CHROMOSOME NUMBER, MORPHOLOGY AND BREEDING BEHAVIOUR IN THE BRITISH SALICORNIAE

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ABSTRACT

Chromosome counts on British *Salicornia* confirm the presence of two series, diploids with $2n = 18$, and tetraploids with $2n = 36$. These two series differ in size of pollen, stomatal guard cells and seeds; and also in general morphology. An attempt is made to correlate these numbers with the taxa generally recognised as being present in the British flora.

The plants are self-compatible, and appear usually to be self-pollinated, though there is limited evidence for occasional anemophily and possible out-breeding. Infra-specific variation may be attributed to the presence of numerous virtually pure-breeding races perpetuated by autogamy.

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INTRODUCTION

The genus *Salicornia* has for many years been a source of trouble to systematists, and we may echo the words of Baxter (1839) : ' Botanists of the highest authority differ in opinion respecting the specific distinctions of the British Salicorniae.' This is especially unfortunate in view of the important role played by these plants in the ecology of saltmarshes and similar habitats. In order to achieve a satisfactory understanding of this group, one must take into account various aspects of the plants' general biology such as breeding behaviour and phenotypic plasticity, which until recently have been neglected or altogether ignored. The taxonomic problems presented by this genus cannot be solved by the study of herbarium material alone.

In the present paper attention is directed mainly to the relationship between morphology and chromosome number, together with a discussion of breeding behaviour. The significance of the variation patterns seen in field colonies, and the particular problems of growth habit and taxonomy, will be elaborated elsewhere.

MORPHOLOGY

Salicornia L., a genus of succulent halophytes belonging to the Chenopodiaceae, is represented in Britain by one perennial and several annual species, limited in distribution to coastal saltmarshes. Free leaves are absent, and the fleshy internodes (' segments ') have apparently been derived from the fusion of the decurrent leaf bases with the outer cortical tissues of the stem (de Fraine, 1913). Branching is regularly decussate, and in large plants

may be of the fourth order. When mature every branch ends in an inflorescence, referred to in this paper as a spike, though perhaps a more correct description would be a ' spike of three-flowered cymules.' Branches which are purely vegetative at maturity are confined to the perennial species.

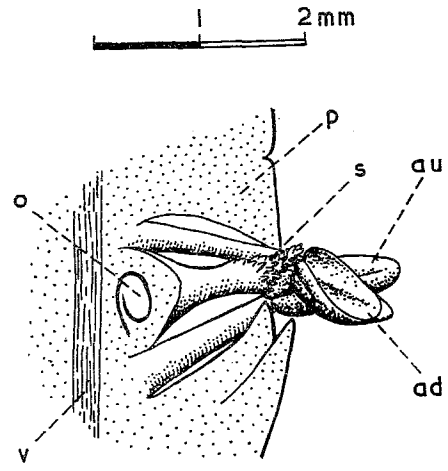

Fig. 1. Longitudinal section through *Salicornia* flower. ad–anther, dehisced, au–anther, unopened, o–ovule, p–perianth, s–stigma, v–vascular strand.

The flowers are much reduced morphologically (Fig. 1), the perianth consisting of three minute flaps and being immersed in the cortical tissues so that its upper surface is flush with that of the stem. Normally each flower contains two stamens, but sometimes only one is present. The solitary ovules (and also the mature seeds) lie transversely in the ovary, parallel to the main axis of the stem, and each with its micropylar end towards the funicle (Fig. 1).

Names used

There is no general agreement as to the number or status of the taxa occurring on our coasts. Illustrative of this variation in personal judgement are the differing treatments of the British species advanced by Tutin (1952,1959) and by Ball & Tutin (1959). Extreme views on the species concept in the genus are those of Wilmott (1939, and unpublished), and König (1960). For reference purposes some taxonomic system must be followed, so the names given by Dandy (1958) are being used in this paper as they conform more closely with the views of the present writer. These are :

Salicornia perennis Mill., Gard. Dict. ed. 8, no. 2 (1768).
S. dolichostachya Moss, New Phytol., **11,** 409 (1912).
S. europaea L., Sp. Pl., 3 (1753).
S. ramosissima Woods, in Henfrey, Bot. Gaz. **3**, 29.
S. pusilla Woods, in Henfrey, Bot. Gaz. **3**, 30 (1851).

Making allowance for the synonymy given by Dandy, these species are interpreted in the sense of Tutin (1952), where references may be found to the appropriate figures in Moss (1914). Ball & Tutin's new species, being published later, are not included by Dandy; reference will be made to these in a subsequent paper.

Chromosome Number

Of the published chromosome counts on European *Salicornia* known to me, those which can be assigned to particular segregates within the genus are included in Table 1.

TABLE 1.

Chromosome counts for European *Salicornia* species.

	Wulff 1936, 1937	Maude 1939	König 1939	Castro & Fontes 1946	Ludwig 1950	Hambler 1954	Ball & Tutin 1959	Dalby unpublished
S. perennis	—	18	—	18	—	18	—	18
S. pusilla	—	—	—	—	—	16?	18	18
S. ramosissima	—	—	18, 36	—	—	18	18	18, 36
S. europaea	38	—	—	18	18, 36	36	18, 36	36
S. dolichostachya	—	—	36	—	—	36	36	36

Some of the counts given above were recorded for taxa not recognised by Dandy (1958). Such taxa have been grouped as far as possible to conform with the species listed by Dandy.

This table shows clearly that there are two chromosome series present, one diploid with $2n = 18$, and the other tetraploid with $2n = 36$. No triploid hybrids have so far been recorded. There is considerable agreement as to the chromosome numbers for each taxon, apart from *S. ramosissima* and *S. europaea*, both of which appear to contain diploid and tetraploid races. It is clear, from other evidence, that these names are being used to cover a range of forms whose precise taxonomic status is open to debate.

With regard to the aneuploid numbers which have been published, Hambler (1954) was uncertain of his own count of $2n = 16$ for *S. pusilla*, and counts by other authors for this very distinct species give uniformly $2n = 18$. Wulff's (1936, 1937) figure of $2n = 38$ needs some comment. He writes (1937) ' Ich fand in zahlreichen Platten eindeutig $2n = 38$ Chromosomen, wodurch *S. herbacea* L. als polyploide, abgeleitete Form gekennzeichnet ist.' His conclusion as to polyploidy is certainly correct, but it is strange that he did not find any plates with $2n = 36$. No plate that I have examined has shown an aneuploid number, all examples where exact counts were possible proving to be euploid 18 or 36.

In the present study, chromosome counts were made from metaphase plates of mitotic divisions of root-tips,obtained from plants in the field and from seedlings in culture.

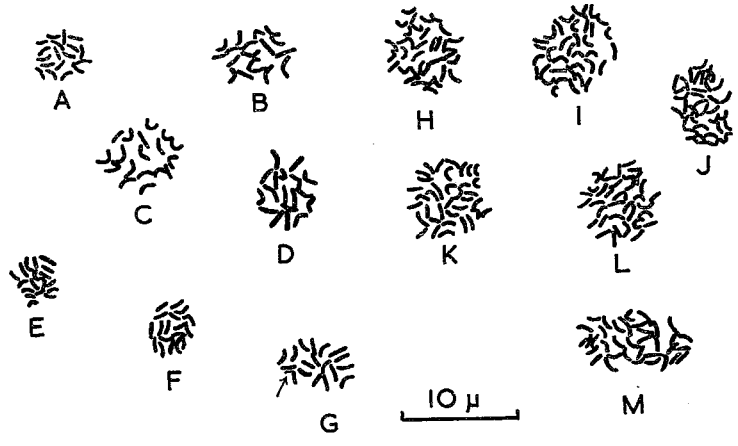

Fig. 2. Metaphase plates from root-tip sections. Diploids ($2n = 18$) A–C, *S. ramosissima*, Hayling Island, Hants (Nos. 68, 55, 69); D, E, *S. ramosissima*, Shingle Street, Suffolk (Nos. 12, 11); F, *S. ramosissima*, Flatford, Suffolk (*s.n.*); G, *S. pusilla*, Hayling Island, Hants (No. 52). Tetraploids ($2n = 36$). H, *S. europaea*, Blakeney Point, Norfolk (*s.n.*); I, *S. europaea*, Colne Point, Essex (No. 35); J, *S. dolichostachya*, Hayling Island, Hants (No. 71); K, *S. europaea*, Hayling Island, Hants (No. 54); L, *S. europaea*, Flatford, Suffolk (No. 19); M, *S. europaea*, Shingle Street, Suffolk (No. 14).

Langlet's modification of Navashin's fixative was used, this fluid also being used for storage until required. The stain used was gentian violet, which was usually taken up well by the chromosomes, and differentiation yielded very satisfactory plates. Some counts were made from acetic orcein squashes of fresh root-tips.

Some examples of metaphase plates are given in Fig. 2. After fixation the chromosomes are small and range from about 0·6 μ to 1·8 μ in length, with very little in the way of distinctive morphology to enable the recognition of homologous chromosomes or particular karyotypes. Nevertheless, diploid plates show sufficient variation in chromosome shape and size to suggest genetic heterogeneity within the scope of the species as recognised in the present study. In two plates at least from plant No. 52 (*S. pusilla*), one chromosome (arrowed in Fig. 2 G) was seen to bear a satellite.

Morphological Differences between Diploids and Tetraploids

It was thought that diploid and tetraploid plants within the genus might well show systematic differences in size or form of their parts, and that this could be used as a primary taxonomic division in the annual species. A range of specimens was therefore examined, including plants from all the species recognised by Dandy (1958). As mentioned above, no definite aneuploid counts were made, and in a few polyploids where clumping made precise counting difficult, they were regarded as having the expected number of $2n = 36$.

(*a*) *Pollen grains*

Pollen grains were taken from mature anthers, and mounted in acetocarmine, their diameters being drawn with a camera lucida at a magnification of × 800. The grains are almost spherical, and their volumes were assumed to be the volumes of spheres with similar diameters. It should be noted that measurements of volume are of greater value than say diameters or lengths, though slightly more difficult to obtain.

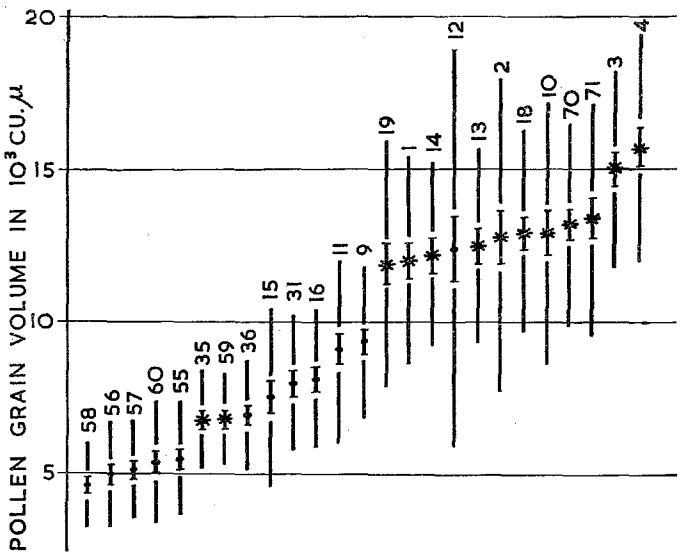

Fig. 3. Pollen grain size for 25 plants of known chromosome number.

Note. In Figs. 3 to 5, dots and asterisks mark the mean values for diploids and tetraploids respectively. The shorter bars above and below mark distances of ± 2 standard error of the mean (non-overlap indicates $p = < 0{\cdot}005$ for samples of similar size). The longer bars mark distances of ± 2 standard deviation, as an estimate of the range. This range will be exceeded by about 1 in 20 in a normal sample.

The data for pollen size are given in Fig. 3, where it is seen that in general the pollen grains are larger in the tetraploids than in the diploids, the change-over being at about $10{\cdot}5 \times 10^3$ cu. μ volume ($27{\cdot}2\ \mu$ diameter).

(*b*) *Stomatal guard cells*

The stomata are rather variable in size, even on a single plant, and vary considerably in frequency, being most numerous towards the tops of the fleshy internodes. They are arranged with their long axes at right angles to the line of the stem, a feature often found in xeromorphs and succulents.

Strips of epidermis were removed from living plants, and placed immediately in absolute alcohol. The length of each stoma was drawn with a camera lucida at a magnification of $\times$ 800, and the volume calculated as that of a sphere with diameter equal to the stoma length. These volumes will always bear a constant relationship to the actual stomatal volumes, provided the stomata are of constant shape. This was assumed to be so.

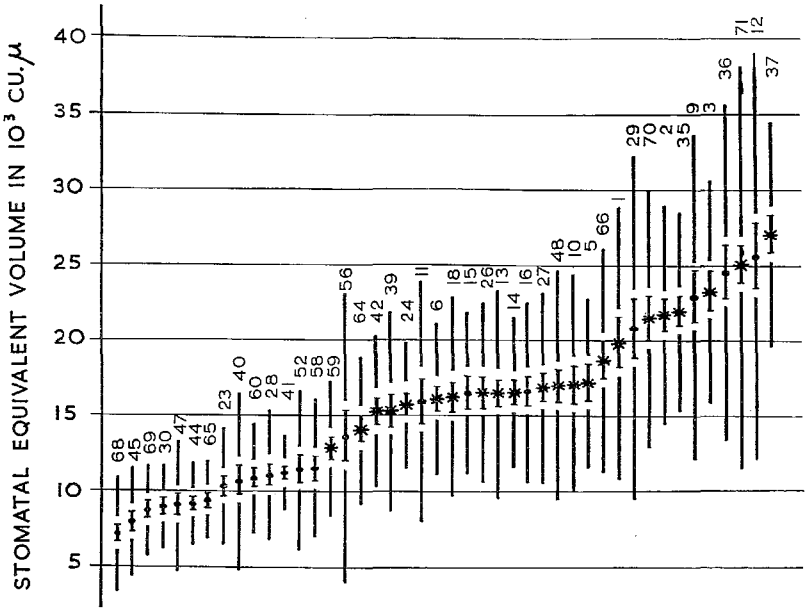

Fig. 4. Stomatal size for 44 plants of known chromosome number. See also note to Fig. 3.

The stomatal sizes are shown in Fig. 4, where, as might be expected, they are generally larger in the tetraploids than in the diploids, the change-over point between the two groups being at approximately 13×10^3 cu. μ for equivalent volume, and $29{\cdot}17\ \mu$ for length. There is however considerable overlap, part of which seems to be due to certain diploid plants having shown unusual vigour in their vegetative growth. These plants, referred to later in this paper, were selected in the field because of their noticeably robust growth and it was expected that they would prove to be polyploids related to, for example, the ' Typ. Nr. 3 ' of König (1939). These plants proved in reality always to be diploids. In this connection, it is interesting that out of four plants whose pollen size was compared with that of their F_1 progeny, the only one to show a significant change in size was one of these robust ' pseudopolyploids.' This was plant No. 11, and the significantly smaller F_1 pollen seemed correlated with poorer vegetative growth.

Clearly pollen size is more closely correlated with chromosome number than is stomatal size in *Salicornia*, but in neither case is the relationship sufficiently precise as to be used alone as a reliable indicator of chromosome number without actually making a count.

(c) *Seed size*

Seeds were taken from the central flowers of cymes on heads of plants of known chromosome number. The seeds from lateral flowers would have been equally satisfactory for this purpose, but seeds from central and lateral flowers should not be mixed, as within each cymule the central flower always has a larger seed than has either of the laterals.

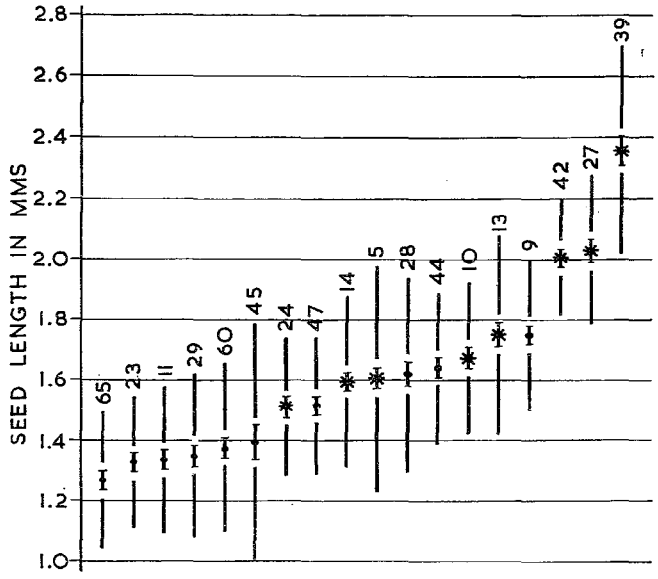

Fig. 5. Seed size for 18 plants of known chromosome number. See also note to Fig. 3.

Seed lengths are shown in Fig. 5, where it is seen that tetraploids have larger seeds than do the diploids, although there is considerable overlapping. The change-over size is at about 1·6 mm. length. Plants 28 and 9 were robust 'pseudopolyploids,' and once again the increase in size of a particular structure seems to follow vigorous vegetative growth in the rest of the plant. The largest tetraploid sample comes from plant 39, a natural mutant of *S. europaea*, in which the cymules are one-flowered. Here, in the absence of competition from the lateral flowers, the central seeds grew to an abnormally large size.

(d) *Ratio of numbers of fertile to sterile segments*

The ratio of numbers of fertile to sterile segments shows a break with very little overlap at about 55,* the data being given in Fig. 6. The ' pseudopolyploid ' plants referred to above are labelled 'A' in Figs. 6 and 7. They are all regarded as belonging to *S. ramosissima*,

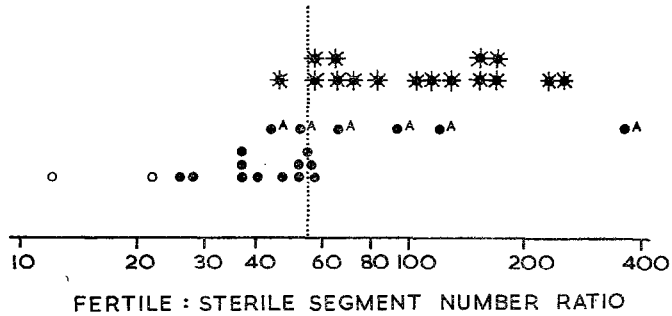

Fig. 6. Ratio of number of fertile to sterile segments for 36 plants of known chromosome number. Rings–diploids (*S. pusilla*), dots–diploids (other than *S. pusilla*), A–robust forms, asterisks–tetraploids. Note. The horizontal scale is plotted logarithmically.

* In this paper, all ratios are expressed as single figures, the second (always 100) being omitted for brevity.

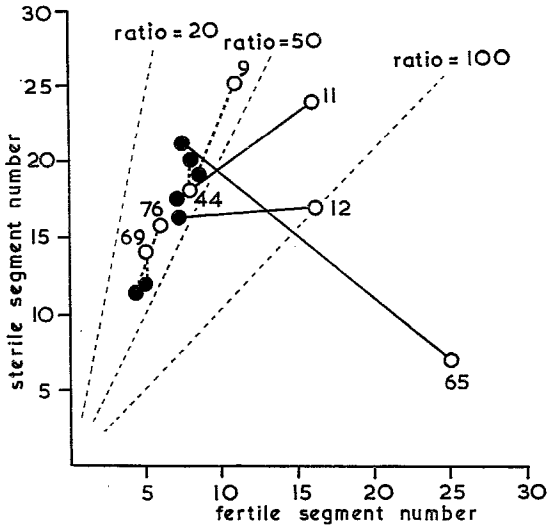

Fig. 7. Change in ratio of numbers of fertile to sterile segments in F_1 progeny in *S. ramosissima*. Open circles–parent plants; solid circles–mean values for F_1 progeny in culture. Lines connecting circles continuous if change is significant ($p = < 0{\cdot}005$), broken if not significant. Plants 9, 11, 12 and 65 were robust 'A' forms, the remainder being of normal size.

some evidence for this being given in Fig. 7, which shows the change in the segment number ratio between several parent plants and their progeny in cultivation. Clearly the 'A' plants lose their high values for the segment number ratio, and assume a constant one of between 40 and 50, typical of normal *S. ramosissima* in the field. One may reasonably assume that in normal circumstances of growth, there is little or no overlap between diploids and tetraploids in their segment number ratio.

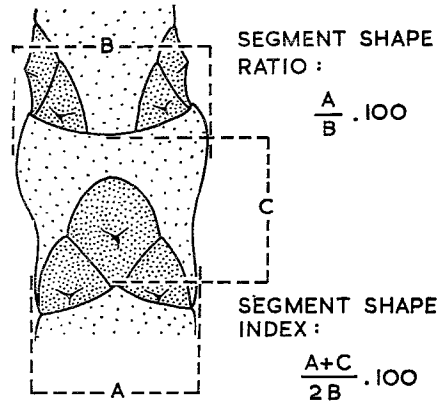

Fig. 8. Derivation of segment shape ratio and index. Means for 2 or 3 segments (central by distance along terminal spike of main axis) used in calculations, except for progeny and field colony samples where only one central segment was measured.

(e) *Segment shape index*

A segment shape index (see Fig. 8) also reveals differences between the two groups. The break is seen in Fig. 9 to be at about 65. Very few diploids overlap the tetraploid range, and those that do are in fact all 'A' plants.

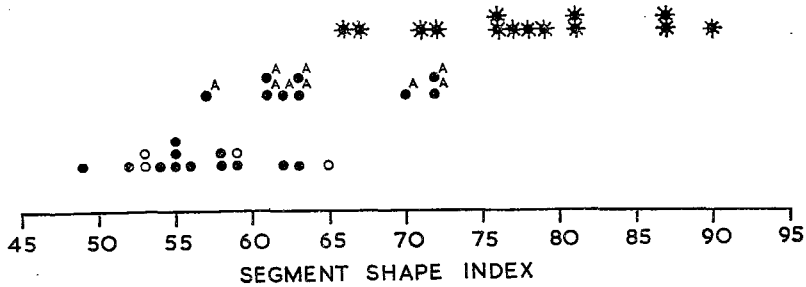

Fig. 9. Segment shape index for 39 plants of known chromosome number. For segment index see Fig. 8. Rings–diploids (*S. pusilla*), dots–diploids (other than *S. pusilla*), A–robust forms, asterisks–tetraploids.

(*f*) *Anthocyanin*

Anthocyanin occurs widely in the European species of *Salicornia*, and its varied distribution and intensity are responsible for their often brilliant autumnal coloration. The presence or absence of anthocyanin in 43 plants investigated is shown in Table 2.

TABLE 2

	Diploids	*Tetraploids*
Anthocyanin present	20	4
Anthocyanin absent	4	15

The correlation between chromosome number and presence or absence of anthocyanin is highly significant, though not absolute (testing for χ^2, $p = 0{\cdot}001$). Anthocyanin is almost restricted to the diploids, though it does occur rarely in tetraploids. Strictly however, it is the ability to produce anthocyanin in favourable circumstances that should be measured, rather than its actual appearance. Too much shading prevents the red pigment being developed, a feature sometimes encountered in prostrate forms which are green beneath yet bright red above.

(*g*) *General conclusions*

The results discussed above show that the two levels of chromosome number are quite distinct morphologically for several characters which can be measured with some precision. Other differences may also be noticed (some are listed by Ball & Tutin (1959) and König (1960)), and it is gratifying to observe the general agreement reached here. One striking difference however, is seen in Ball & Tutin's data for pollen size. They regard a pollen diameter of about 29·5 μ as marking the change from diploid to tetraploid, whereas the present writer would put it at 27·2 μ. Approximately half the tetraploids plotted in Fig. 3 come within Ball & Tutin's diploid range for mean grain size. Their data for stoma and seed size are however almost identical with those given in this paper.

The assigning of chromosome numbers to the different species of *Salicornia* is a difficult problem, and will not meet with the same general agreement as has been reached over the correlation between gross morphology and chromosome number. This is because of the instability of the systematic treatments of the genus referred to at the start of this paper. Thus although *S. pusilla* is definitely a diploid, and *S. dolichostachya* is definitely a tetraploid, both *S. ramosissima* and *S. europaea* appear to contain diploid and tetraploid forms. It is from this *S. ramosissima–europaea* complex that several new species have recently been separated, and doubtless others could too with equal justification.

It seems to me that it is in this *S. ramosissima–europaea* complex that we should seek a basic *Salicornia*-type from which the other forms have been derived. This is wholly opposed to Salisbury's (1940) views, where he believed *S. dolichostachya* to be a basic type, allied to *S. perennis*. In the first instance, *S. dolichostachya* is polyploid, and so cannot be regarded as ancestral to the diploid species. Secondly it is very close morphologically to some forms of *S. europaea*, and differs quite markedly from *S. perennis*. These differences are in fact so great as to have led Moss (1948) into transferring the latter species from *Salicornia* to *Arthrocnemum*.

Breeding Behaviour

Genera showing taxonomic difficulties often possess reproductive peculiarities, and as little is known of the reproductive methods in these plants, the remainder of this paper is devoted to the pollination and fertilisation of *Salicornia*.

(*a*) *Pollen fertility*

The fertility of pollen from a number of plants was determined by mounting fresh grains in acetocarmine; those which took up the stain deeply being considered fertile, whilst those which remained colourless or pale, and which were usually mis-shapen or shrunken, were regarded as being sterile. Data for pollen sterility are given in Table 3.

Table 3
Percentage sterility of *Salicornia* pollen.

$2n = 18$ (counted)		$2n = 18$ (inferred from morphology)	
Shingle Street	10·5	Colne Point	8·5*
	8·5	Hayling Island	15·0
	6·0		9·5
	5·5		6·8
	3·0		
Colne Point	1·5		
$2n = 36$ (counted)		$2n = 36$ (inferred from morphology)	
Blakeney	5·0	St. Mary's Bay	100·0**
	3·5		9·1***
	3·3***		1·5
	2·0		1·0
Shingle Street	5·0	Dovercourt	10·3***
	2·5		7·5
	0·0		5·0
Colne Point	82·0		3·0
Hayling Island	2·5		2·0
	1·5		

* – 100 grains examined.
** – 83 grains examined.
*** – c.150 grains examined.
At least 200 grains examined from each plant unless otherwise stated.

From these figures it is seen that normal plants show a fertility of between 90% and 100%, whether they are diploid or tetraploid. From this one may suppose that the tetraploids are, in general, allo- rather than autoploids. The markedly reduced fertility of some specimens indicates some genetic unbalance, possibly resulting from the hybridisation of related, but not identical, biotypes.

Pollen tubes were seen in abundance on gynoecia dissected out and mounted whole, although efforts to germinate pollen artificially met with no success. Fresh stained dissec-

tions have revealed pollen tubes within the stylar tissues, and sections have shown traces of what are probably pollen tubes at the entrance to the micropyle. Such serial sections of flowers cut at and soon after pollination have cast little light on the actual process of the presumed sexual fusion. The embryo sac appears to have eight nuclei, and the embryo develops normally from the micropylar end. An endosperm is formed, though scanty in amount, as is correctly recorded by Volkens (1893), though overlooked by Moss (1914) and Tutin (1952).

(*b*) *Pollination*

Knuth (1909) quotes Schulz as saying that the flowers of *Salicornia* are feebly protogynous, but possess persistent stigmas so that in consequence of the proximity of the anthers automatic self-pollination is easily possible. Moss (1912) says 'The species of *Salicornia* are wind-pollinated; and hybrids are often abundant when allied species grow together.' Ball & Tutin (1959) describe a species *S. obscura* with 'usually cleistogamous flowers.'

My own observations suggest that it is very likely that many of the annual forms are self-pollinated in nature, as ripe dehiscing anthers may be seen in contact with presumably receptive stigmas, and their pollen spilling on to the stigmatic papillae (see Fig. 1).

Usually it seems that *Salicornia* is weakly protogynous, and sometimes it may be markedly so (as for example *S. perennis*). Often, however, stigmas and anthers appear simultaneously, and even when protogynous, pollen from earlier flowers on one part of a plant may be transferred to stigmas on later flowers on another part of the same plant.

The possibility of wind-pollination sometimes happening must therefore be considered, though without an experiment using distinctive marker-genes, it may not be possible to prove. The experiment described below was carried out at Blakeney Point, Norfolk, to help in assessing the possibility of anemophily in *Salicornia*.

Blakeney Point was selected because there is, on the '*Pelvetia* Marsh,' a great expanse of almost pure *Salicornia* which comes to an abrupt stop on the northern edge of the marsh against sand-dunes, where the vegetation is almost solely *Ammophila arenaria*. On the southern side of the marsh there is about ½ to ¾ mile of bare mud or water, and then more saltmarsh with much *Salicornia*.

A day was selected when the wind was blowing steadily from the south, and *Salicornia* on the marsh was shedding its pollen. Microscope slides coated thinly with gelatin contain-

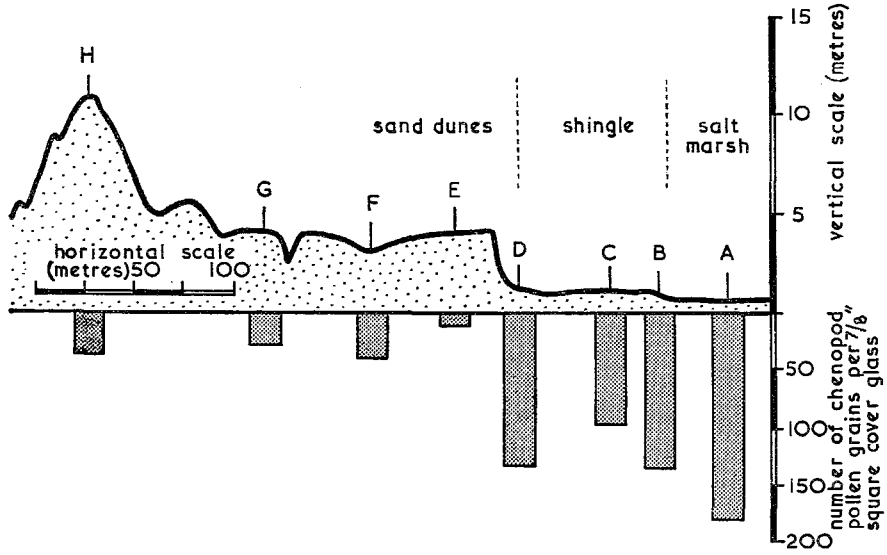

Fig. 10. Wind dispersion of pollen along transect from saltmarsh to sand dunes, Blakeney, Norfolk. The lines marking the sampling points A to H are not drawn to scale vertically.

ing a little acetocarmine were exposed vertically at about one foot above the ground at intervals along a transect running from saltmarsh to dune-crest (see Fig. 10). After 12 hours, the slides were taken indoors, coverslips placed in position and the slides warmed gently to melt the gelatin. The catch for total Chenopodiaceae-pollen is shown below each sampling point in Fig. 10. The catch at D is rather larger than might have been expected, probably because the freshening wind raised grains which had come to rest on the shingle (the slide was covered with wind-blown sand). In contrast, the catch at E is smaller than to be expected, as the wind was deflected clear of this sampling site on rising from the blow-out.

This experiment certainly proves that pollen of Chenopodiaceae is carried by the wind, and knowing that *Salicornia* was by far the most numerous genus at anthesis on the marsh, we may well assume that the majority of this wind-blown pollen did in fact come from that genus. It should be mentioned that related genera in the Chenopodiaceae have very similar pollen grains, differing only very slightly in size and sculpturing of the exine.

(*c*) *Self-compatibility*

The compatibility relationships of several plants were examined by considering specimens gathered from different saltmarshes before the flowers had opened. The flowering branches were washed carefully to remove any grains that might be adhering, and the selected spikes were enclosed in small polythene bags tied loosely over cotton-wool plugs. Other branches were left as controls. When the control branches had set seed, the 'bagged' branches were dissected, and the number of seeds set counted. In all instances counts were restricted to the central flowers of the cymules. The results are set out in Table 4.

TABLE 4.

Effect of 'bagging' on setting of seed in *Salicornia*.

	Control		*Experimental*	
	Maximum potential seed number	*Number actually set*	*Maximum potential seed number*	*Number actually set*
S. ramosissima				
Hayling Island				
a	—	—	21	17
b	—	—	22	18
Shingle Street				
c	5	2	12	7
d	13	8	18	10
e	16	11	26	12
S. europaea				
Pagham				
f	22	15	26	15
g	33	31	28	23
h	21	17	30	21
S. dolichostachya				
Blakeney				
i	10	10	23	18
j	—	—	28	13

It will be seen that 'bagging' has caused a slight but significant reduction in the quantity of seed set ($\chi^2 = 5{\cdot}93$; $0{\cdot}025 > p > 0{\cdot}01$). Assuming reproduction to be sexual, it is clear from the substantial quantity of seeds set that the plants used in the experiment were self-compatible. A further conclusion is that the physical effects of the 'bagging' (eli-

mination of air currents near the anthers) have reduced the chances of pollination taking place. Thus though these plants are self-compatible, we may assume that in nature some pollen transfer takes place from flower to flower, and possibly from plant to plant.

(*d*) *Apomixis*

There still remains the possibility that some species of *Salicornia* may be apomictic, which might explain their taxonomically critical nature.

Plants of *S. europaea* from Pagham, Sussex, were used in a simple experiment in which the stigmas were removed from 17 protogynous flowers by making a cut parallel to the segment surface. 16 of the experimental flowers failed to set seed during a period when uncut control flowers did so. The single seed set may have been due to pollination having taken place before the experiment began.

This evidence, though scanty, is against autonomous apomixis in *S. europaea*, but would not of course indicate the absence of pseudogamous apomixis. The evidence in favour of sexual reproduction is, however, strong, though not yet conclusive.

(*e*) *General conclusions*

The main significance of the work described above lies in its bearing on specific variation limits in the genus. Hybrids may sometimes occur, although as far as the writer knows there have not yet been any proven records of hybridity in this genus. Hybridisation could certainly be a physical possibility, as *Salicornia* pollen may be carried in considerable quantities for short distances by the wind. The reduced pollen fertility sometimes encountered is evidence for crossing, possibly between related, but not identical, biotypes.

Reproduction is considered to be sexual, whilst the preponderance of self-fertilisation would be expected to produce more or less pure-breeding lines which could be regarded taxonomically as microspecies. Segregates from the occasional crosses between different lines could then act as the sources of new lines. This pattern of variation is wholly in keeping with the views expressed by Stebbins (1958) in considering the advantages to an annual species following self-fertilisation.

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