristic is presumably brought about by polymery involving two factors. In populations of *S. media* plants with narrowly winged seeds may arise as the result of genetic recombination, which individuals may have a high survival value in certain environments, but in *S. marina* such phenotypes – which have hardly any adaptive significance or none at all – do not arise.

The degree of outbreeding in populations of *S. media* is estimated at 8 to 15 per cent, in populations of *S. marina* at 1 to 2 per cent.

The different genotypic determination of the degree of wing development of the seed and the different rates of outbreeding and inbreeding are most probably attributable to the different ecological situations in which the two species occur in nature.

1. INTRODUCTION

Spergularia media (L.) C. Presl and *S. marina* (L.) Griseb. are polymorphic species. The distinction between these taxa has in the past often caused difficulties by the considerable overlap of characters supposed to be of diagnostic value. One of these characters is the degree of development of the seed wing, *S. media* being supposed to have chiefly winged seeds and *S. marina* unwinged ones. It has been demonstrated that among populations of both species individuals occur which produce winged seeds as well as individuals producing unwinged ones (STERK 1969a,b). Plants with winged seeds and plants with unwinged ones differ in their ecological tolerance and preference. Phenotypes of *S. marina* with winged seeds are very rare in the Netherlands and elsewhere along the coasts of Western Europe. In the Netherlands only a single population was recorded on the North Sea Island of Terschelling (De Grie).

In view of the strong correlation between the type or habitat and the degree of seed wing development, the presence or absence of the wing has presumably a considerable adaptive significance. As a continuation of previously published studies, hybridization experiments between plants with broadly winged and plants with unwinged seeds of both species were carried out. These crosses have yielded an insight into the genetic determination of the development of the seed wing and into the possible relation between genetic factors and the adaptive meaning of the winged or unwinged seed types.

2. HYBRIDIZATION EXPERIMENTS WITH S. MEDIA

The development of the seed wing in *S. media* is subject to an appreciable variation, and for the evaluation of the progenies of crosses the following classification was used:

1. unwinged to subalate seeds (*urw*-seeds, width of the wing 0.0–0.15 mm),
2. narrowly winged seeds (*nw*-seeds, width of wing 0.15–0.30 mm), and
3. broadly to very broadly winged seeds (*bvw*-seeds, width of wing >0.30 mm).

Some types of seeds are shown in *fig. 1.*

In the proximally situated capsules of *S. media* seeds of one kind predominate. On this basis the plants are classified in *URW*-plants (with exclusively or mainly *urw*-seeds); *NW*-plants (with exclusively or mainly *nw*-seeds); and *BVW*-plants (with exclusively or mainly *bvw*-seeds), respectively. The capsules borne more distally on the inflorescences contain more seeds of "aberrant" types (in this taxon: seeds with a narrower wing) than the proximal capsules, the *NW*-plants exhibiting the greatest variation.

The breadth of the wing is not only dependent on the location of the capsule but also on the conditions obtaining during the growth of the plant. In unfavourable circumstances, such as a poor substratum, the wings are narrower than those of plants that grew on a much richer soil type (Sterk 1969a). The great phenotypic plasticity of the seed wing character is manifest, and that is why during the genetical analysis only the contents of the proximal capsules of plants reared under similar conditions were included in the counts.

The genetical analysis was carried out with plants reared from seeds of the exclusively *BVW*-population of Het Zwin (Zeeuws-Vlaanderen, Netherlands) and with plants reared from seeds of the exclusively *URW*-population from the Danish North Sea Island of Rømø. These plants appeared to be homozygous for the characters "broad-winged" and "unwinged". In the Netherlands not a single population was found consisting of exclusively *URW*-plants (this

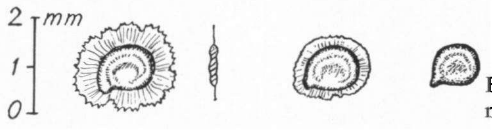

Fig. 1. *S. media.* Broadly winged seed, narrowly winged seed and unwinged seed.

phenotype occurs in populations containing also *BVW*- and *NW*-individuals), so that, owing to the partial outbreeding in natural stands, there was no *a priori* certainty of the homo- or heterozygoty of the *URW*-plants and of their seeds in such "mixed" populations (Sterk 1969a). Some of the investigated *BVW*- and *NW*-individuals of "mixed" populations indeed appeared to produce progenies with segregation into phenotypes exhibiting different degrees of seed wing development.

The crossings were made according to the following scheme, the F2 generation being produced by selfing of F1 plants. (In the scheme, *BVW* stands for plants with exclusively broad-winged seeds, *NW* for individuals with only narrow-winged seeds, and *URW* for phenotypes with only exalate seeds).

P:	♀ BVW × ♂ URW	♀ URW × ♂ BVW
	↓	↓
F1:	BVW	BVW
	↓	↓
F2:	167 BVW: 30 NW: 14 URW	163 BVW: 39 NW: 10 URW

The distribution of the two progenies agrees very well (in the homogeneity test: $\chi^2 = 1.8869$; df = 2; p = 0.50–0.30). The sum total of both segregation ratios is: 330 BVW: 69 NW: 24 URW, i.e., approximately 12:3:1. This segregational distribution can be explained by assuming that two independent factors are involved, *viz.*,

1. one factor responsible for the difference between "narrowly winged" and "exalate" (and the ratio between the *NW* and *URW* phenotypes in the F2 is indeed 69: 24, *i.e.*, approximately 3:1, $\chi^2_{3:1} = 0.023$, p = 0.90–0.80, in other words, the segregation ratio found does not differ significantly from the expected 3:1 ratio) and
2. one factor responsible for the difference between "broadly winged" and the remaining phenotypes, which factor is epistatic in respect of the factor mentioned sub 1 (the ratio of segregation between the *BVW* phenotypes and the other phenotypes together is 330 BVW: 93 NW + URW, *i.e.*, approximately 3:1, $\chi^2_{3:1} = 2.0496$, p = 0.20–0.10, in other words, the actual ratio does not differ significantly from the anticipated 3:1 relation).

F1 hybrids were subsequently crossed back with the recessive unwinged parent URW:

P:	♀ BVW × ♂ URW
	↓
F1:	♀ BVW × ♂ URW (P)
	↓
B1:	146 BVW: 62 NW: 77 URW

Starting from the above-mentioned hypothesis, a ratio of segregation of 1:1 between *NW* and *URW* phenotypes, and between the *BVW* and the other phenotype groups together, might be expected. The actual numbers were:

NW: URW = 62:77 ($\chi^2_{1:1} = 1.6187$, $p = 0.30$–0.20)

BVW: (NW + URW) = 146:139 ($\chi^2_{1:1} = 0.1719$, $p = 0.70$–0.50).

The experimental segregation ratio does not significantly differ from the expected one.

The final conclusions that can be drawn from the crossing experiments are:

1. the factor responsible for the phenotypic character "broadwinged seeds" is a dominant one (in respect of "unwinged seeds"), and
2. both the segregation ratio of the F2 and that of the backcross can be explained by a bifactorial hybridization in which one of the genes involved is epistatic in respect of the other.

3. HYBRIDIZATION EXPERIMENTS WITH S. MARINA

As in *S. media*, the seeds of *S. marina* may exhibit a considerable variation in the degree of development of the wing from broadly winged to exalate. The seeds of *S. marina* resembling those of *S. media* in both size and shape, the same classification in seed wing classes as that for *S. media* was used (see p. 482). The scarcity of phenotypes with *nw*-seeds is striking (Sterk 1969b). The seeds in the proximal capsules of the inflorescence being predominantly of one wing-class only, for convenience a classification in *BVW*-individuals (with *bvw*-seeds) and *URW*-plants (with *urw*-seeds) was used; specimens with chiefly *nw*-seeds in their proximal capsules are lacking.

As in *S. media*, the seed wings are narrower in the distal capsules than they are in the proximal ones, so that for an analysis of the genotypic constitution exclusively seeds from proximal capsules were included in the investigation. The search for homozygous parent plants did not cause appreciable difficulties, since the high degree of incidence of autogamy results in the predominance of homozygous individuals of the different phenotypes.

Reciprocal crosses were made between *BVW*-individuals reared from seed collected in Terschelling and *URW*-plants reared from seed of a population from Het Zwin (Zeeuws-Vlaanderen).

P:	♀ BVW × ♂ URW	♀ URW × ♂ BVW
	↓	↓
F1:	URW	URW
	↓	↓
F2:	24 BVW: 256 URW	17 BVW: 235 URW

The segregation ratio of the sum of the phenotype classes is:
41 BVW: 491 URW (*i.e.*, approximately 1:15).

Such a ratio can be explained by assuming the presence of two independent and completely dominant factors producing the same phenotypic expression (*i.e.*, polymery by two factors). The probability test shows that the distribution is in good agreement with the ratio of segregation to be expected on the basis of this hypothesis:

$$\chi^2_{15:1} = 1.9268, \; p = 0.20\text{–}0.10.$$

A back-cross was subsequently carried out with Fl-hybrids and the recessive (wing-seeded) parent type BVW:

P: ♀ BVW × ♂ URW
↓
F1: ♀ URW × ♂ BVW (P)
↓
B1: 121 URW: 38 BVW

Starting from the above-mentioned supposition the ratio URW:BVW to be expected is 3:1; the recorded numbers were 121:38 ($\chi^2_{3:1} = 0.1027$, $p = 0.80$–0.70), so that the ratio URW:BVW does not differ significantly from the theoretical one.

The final conclusions are:

1. the phenotypic character “seed unwinged” is dominant over the character “seed winged”, and
2. the segregation ratio of the F2 as well as that of the back-cross can be explained by assuming hybridization involving two completely dominant factors with the same phenotypic effect (bifactorial polymery).

4. REPRODUCTION IN S. MEDIA AND S. MARINA

Previous anthecological and anthomorphological studies yielded indications of a predominantly autogamous reproduction with some outbreeding in *S. media* and an almost exclusive autogamy in *S. marina* (STERK, 1969d), but quantitative data concerning the ratios between selfing and outbreeding were lacking.

After the crossing experiments had shown the dominance of the “winged seed” character in *S. media* and of the “unwinged seed” character in *S. marina*, the possibility arose to procure information on the rates of outbreeding and inbreeding by a genetical approach.

An experiment was set up in the experimental garden in which homozygous recessives and homozygous dominants were planted in a pattern shown in

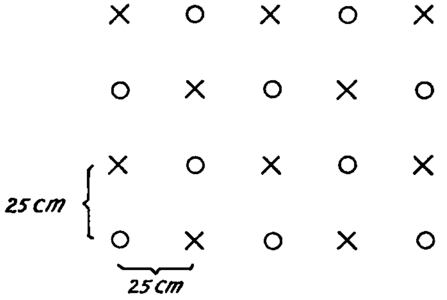

Fig. 2. Planting scheme.
O homozygote recessive individual,
X homozygote dominant individual.

fig. 2, the total numbers of each phenotype being equal. Pollination took place in the natural way.

In this experiment the following possible models of pollination of the recessives were present:

a. strict autogamy (selfing of one flower), maintaining the recessive character in the (homozygous) progeny;
b. geitonogamy (pollination between flowers of one individual), also yielding homozygous recessives;
c. outbreeding (allogamy) in which the pollen hails from
   1. a different recessive homozygous plant, again yielding a completely homozygous progeny of recessives, and
   2. a different dominant phenotype, leading to the appearance of the dominant expression of the seed wing character in the progeny.

In the experiments 100 capsules were harvested from the recessive plants (excluding the plants of the outermost rows), which would theoretically yield (taking 90 as the mean number of seeds per capsule in *S. media* and 49 seeds per bvw-capsule in *S. marina*) about 9,000 seeds in *S. media* and about 4,900 seeds in *S. marina.*

From the seeds actually obtained from the ripe capsules of each species, 944 plants of *S. media* and 1060 plants of *S. marina* were reared. Of the 944 plants of *S. media* 845 (*i.e.*, about 89 %) were *URW*-recessives and 99 (or about 11 %) heterozygous *BVW*-phenotypes; of the 1060 plants of *S. marina* 1034 (or about 98 %) were homozygous *BVW*-recessives, and only 26 (about 2 %) heterozygous *URW*-plants.

It is quite clear from these ratios that outbreeding plays a much greater rôle in *S. media* than in *S. marina.* This is a confirmation of suppositions concerning the mode of pollination in the two species based on morphological and ecological studies of the flowers (STERK 1969d).

In the experiment under discussion an unexpected luxuriant growth of the plants in the experimental plot resulted in a rather extensive intermingling of the plants, which caused an intermingling of their flowering branches and unduly favoured the chances of cross-pollination between adjacent individuals. The actual percentages in *S. media* indicate a pollen transfer from the dominant *BVW*-plants to the recessive *URW*-plants in about 11 % of the cases. Considering an individual *URW*-plant in the experiment (*fig. 2*) we may accept that the adjacent *BVW*-plants are closer to each *URW*-plant than the nearest four *URW*-plants, which effect is enhanced by the greater intermingling by the *BVW*-neighbours. Altogether, the chances of outbreeding by a pollen transfer from a *BVW*-plant are considerably greater than pollination with pollen from a different *URW*-plant. If we estimate the latter chance at a little over 1/2, the percentage of outbreeding in this experiment must be about 1.5 × 11%, *i.e.*, between 15% and 20%. Similar considerations obtain in the case of *S. marina*, and this would yield an outbreeding percentage of 2–4% under the experimental conditions. The ecological situation in natural stands in salt-marshes differs appreciably from that in the garden. The plants of *S. media* are usually smaller in natural habitats and the population density is but rarely so high that plants intermingle (STERK 1969c). The greater distance between plants in natural sites undoubtedly renders the percentage of autogamy and geitonogamy higher than it is in the experimental plot. An additional factor is the appreciable sensitivity of the flowers to unfavourable weather conditions, which affects the duration of their opening. During the experiments the meteorological conditions were very favourable; there was hardly any rainfall, the temperature was rather high, and there were long periods of sunshine. Also insects were very active in this period. In the natural habitats along the coast the conditions are on the whole less favourable during the flowering season, with a greater number of days with overcast skies, lower temperatures, and more rainfall. As a consequence of this there are more days on which the flowers remain closed. Accordingly, the percentage of heterogamous reproduction is, on the average, lower in natural populations than it is under the experimental conditions just described, and presumably lies between 8% and 15%.

In much trodden sites and in pools that have recently fallen dry *S. marina* may occur in population densities approximating the conditions prevailing in the experiment with a close proximity and even intermingling of the individual plants, but the flowers are even more sensitive to unfavourable weather conditions than those of *S. media*, so that on the whole the percentage of outbreeding in natural stands must be lower than under experimental conditions and is estimated at between 1% and 2%.

5. THE RELATION BETWEEN THE ECOLOGICAL SIGNIFICANCE AND THE GENETIC DETERMINATION OF THE SEED WING

Earlier studies have shown that plants of *S. media* with broadwinged seeds and plants with unwinged seeds have a different ecological preference (STERK 1969c). Populations of relatively stable environments with a closed stand of vegetation on clayey soils consist completely or predominantly of *BVW*- and *NW*-individuals, whereas populations of more unstable environments consisting of sparse stands on sandy soils contain an appreciable proportion of *URW*-plants.

The situation in *S. marina* is in so far rather similar that its populations, which occur only in unstable, disturbed and open stands of vegetation, contain exclusively *URW*-plants. Apparently a similar selection pressure has resulted in both species in the development of populations with exalate seeds in unstable types of environments. In this train of thought it is conceivable that *S. marina*, a species of disturbed habitats, has only in exceptional cases populations with broadly winged seeds, because this character has, as in *S. media*, no survival value in disturbed habitats. For the possible adaptive significance of the seed wing the reader is referred to STERK (1969c).

S. media has a wider ecological amplitude than *S. marina* and occurs in a range of different habitats exhibiting, among other things, different degrees of stability (STERK 1969c). There is a distinct correlation between the type of environment and the degree of development of the seed wing in different populations of *S. media*. There are populations in which not only broadly winged seeds occur, but also narrowly winged to exalate seeds. The ratios in which these three seed classes are represented in a population are largely dependent on the degree of stability of the environment, the percentage of broad- to narrow-winged seeds decreasing, and that of the exalate seeds increasing, according as the habitat is less stable. If the selective pressure favouring the incidence of unwinged seeds is strong and persistent enough, ultimately populations may arise containing exclusively plants with exalate seeds. If selective pressure works in the opposite direction, in more stable situations, ultimately populations with exclusively winged seeds develop. Assuming that the degree of seed wing development has indeed an adaptive significance in relation to the stability of the environment, it is permissible to conclude that *S. media* is capable to adapt itself to various degrees of environmental stability by means of different degrees of seed wing development. This adaptation is possible owing to both the genetical control and the phenotypic plasticity of the seed wing character. The genetical basis is different in the two species of *Spergularia* under discussion, and it is possible to correlate the genetical differences with ecological differences.

Within the range of distribution of *S. media* in the Netherlands and elsewhere in Western Europe, and presumably also in the remaining area of distribution, the populations containing exclusively or predominantly winged seed form the majority (RATTER 1964, STERK 1969a, 1969b). Apparently the selective pressure favouring the survival of plants with alate seeds prevails in a considerable part of the habitats. The situation is the reverse in *S. marina*, the selective pressure favouring the predominance of exalate seeds. If these data are related to the results of the hybridization experiments, a correlation between genetic dominance of the seed wing character and the prevailing selective pressure becomes evident: in *S. media* the selective pressure normally favours the incidence of winged seeds and the phenotype "winged seed" is dominant over "unwinged", whereas in *S. marina* the selection tends to eliminate the winged seed character and "unwinged" is dominant over "winged". The adaptation of populations of *S. media* to the rather varied environment (as far as stability is concerned) is brought about by another hereditary factor. The crossing experiments indicate a bifactorial determination of the character "seed winged", one factor being epistatic in respect of the other, so that three genetically determined phenotypes may occur, with broadly winged seeds, narrowly winged seeds, and exalate seeds, respectively. The segregation ratios in the F2 generation indicate that the genetic determination of these phenotypic characters can not be attributed to polygenic factors; for, if this would be the case, a cross between homozygous *BVW*- and homozygous *URW*-parents would result in a predominance of *NW*-plants in the F1 and F2 generations. The non-polygenous genetical basis of the character permits the occurrence of *NW*-plants which have a high survival value in certain environments, but the emphasis clearly lies upon the production of *BVW*-plants, which exhibit the highest selection coefficient in the majority of the habitats.

The ecological situation is altogether different in the case of *S. marina* and the different genetical control of the seed wing character is correlated with the different ecological requirements. *S. marina* has a narrower ecological amplitude and is exclusively found in unstable environments where a strong selective pressure acts in favour of the phenotype with unwinged seeds. *S. marina* does not withstand interspecific competition and disappears when the vegetation cover becomes closed and the milieu more stable. As in *S. media*, the genetic control of the seed wing character is bifactorial, but in *S. marina* two polymerous factors with complete dominance are involved. The genetic composition is such that phenotypes with *nw*-seeds, which have but little adaptive significance in the unstable environments, do not occur; any incidental crosses favour the production of *URW*-plants, which have the highest selection coefficient. As in *S. media*, the character of "presence of wing" is not polygenously determined.

Finally, there is some correlation between the mode of reproduction and the ecological variation of the two species under discussion. *S. marina* is a predominantly annual taxon from pioneer vegetation, and, like many other annuals from pioneer sites, reproduces mainly autogamously. There is a fairly general consensus of opinion that a rapid building up of a population is of paramount importance to annual species, which is achieved, among other things, by a considerable degree of homozygoty in the population resulting in a small loss of individuals by the segregation of not so well adapted genotypes as would be the case if allogamy prevailed. *S. media* is a perennial species with a relatively short life-span. The appreciable variation within the habitat and the rapid changes often taking place in the dynamic environment of salt marshes require an appreciable genetical variation, which is achieved, among other things, by the outbreeding taking place in the populations. The degree of allogamy (8–15%) seems to be on the low side, but if the selection coefficients of the various genotypes present in the population differ appreciably (more particularly: if the heterozygous genotypes have higher selection coefficients than the homozygous ones), which happens especially when the environment is changing, even a relatively low rate of natural outbreeding (below 10%) may result in a high incidence of heterozygoty (ALLARD 1960).

The relative degree of seed wing development is, at least in coastal populations of *S. media* and of *S. marina*, associated with the size of the seed body (*i.e.*, the seed without the wing): winged seeds have, on the average, a larger seed body than exalate ones. As a consequence, the young seedlings developed from winged seeds are, on the whole, larger than those from unwinged seeds. The seed wing characters are clearly connected with other structural characters of the seed, and this whole integrated complex of characters must be of considerable importance in the maintenance of the species.

The present investigation has yielded evidence of a relation between the genetic control of the seed wing characters and the prevalent selection pressure. This relation was to be expected since such phenomena as dominance and genetic determination of characters are subject to natural selection (and originate, in point of fact, by the action of natural selection). In many species studied, selection will tend to make the favourable effects of the gene dominant and the unfavourable ones recessive (FORD 1964). Studies by several workers, *e.g.*, those of GREGOR (1938, 1939) on *Plantago maritima*, and those of MARSDEN-JONES & TURRILL (1957) on *Silene maritima* and *S. vulgaris*, have shown that characters of an appreciably adaptive value for the requirement of delicate adjustment to various habitats are polygenic. The seed wing characters of the *Spergularia* species studied also belong to that group of characters of adaptive significance, but the close adaptation to various habitats is not brought about by polygeny, but by the combined action of a small number of genes and the phenotypic plasticity of the character.

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