

# Seed heteromorphism in a population of *Spergularia media* in relation to the ambient vegetation density

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## SUMMARY

This paper presents basic data regarding the seed heteromorphism in a population of the short-lived perennial halophyte *Spergularia media*. Essentially two seed types exist, unwinged and winged seeds. The variation in seed size and the existence and the extent of seed wings was investigated in a population from the western coast of Sweden. Seeds were collected both directly from plants growing under natural conditions, and from plants developed out of soil samples brought into a greenhouse after the seed set in the autumn. The seed size varied considerably and the width of the seed wing was positively related to the length of the seed body, but in contrast to the situation in the closely related annual *S. marina* (where the winged seeds have appreciably larger seed bodies than the unwinged seeds), the average seed body length differed only marginally (but in the same direction) between the seed types in *S. media*. Most of the plants produced either exclusively winged or unwinged seeds, but still 45%<sub>Field</sub> or 10%<sub>Greenhouse</sub> of the plants were found to produce capsules with heteromorphic seeds (strongly dominated by the winged seed type). The spatial distribution of the different seed types in an environmental gradient comprising surrounding vegetation of sparse, intermediate and dense covering was also investigated. Seed capsules containing only winged seeds were more common in the dense vegetation. Inversely, capsules with unwinged seed contents were more frequently encountered in open areas. No such relation was found between the vegetation density and the proportion of capsules with heteromorphic seeds. A hypothesis is presented saying that the production of two seed types in *S. media* is dictated by the pressure for greater efficacy in seed dispersal in combination with differential survival and reproduction of the two different seed morphs.

*Key-words:* halophyte, seed heteromorphism, seed size, seed wings, *Spergularia media*.

## INTRODUCTION

Various kinds of seed heteromorphism have been demonstrated and examined in a considerable number of species (Dowling, 1933; Cole 1961; Grant Lipp & Ballard 1964; Cavers & Harper 1966; Ungar 1979; Baker & O'Dowd 1982; Kalisz 1986; Venable *et al.* 1987). This phenomenon, which can be defined as the 'production by single individuals of

seeds (or sometimes single-seeded fruits) of different form or behavior' (Venable 1985), is often adaptively interpreted in terms of risk spreading and colonizing ability in spatially and temporally varying environments (Stebbins 1974; Harper 1977; Ernst 1981; Schat 1981; Westoby 1981; Schoen & Lloyd 1984; Silvertown 1984; Venable 1985; Kalisz 1986). This interpretation is based on the implicit assumption that the different seed morphs show differential behaviour, and in a model Lloyd (1984) stated that the evolution of seed heteromorphism presupposes that the fitness of the different seed types is not correlated in time or space. The seed traits usually considered concern dormancy, size and dispersal characteristics (e.g. McEvoy 1984; Venable & Levin 1985).

As reported in most modern floras, the short-lived perennial halophyte *Spergularia media* (L.) C. Presl. produces varying proportions of its small ovate seeds either with or without a membranaceous border. Sterk (1969), who investigated the morphological variation of *S. media* in relation to the environmental conditions in The Netherlands, found local populations with predominantly winged seeds in sites where the vegetation cover was dense and the fluctuations in the factors involved in the water- and salt relations less variable than in those places where the unwinged seed type dominated in the populations. In discussing the seed heteromorphism of the closely related and ecologically similar *S. marina* as an adaptation for differential dispersal distances, Telenius & Torstensson (1989) showed that under certain conditions the two seed types differ in their dispersal ability. Considering these findings and keeping in mind that the production of either type of seed appears to be largely genetically determined (Sterk & Dijkhuizen 1972), it is reasonable to assume that the spatial pattern of individual plants producing varying proportions of the different seed types in nature reflects either the interaction between dispersal and/or demographic processes (Wilson 1983; Telenius & Torstensson 1989, 1991).

This paper provides basic information on the seed size variation and the degree of wingedness at the intra-individual and intrapopulation levels in *S. media*. It also contains an account of the actual pattern of seed type occurrence in a population under field conditions. The result derives from two sources; direct sampling in the field, and sampling from plants grown out of the active part of the soil seed bank in a greenhouse (in order to circumvent 'the environmental sieve' (*sensu* Harper 1977)). The spatial distribution of the seed types was established from both sources, whereas the data on the variation in seed length and seed wing width was collected from the latter plants only. These plants also provided information regarding the relative onset of the flowering period, and the amount of seeds produced per capsule.

## MATERIALS AND METHODS

### *Study area*

The seeds and the soil samples were collected in August 1982 and in November 1984 respectively, in a cattle-grazed sea-shore meadow situated near Vallda Sandö (latitude 57°28'39"N, longitude 11°56'30"E) c. 30 km south of Göteborg on the western coast of Sweden. Here the population of *S. media* grows scattered among *Puccinellia maritima* (Huds.) Parl., *Salicornia europaea* L. (coll.), *Plantago maritima* L., *Halimione pedunculata* (L.) Aell. and *Juncus gerardii* Lois. in a c. 2-m wide belt, which ranges vertically between 0.1 and 0.6 m above mean sea level. As the diurnal tidal variation in this area is less than 0.3 m, the sea-shore meadow is only rarely flooded and then due to periodical, climatically induced seasonal fluctuations in the sea-water level. This happens normally in the late

summer and in the autumn concomitant with the seed maturation and dispersal. The variation in the density of the vegetation cover is marked even on a small scale. This means that within a 40 cm × 40 cm frame (the size of the permanent plots in a demographic investigation of *S. media* at the same site [A. Telenius, in preparation]), all degrees of vegetation closure from open to completely covered ground may occur.

#### *Seed type distribution in the field*

*Field plants.* In 1982 one seed capsule per plant (the lowermost where applicable) was collected straight from each of 3 × 100 individuals growing at least 2 m apart under conditions of sparse, intermediate and dense vegetation cover. The classification of the density of the vegetation that surrounded each individual plant was in this case made subjectively using the following criteria: areas with less than approximately 50% vegetation cover were designated as 'sparse'; areas with more than 50% cover, but with still some bare ground visible were considered as 'intermediate', and areas with a complete vegetation cover were regarded as 'dense'. The contents of the capsules were inspected and the relative proportions of winged and unwinged seeds were determined.

*Greenhouse plants from the soil seedbank.* In November 1984 (after the seed set) 72 cylindrical soil cores (diameter 60 mm, height 30 mm; 10 from sparse, 40 from intermediate and 22 from dense areas respectively — the unequal sample size were due to the location of the soil cores by the aforementioned permanent plots) were sampled and transported into a greenhouse. After being moved indoors the cores were depleted of above-ground vegetation, the soil was crumbled and the samples were spread out in Petri dishes. The soil was kept moist and was stirred repeatedly at 30-day intervals to increase the probability that all seeds gained access to light. Lighting was provided by Philips HPI/T metal halide lamps producing  $250 \mu\text{Em}^{-2} \text{s}^{-1}$  with a high red/far red ratio. The germination took place between the end of November 1984 and the beginning of March 1985 at 18-h day/6-h night conditions, with temperatures set at 18°C and 12°C respectively. Seedling appearance was recorded every 10th day and at each inspection the newly germinated seedlings were transplanted into individual plastic pots (50 mm × 50 mm × 55 mm). The plants were grown in a mixture of one-third sand and two-thirds compost. As in the equally halophytic *S. marina* the proportions of winged and unwinged seeds is not significantly affected by the addition of salt water to plants grown under experimental conditions (P. Torstensson, unpublished observations) it was decided not to impose such a treatment in this experiment. Altogether 626 plants were reared. At the time of budding, the floral parts of the main stem were enclosed in an emptied nylon tea-sachet. This was done in order to facilitate the collection of the contents of the dehisced capsules afterwards, but at the same time the possibility of cross-fertilization was eliminated. Finally, the number of nodes from the cotyledons to the first flower-producing node was also noted as a measurement of the 'time' to first flowering. When mature, the seed capsules from these plants were sampled (preferably two [the first and the last] but at least one seed capsule per individual shoot [normally four shoots per plant]) and their contents examined.

#### *Overall seed size variability*

The seeds were counted and in a few selected capsules the length of all seeds were measured at the longest axis. Frequency distributions of the length of the seeds within these capsules were calculated. Based on the size distribution thus found, it was

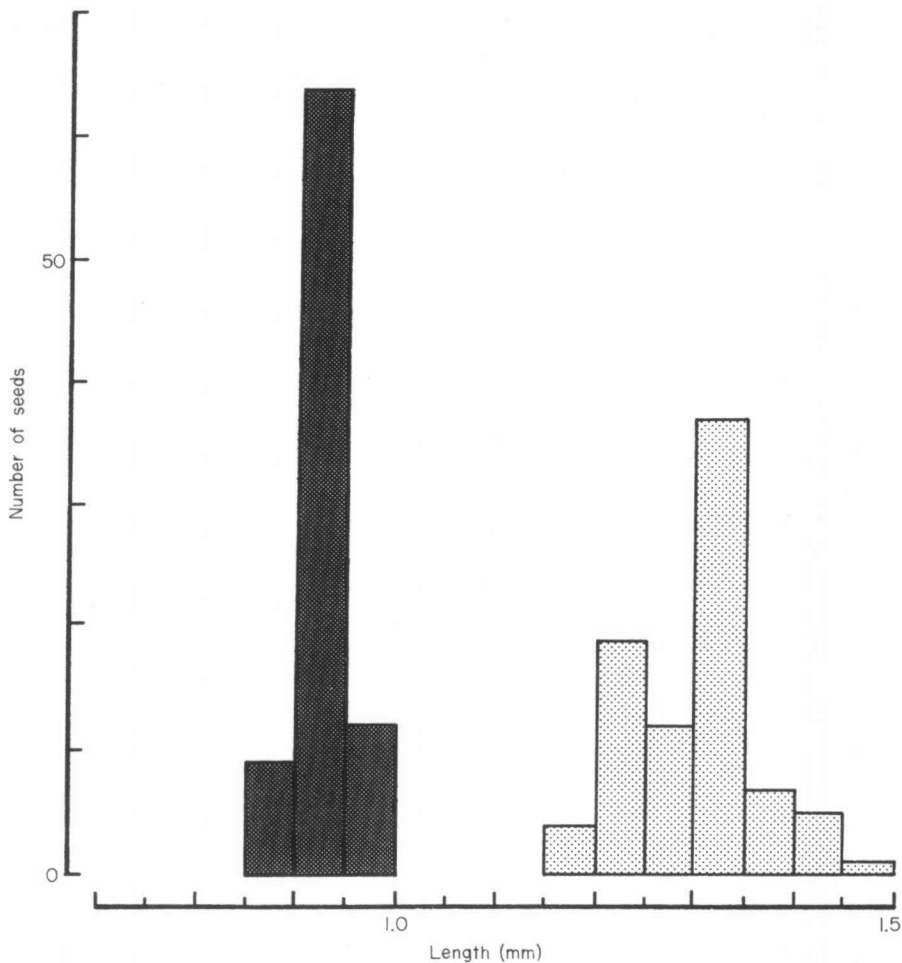


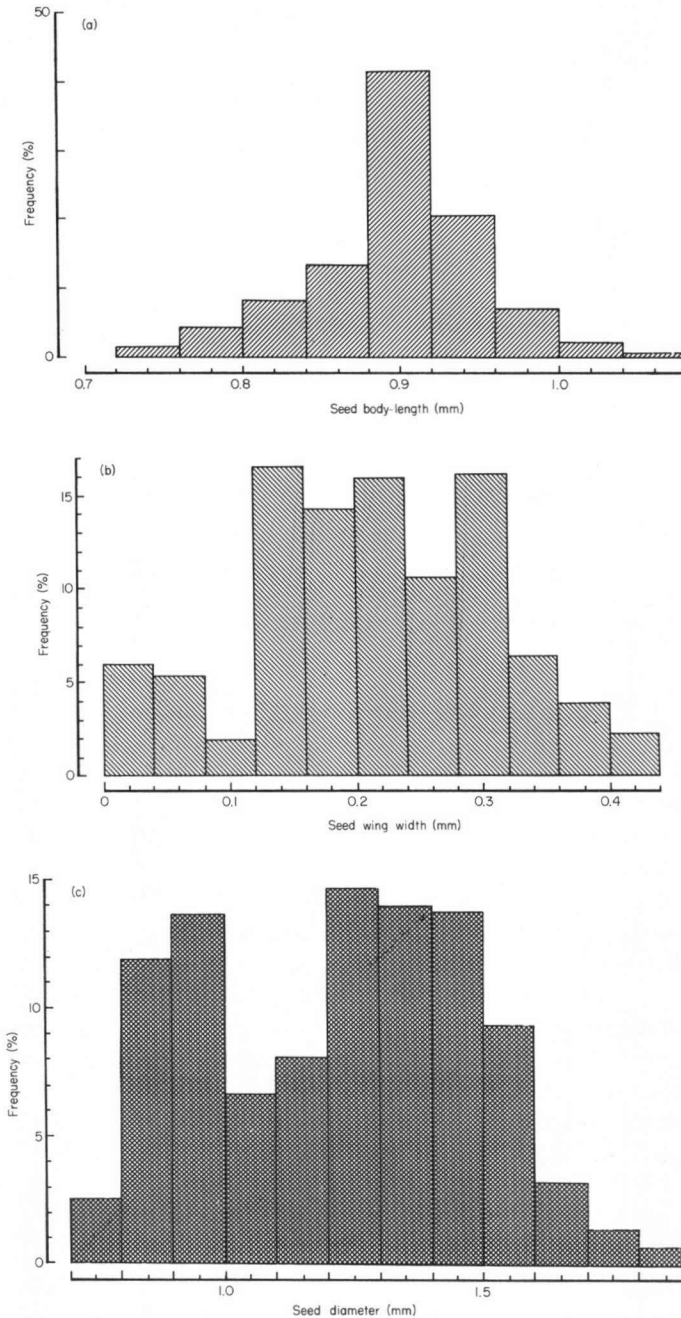
Fig. 1. The seed length variation within one *S. media* capsule containing only winged seeds. The heavily shaded area denotes the variation in seed body length, and the lightly shaded areas denotes the seed body length + 2 × seed wing width (= seed diameter). The capsule was collected from a greenhouse plant.

considered sufficient for the present purpose to subjectivity choose and measure only one 'representative' seed per capsule (i.e. per individual plant), or when more than one distinct type of seed occurred, one seed per estimated seed type. All size measurements were made using a binocular microscope fitted with a measuring eyepiece.

## RESULTS

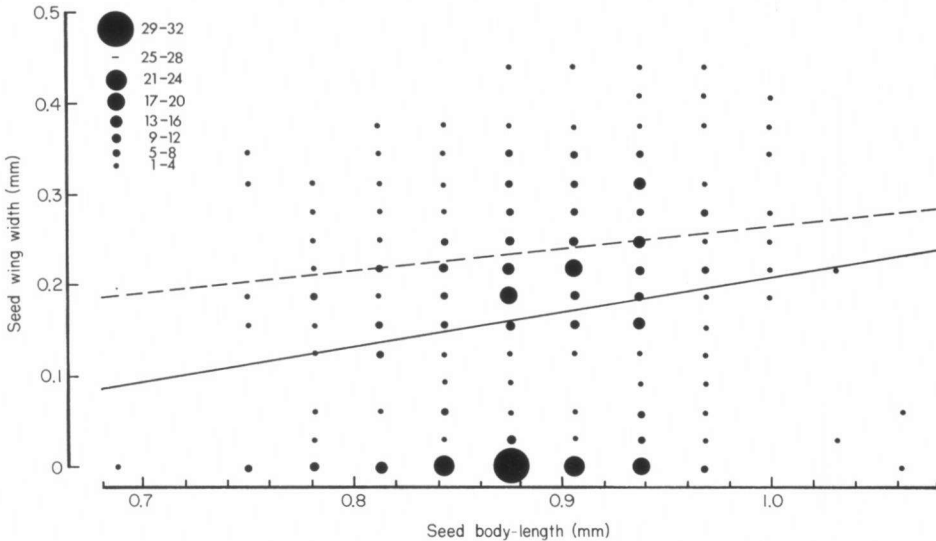
### *Seed size variation in the greenhouse population*

Figure 1 shows an example of the variation in seed length within a single seed capsule containing exclusively winged seeds. The variation in the mean seed body length, the width of the wing and the total seed diameter (i.e. seed body-length + 2 × wing width at the longest axis) in the entire population based on the measurement of one 'representative'



**Fig. 2.** The variation in (a) seed body length (b) seed wing width, and (c) seed diameter (seed body length +  $2 \times$  seed wing width) in *S. media* capsules collected from greenhouse plants. NB! Note the different scales.

seed per individual plant (as explained above) is shown in Figure 2. The length of the seed body varied between 0.72 and 1.08 mm, and the winged margin was up to 0.44 mm wide. The seed diameter varied between 0.72 mm and 1.84 mm in the investigated seed capsules.



**Fig. 3.** The relation between seed body length and seed wing width in *S. media*. The solid regression line refers to winged and unwinged seeds collectively, whereas the hatched line refers to winged seeds only. The seeds were collected from plants grown in a greenhouse.

The regression of seed wing width on seed body length (including the unwinged seeds) showed a positive relationship ( $F_{1,556} = 17.5$ ,  $P < 0.001$ ,  $r = 0.175$ ,  $y = 0.38x - 0.17$ ) (Fig. 3). The omission of the unwinged seeds from the test conferred only a minor change to the slope of the regression line ( $F_{1,372} = 9.99$ ,  $P < 0.01$ ,  $r = 0.162$ ,  $y = 0.22x + 0.04$ ).

In spite of the continuously varying seed body length the qualitative distinction between winged and unwinged seeds suggested by the previous authors (e.g. Salisbury 1958; Sterk 1969 [who, however, also identified a group of narrowly winged seeds]) appears to be fairly relevant. This can be seen in Figure 2c, where two peaks emerge, and in Figure 3, showing two 'clouds' of seeds. Thus, henceforth completely unwinged seeds, and seeds with a vestigial wing (up to 0.1 mm width) covering all or part of the rim are designated as 'unwinged', and the rest of the seeds are considered to be 'winged'. The diameter of these unwinged seeds varied between 0.72 and 1.19 mm, whereas the winged seeds were between 1.03 and 1.84 mm wide. The comparison of the average seed body length in the two groups showed a considerable overlap. The seed body was only slightly larger (but statistically significant;  $t = 2.77$ ,  $df = 556$ ,  $P < 0.01$ ) in the winged group than in the unwinged group: 0.89 mm (SD = 0.054) as opposed to 0.88 mm (SD = 0.060).

#### *Seed type distribution in the field*

Although the relative frequencies of capsules containing either exclusively winged or unwinged seeds and of capsules with heteromorphic seeds differed markedly between the mature field plants and the greenhouse plants grown from the soil seedbank ( $\chi^2 = 321$ ,  $df = 1$ ,  $P < 0.001$ ), both sets of data demonstrated a majority of capsules containing seeds of one type only (Table 1). The proportion of 'heteromorphic capsules' was more than four times as high in the field capsules as in the greenhouse capsules (45% vs. 10%). In the field material 76% of the 'monomorphic capsules' contained winged seeds. The corresponding figure in the greenhouse was 63% ( $\chi^2 = 229$ ,  $df = 1$ ,  $P < 0.001$ ). The mixed

**Table 1.** The distribution in a vegetation density gradient, of seed capsules from *S. media* containing either exclusively winged or unwinged seeds, or with mixed contents. The results presented refer to capsules collected in the field and from plants grown in a greenhouse respectively. The greenhouse plants were reared from seeds present in soil cores in correspondence with the distribution of sparse, intermediate or dense vegetation-cover in the field

	Sparse n%	Intermediate n%	Dense n%	Total n%
<b>Field</b>				
Winged	39 (39.4)	31 (31.3)	54 (55.1)	124 (41.9)
Unwinged	16 (16.2)	16 (16.2)	8 (8.2)	40 (13.5)
Heteromorphic	44 (44.4)	52 (52.5)	36 (36.7)	132 (44.6)
Total	99 (100)	99 (100)	98 (100)	296 (100)
<b>Greenhouse</b>				
Winged	8 (26.7)	159 (51.6)	149 (67.7)	316 (56.7)
Unwinged	20 (66.7)	117 (38.0)	47 (21.4)	184 (33.0)
Heteromorphic	2 (6.7)	32 (10.4)	24 (10.9)	58 (10.3)
Total	30 (100)	308 (100)	220 (100)	558 (100)

capsules were strongly dominated by winged seeds (many of which however carried only a brief margin, Fig. 4). Altogether four out of five of the seeds carried a winged margin in the field capsules examined, whereas only two-thirds of the seeds were winged in the greenhouse capsules.

The spatial pattern of winged, unwinged and heteromorphic phenotypes from both the field and the greenhouse collections is also given in Table 1. All three groupings occur in each of the three vegetation density classes but the plants producing solely winged seeds are more common in the intermediate and dense vegetation classes ( $\chi^2_{\text{Field}} = 6.60$ ,  $df = 2$ ,  $P < 0.05$ ;  $\chi^2_{\text{Greenhouse}} = 135$ ,  $df = 2$ ,  $P < 0.001$ ) than in the sparse class. On the contrary, although the test result is not significant in the field material, the plants producing only unwinged seeds appear more frequently in the more open vegetation types ( $\chi^2_{\text{Field}} = 3.21$ ,  $df = 2$ ,  $P > 0.05$ ;  $\chi^2_{\text{Greenhouse}} = 81.8$ ,  $df = 2$ ,  $P < 0.001$ ). The heteromorphic capsules are rather evenly distributed among the plants from all classes in both collections ( $\chi^2_{\text{Field}} = 2.91$ ,  $df = 2$ ,  $P > 0.05$ ). In the greenhouse material one of the cells consists of only two capsules, making  $\chi^2$  an improper test method.

Reconsidering Table 1 from another angle, the unwinged phenotypes are found to be the least common type in the sparse grouping in the field ( $\chi^2_{\text{Field}} = 13.5$ ,  $df = 2$ ,  $P < 0.01$ ), whereas in the greenhouse the unwinged type of plant is actually the most frequent in this density category (however, again goodness-of-fit testing is not applicable). In the intermediate density the unwinged plants are again rarer than any of the other types in the field ( $\chi^2_{\text{Field}} = 19.8$ ,  $df = 2$ ,  $P < 0.001$ ), but in the greenhouse this situation has changed into a scarcity of 'heteromorphic plants' ( $\chi^2_{\text{Greenhouse}} = 81.5$ ,  $df = 2$ ,  $P < 0.001$ ). Finally, in the dense vegetation the 'unwinged plants' are scarce in the field ( $\chi^2_{\text{Field}} = 32.6$ ,  $df = 2$ ,  $P < 0.001$ ) and only twice as common as the fairly rare (11%) heteromorphic plants in the greenhouse ( $\chi^2_{\text{Greenhouse}} = 121$ ,  $df = 2$ ,  $P < 0.001$ ).

The more frequent occurrence of seeds with wings in plants growing in intermediate and high vegetation density once again occur in the seed size variation data presented in Table 2. The average overall seed length increases from 1.06 mm in sparse areas to

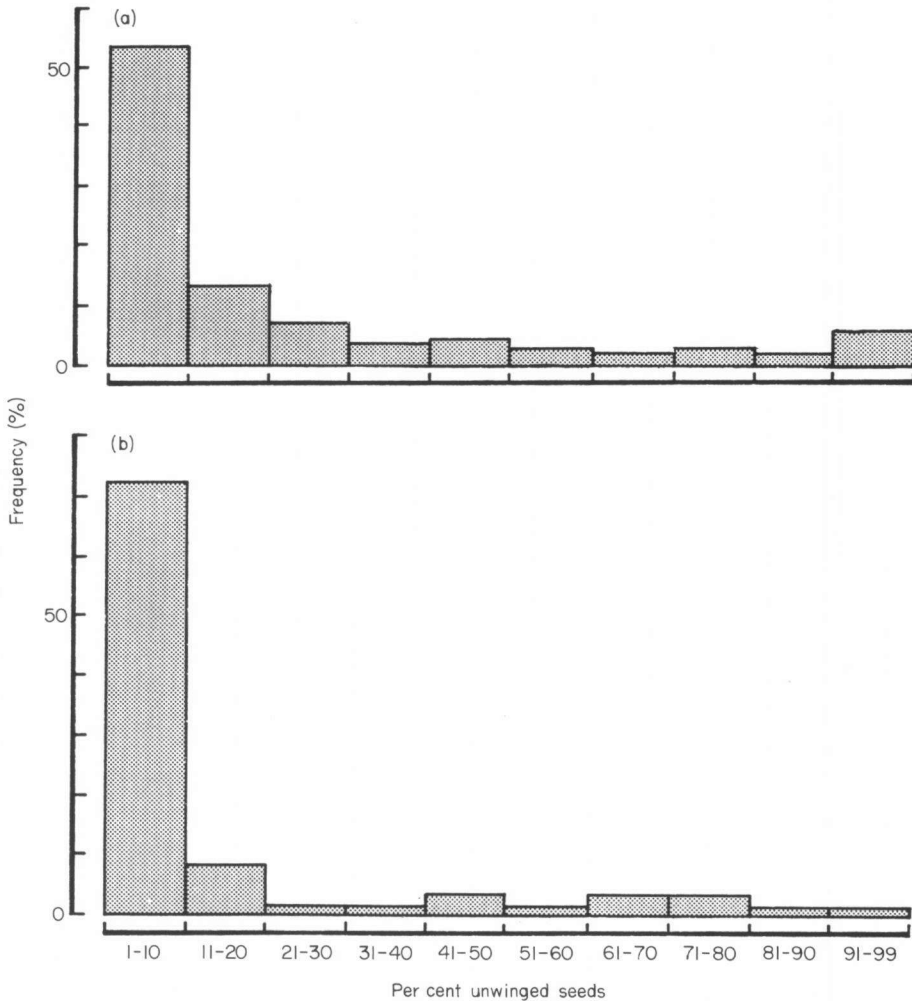


Fig. 4. The frequency distribution of winged and unwinged seeds in heteromorphic *S. media* capsules (a) collected in the field, and (b) collected from plants grown in a greenhouse.

1.28 mm in dense areas. Notably however, the seed body length is nearly unchanged, which means that the difference is almost exclusively derived from the increased presence and extent of seed wings as the vegetation density increases.

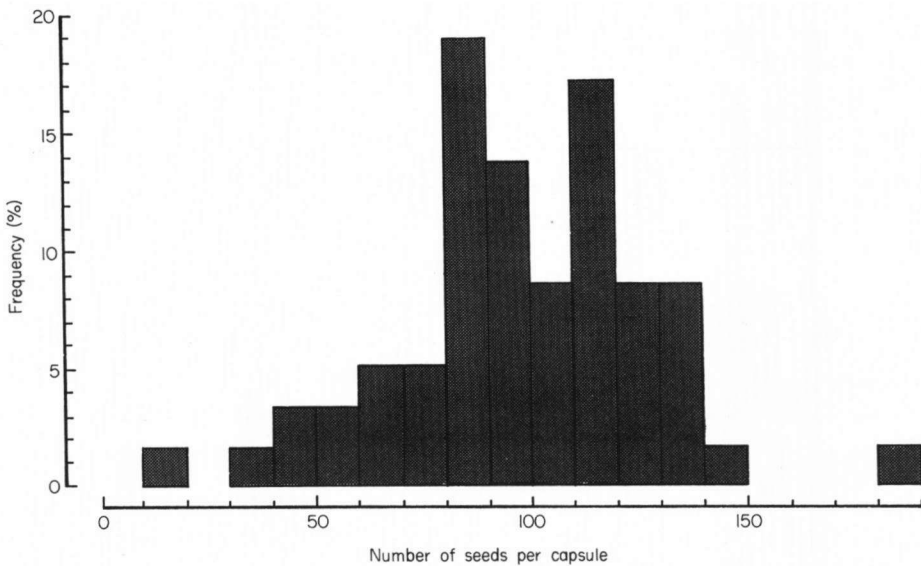
The number of seeds produced per capsule varied more than 30-fold from 6 to 196 (average 94.4, Fig. 5). Such great variability certainly reflects the influence of several factors determining the reproductive success, such as positional effects, compatibility variation among the plants (leading to differential efficiency in the pollination and fertilizing procedures) and chance events. The seed body length and the seed number per capsule both decreased with increasing height in the inflorescence (Table 3). The number of seeds per capsule did not differ between capsules containing heteromorphic seeds or exclusively winged or unwinged seeds ( $F_{2,583} = 0.595$ ,  $P > 0.05$ ). In the greenhouse experiment the seed production was invariant among the vegetation density categories ( $F_{2,583} = 0.456$ ,  $P > 0.05$ ) and along the elevational gradient ( $F_{1,584} = 0.00804$ ,  $P > 0.05$ ,



**Table 2.** The variation in seed body length and seed length including seed wings in *S. media*, in a gradient of increasing vegetation density. The plants were grown in a greenhouse and were reared from seeds present in soil cores collected in correspondence with the distribution of sparse, intermediate or dense vegetation-cover in the field

Vegetation density	Seed body length (mm)	Seed length (mm)
Sparse	0.89	1.06
Intermediate	0.88	1.20
Dense	0.89	1.28
	$F_{2,555} = 1.97 \dagger$	$F_{2,555} = 12.6$ $P < 0.001$

†Not significant.



**Fig. 5.** The distribution of the number of seeds per capsule in *S. media*. The plants were grown in a greenhouse.

$r = 0.0371$ ), but in the field-collections the dense capsules contained more seeds than did the sparse and intermediate capsules ( $F_{2,293} = 15.0$ ,  $P < 0.001$ ). The seed body length increased as the start of flowering was postponed (Table 4). The full regression of seed number per capsule on seed body length, vegetation density in the soil cores and the node where the first flower was produced, showed an inverse relationship between the first two variables only (Table 4).

Finally, turning to the onset of the reproduction, the flowering was initiated between node numbers 7 and 31, with an average at 12.7 (Fig. 6). Plants producing winged, unwinged or dimorphic seeds did not differ in this respect ( $F_{2,594} = 2.37$ ,  $P > 0.05$ ).

**Table 3.** Regression of seed body length and number of seeds per capsule respectively, on the relative position on the inflorescence in *S. media*. The plants were grown in a greenhouse and were reared from seeds present in soil cores collected in correspondence with the distribution of sparse, intermediate or dense vegetation-cover in the field

Independent variable	Relative position in the inflorescence (1-5)	
	Seed-body length	Number of seeds/capsule
<i>k</i>	-3.45	-9.85
<i>F</i> -ratio	$F_{1,556} = 11.9$	$F_{1,584} = 24.3$
<i>P</i>	<0.001	<0.001
<i>r</i>	0.145	0.200

**Table 4.** Multiple regression of seed body length, number of seeds per capsule, first flowering node and vegetation density in *S. media*. The plants were grown in a greenhouse and were reared from seeds present in soil cores collected in correspondence with the distribution of sparse, intermediate or dense vegetation in the field

Dependent variable	Independent variable	<i>k</i>	<i>t</i>	<i>P</i>
Number of seeds per capsule	Seed body length	-113	4.60	<0.001
	Vegetation density	0.141	0.556	>0.05
	First flowering node	-0.201	0.0592	>0.05
Seed body length	Vegetation density	0.00707	1.76	>0.05
	First flowering node	0.00212	3.50	<0.001
First flowering node	Vegetation density	-0.510	1.82	>0.05

## DISCUSSION

The size of the seeds of *S. media* shows substantial variation and the width of the seed wing is weakly positively related to the length of the seed body. The latter aspect is not controversial *per se*. As pointed out by Willson *et al.* (1990) 'If selection favors maximal dispersal distances, large wind-dispersed seeds might be expected to have larger dispersal devices than small seeds in the same seed-crop'. Formerly Telenius & Torstensson (1989) have demonstrated a stronger positive relationship between the seed size and the wing width in *S. marina*, and that when dispersed by wind, the occurrence of a seed wing actually helps the heavier seeds to at least attain the same dispersal distance as the lighter, unwinged seeds. Instead it is rather the weak correlation that needs explaining. Such an explanation cannot be given at ease and whether it lends itself to an adaptive interpretation is uncertain at the moment.

Some aspects on the variation in seed size are perhaps more difficult to understand than it appears at first sight. First, even the sheer existence of this magnitude of variation

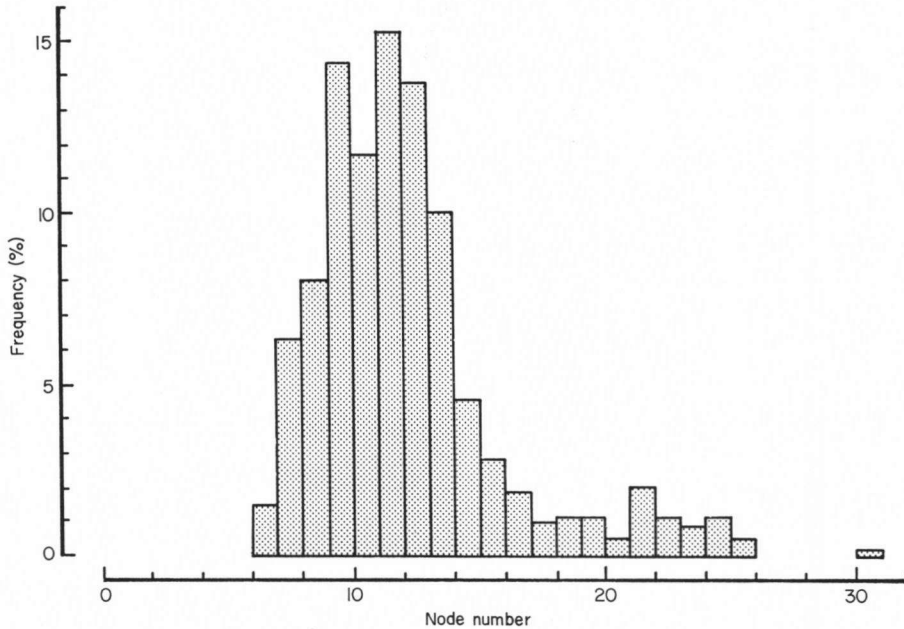


Fig. 6. The distribution of the time of first flowering in *S. media*, counted as the node where the first flower appeared. The plants were grown in a greenhouse.

may cause some worry but referring to a number of recent studies Silvertown (1989) questioned that seed size is under stabilizing selection, saying that many wild plants show marked phenotypic plasticity and low heritability of seed size. He argued that the traditionally expected 'constancy of mean seed size may be due to developmental canalization, of which selection is the ultimate but not the immediate cause'. In other words, in data that is collected in nature, seed size variation should not surprise anyone. However, in the circumstance of the equable conditions in the greenhouse met with here might be of heritable origin. Secondly, in spite of the comparatively large variation in seed body length (indicating the possibility of a differentiation in the size of the winged and the unwinged seeds as shown by Telenius & Torstensson 1991, where the presence of seed wings in the entire genus *Spergularia* was linked with large seed size) there is an almost complete overlap in regard to the seed size between the seed types in this investigation: there exist both large and small seeds with or without a seed wing. In *S. marina* the average size of the body of the winged seeds was considerably larger than that of the unwinged seeds and the overlap much less (Telenius & Torstensson 1989). However, Sterk (1969) gave evidence of such a difference in size between the two types of seeds even in *S. media* and, in making a broad comparison of seed sizes in relation to the occurrence of seed wings in the genus *Spergularia* Telenius & Torstensson (1991 and unpublished observations) also found considerably larger winged than unwinged seeds in this species. Here the average length of the seed body of the unwinged seeds was 0.78 mm (SD=0.06;  $n=59$ ) and the winged seeds were almost 9% larger (0.85 mm; SD=0.06;  $n=75$ ). Yet this difference is still less than in *S. marina*. Besides, neither body size nor wing width was correlated in this sample. Again the major difference amongst the seed measurements in these four cases is that in the earlier three (Sterk 1969, Telenius &

Torstensson 1989, 1991) the seeds were collected in the field whereas in the present investigation they were taken from plants that lived for their entire lives in a greenhouse under optimal conditions as regards the temperature regime, the availability of water and nutrients, and complete lack of herbivory. When grown under similar circumstances in the greenhouse *S. marina* shows a very small overlap in size between its winged and its unwinged seeds. Sterk & Dijkhuizen (1972) estimated the degree of outbreeding in *S. media* to be 8–15% in nature, in the greenhouse each shoot was provided with a nylon envelope that almost completely eliminated the possibility of cross-pollination. Apart from any anomalies due to the source of the seeds collected, in my opinion the most reasonable explanation for the greater overlap in seed size between winged and unwinged seeds in *S. media* is that the presence or absence of seed wings is selected *per se* and in front of seed body size.

The assumption that each genotype is adequately represented by one examined seed capsule is implicit in the investigation of the spatial distribution of the seed types. Intra-individual variation must not be ignored, but in the majority of the individuals where more than one capsule was examined the contents was remarkably similar in both size and presence or absence of seed wings within and between the branches. The meaning of this is that the initial assertion is probably acceptable but one must be cautious when alleging that one individual is 100% winged or unwinged and restrict the purport of the assertion to saying that almost all seeds are of the same kind, but that a few of the opposite type may also be present. Thereby all plants should in theory be classified as heteromorphic although the situation with 50% of each seed type is very rare. Results regarding *S. marina* (P. Tortensson, pers. comm.) speak of the same situation in that species in spite of its greater variation in seed body size between winged and unwinged seeds.

Far from being mutually exclusive the frequency of plants producing winged or unwinged seeds shifted between the open areas and those with a dense cover of vegetation. As the dominance of either winged or unwinged genotypes in their respective, most-favoured habitats is restricted to *c.* around 50% in the material collected in the field, and *c.* 40% in the greenhouse material, the selective forces cannot be particularly strong for either type of seed along the gradient. Besides, '... if the selection coefficients of the various genotypes present in the population differ appreciably ... , which happens especially where the environment is changing, even a relatively low rate of natural outbreeding (below 10%) may result in a high incidence of heterozygosity' (Sterk & Dijkhuizen 1972). The admittedly heteromorphic portion of the genotypes is nearly one-third in all categories of vegetation density. There is a marked difference between the field and the greenhouse material as to the proportion of seed capsules that are really heteromorphic. The greater share of such capsules in the field material may be due to environmentally induced plasticity in size, but it may also reflect the significance of recombination through cross-pollination to the maintenance of the heteromorphic condition. A third reason for this divergence could be that the 2 years that lapsed between the collection of the data sets conceal a change in the frequency of the genotypes in the field due to climatical fluctuations or chance. Also in the soil samples all seedlings were taken care of and although some seeds might have failed to germinate, certainly no seedling mortality occurred (which could have been biased towards either kind of seed type).

The seed heteromorphism of *S. media* has been explained by reference to both increased demographic variability (Sterk 1969) and dispersal (Willson 1983). Neither of these explanations can be entirely refuted in the light of the result from this investigation. After all, a seed size variation as the one shown should confer differential survival probability to

the seedlings, that is useful under temporally and spatially fluctuating conditions of germination and growth. Furthermore, although in the greenhouse plants the two seed types do not differ as to the number of seeds produced per capsule (which is due to the great overlap in size between the two types), keeping in mind the inverse relation between seed size and seeds per capsule and that in nature the winged seeds are actually larger than the unwinged ones, a demographic trade-off may be envisioned which should contribute to the preservation of the heteromorphism.

On the other hand, adding to the above discussion of wind dispersal, the importance of secondary dispersal by water of the seeds of the salt-marsh species *S. media* must not be overlooked. When dispersed by water (and in the presence of vegetation) increased seed diameter might act as a hindrance to the loss of seeds into the sea or into the sediment (as shown for *S. marina* (Telenius & Torstensson 1989), contributing also to the complex pattern of seed dispersal in this species. Thus, heteromorphic seeds may be a useful tool in achieving a more even scatter of the seeds. Direct observation of the dispersal of the seeds of *S. media* under natural conditions is an intriguing exercise that would help to solve the question of the significance and the origin of seed wings and seed heteromorphism in the species and remains to be done.

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