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A Biosystematic and Ecological Study of *Salicornia* in the Dee Estuary

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ABSTRACT

Populations of *Salicornia* in the salt marshes of the Dee Estuary (Cheshire, England) are composed of *Salicornia europaea* L. ($2n = 18$) and *S. dolichostachya* Moss ($2n = 36$) growing intermingled. It is shown that nearly all individuals can be identified by means of a number of morphological features, but anther-size is the most reliable character. *S. dolichostachya* was the commoner species in the most open habitats. It was found that the radicle of seedlings of *S. dolichostachya* elongated more rapidly than that of *S. europaea* and it is suggested that this may to some extent explain the greater frequency of *S. dolichostachya* in the open habitats. *S. europaea* was more frequent than *S. dolichostachya* in areas where there was a relatively high cover of *Puccinellia maritima* (Huds.) Parl. and *Spartina* '*townsendii*', and it was found that many individuals of *S. dolichostachya* died without producing seed in these areas. It would seem that *S. europaea* is better able to withstand competition from perennial grasses than is *S. dolichostachya.*

INTRODUCTION

The genus *Salicornia* has always presented considerable taxonomic difficulty and, despite extensive investigations in a number of European countries in recent years, there is no general agreement as to the number of species which occur in Europe. Whilst it is usually possible to recognise a number of taxa in a given locality, difficulties often arise when attempts are made to correlate the taxa from different localities. Because of these taxonomic difficulties most ecological data have been recorded under the generic name only, or under a collective specific name. In those cases where attempts were made to be more precise, the information is of rather uncertain value as the criteria used in the past to recognise species have been shown to be very unsatisfactory (Ball & Tutin 1959, Ball 1960). The observations presented here are an attempt to combine a morphological study with a preliminary autecological investigation. Because of the necessity to examine each individual with some care, the quantity of material used was relatively small. This was partly due to the time needed to record the data, and partly to a desire not to deplete the numbers of *Salicornia* plants in the areas investigated, since each sample examined had to be removed from the marsh.

LIFE HISTORY

The life-history of *Salicornia* is very similar to that of many other annual Chenopodiaceae. Seeds usually germinate in April or May and the plants grow vegetatively until July or August, when fertile segments are produced, and flowering commences soon after this (see Ball & Tutin (1959) for a detailed morphological description). By the end of August to mid-September the plants have ceased to grow and they have usually completed flowering by the end of September, although a few flowers can often be found until well into October. Seed reaches maturity from about mid-September onwards when the plants begin to die. Seed is usually shed by falling out of the dead or dying parent plant, but it is not unusual to find that the seeds have not been shed and have germinated *in situ* the following spring, by which time the parent has often fallen over and been buried.

MORPHOLOGICAL INVESTIGATIONS

The salt marshes of the Dee estuary in Cheshire are of recent origin and are still expanding rapidly. The area that has been examined in some detail is that between Parkgate and Neston (Grid ref. SJ 2777). This marsh is known to have developed since about 1930 and it now extends for up to 1 km beyond the seawall. *Salicornia* occurs mainly towards the lower edge of the marsh and in many places is colonizing open sand or muddy sand. A small number of plants were examined in 1955 and the population has been examined each year since then by one of us (P.W.B.). This population is composed of two species, identified as *S. europaea* L. ($2n = 18$) and *S. dolichostachya* Moss ($2n = 36$) by Ball & Tutin (1959). Table 1 summarizes the morphological differences between the two species, and it can be seen from this that no single character apart from the chromosome number gives an absolute distinction between them. The chromosome numbers were determined on a small number of plants collected in 1955 and 1956, and in 1957 a large sample was collected in order to obtain further information about the variation that occurred. Figure 1 illustrates some of the results obtained from this sample. The two characters selected—the number of fertile segments in the terminal spike and the ratio 'maximum width of the fertile segment/width at the base of the fertile segment'—give a clear division into two taxa. The ratio chosen corresponds approximately to the fertile segment shapes used in the 1966 study (Fig. 2). Plants with a ratio of 1·17 or

TABLE 1. COMPARISON OF *SALICORNIA EUROPAEA* AND *S. DOLICHOSTACHYA* (AFTER BALL & TUTIN 1959).

Character	*S. europaea*	*S. dolichostachya*
Colour	Often red or purple	Green or yellow, rarely reddish
Angle between main stem and base of uppermost branches	c. 45°, branches straight	45–90°, branches curving upwards
Terminal spike	(2–)5–9(–16) fertile segments	(7–)12–25(–30) fertile segments
Fertile segments		
Length	(2·2–)2·5–4(–5·5) mm	3–6 mm
Diameter at base	2–4·5 mm	3–6 mm
Maximum diameter	(2·5–)3·5–6 mm	3–6 mm
Shape	A, rarely B (Fig. 2)	C, rarely B (Fig. 2)
Central flower	1·7–2·5 × 1·7–2·5 mm	2·4–4·0 × 1·9–2·9 mm
Lateral flowers	1·6–2·0 × 1·3–1·8 mm	1·8–3·0 × 1·5–2·3 mm
Stamens	Usually 1, exserted or not, usually dehiscing before exsertion	1–2, always exserted, not dehiscing before exsertion
Anther size	0·3–0·5 mm	(0·5–)0·6–0·9 mm
Pollen grain diameter	(20–)24–28(–31) μm	(27–)31–34(–42) μm
Stomata (length of guard cells)	(20–)24–30(–33) μm	(27–)29–36(–42) μm
Seed size	1·0–1·7 mm	1·5–2·3 mm
Chromosome number	$n = 9$	$n = 18$

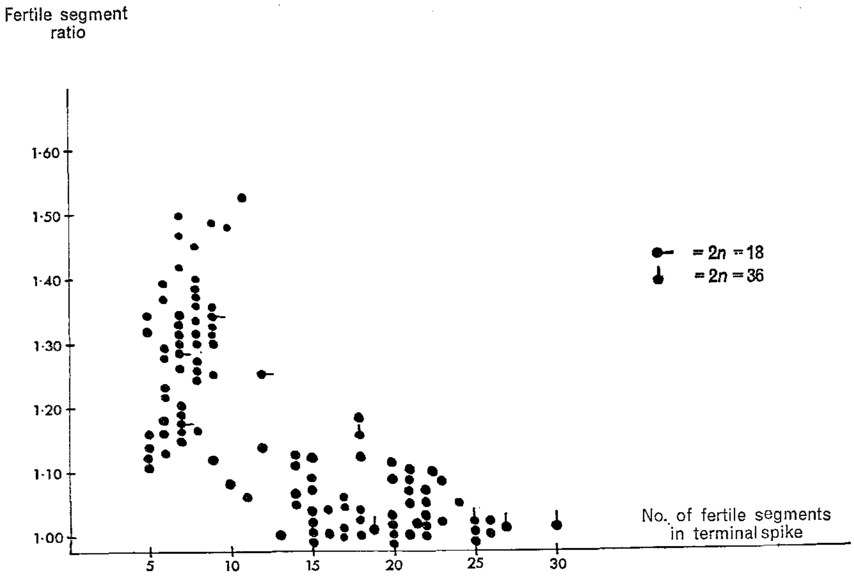


FIGURE 1. Scatter diagram of sample collected in 1957 and individuals of known chromosome number collected in 1955–6.

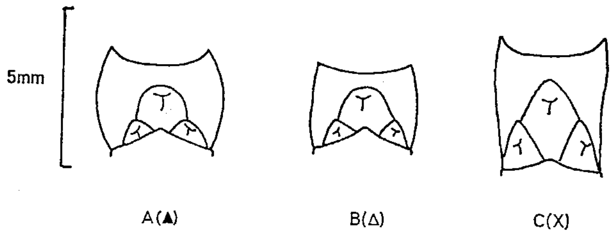


FIGURE 2. Fertile segment shapes used in the 1966 study.

more correspond to Shape A, those with a ratio of 1.12 or less correspond to Shape C, the intermediate ones being similar to Shape B. The plants whose chromosome numbers were determined in 1955 and 1956 have also been included on this diagram, and it can be seen that the difference in chromosome number is correlated with the morphological separation. In the revision by Ball & Tutin (1959) it was emphasized that damaged and depauperate plants often presented considerable difficulties and they were excluded from these samples.

In 1966 it was decided to make a comparative ecological study of the two species. It was apparent from the previous investigations that they were growing side by side in the lower parts of the marsh although the proportions of each varied considerably from one habitat to another. If the results obtained were to have any validity then it would be necessary to identify all individuals in any condition. The first part of the 1966 investigation was therefore aimed at checking the reliability of a variety of characters that might be used to identify the individuals in this particular population. Two main areas (A and B) were selected for sampling and small samples were also taken from two others

(C and D). Area A was a low mound, about 140 metres in diameter, on the seaward side of the marsh. It was surrounded by broad shallow channels on all sides, these having *Puccinellia maritima—Spartina* marsh on the opposite bank on 3 sides and almost bare sand and mud on the fourth side. The vegetation on the central part of the mound comprised a dense sward of *Suaeda maritima*, with up to 2000 plants per sq. metre, and relatively few *Salicornia* plants. Around the perimeter was a more open community of *Salicornia* and *Suaeda maritima*. Area B was a transect taken from the lower edge of the marsh from bare sand through an open *Salicornia* community into a closed *Puccinellia maritima–Spartina* marsh. Area C was about half-way between the edge of the *Puccinellia maritima–Spartina* marsh and the mean high water level, whilst Area D was at about the maximum high water level with *Festuca rubra* as the dominant species. Areas C and D contained only *S. europaea*, so although they were of interest when examining the variation found in this species they were not used for the later comparative studies. For the detailed investigations a 2-metre quadrat in the middle of a transect through Area A was chosen and a sample of 50 plants taken. Another sample was taken from the perimeter of A, and others were obtained by means of random 0·5 metre quadrats. Similar samples were taken from Area B. Small collections were also made from Areas C and D. The previous studies of *Salicornia* in this locality had indicated that only a limited number of characters were likely to be of value in separating the two species so only the following data were recorded: (i) height of plant (ii) total number of branches, or total number of fertile segments (iii) number of fertile segments in the terminal spike (not recorded if damaged) (iv) length of the 2nd–4th fertile segments in the terminal or a major lateral spike (v) shape of the fertile segments (A, B or C, Fig. 2) (vi) anther length (when available) (vii) length of guard cells of stomata (epidermis taken from the sterile segment at the base of the terminal or a major lateral spike). Figures. 3–7 were prepared from this data.

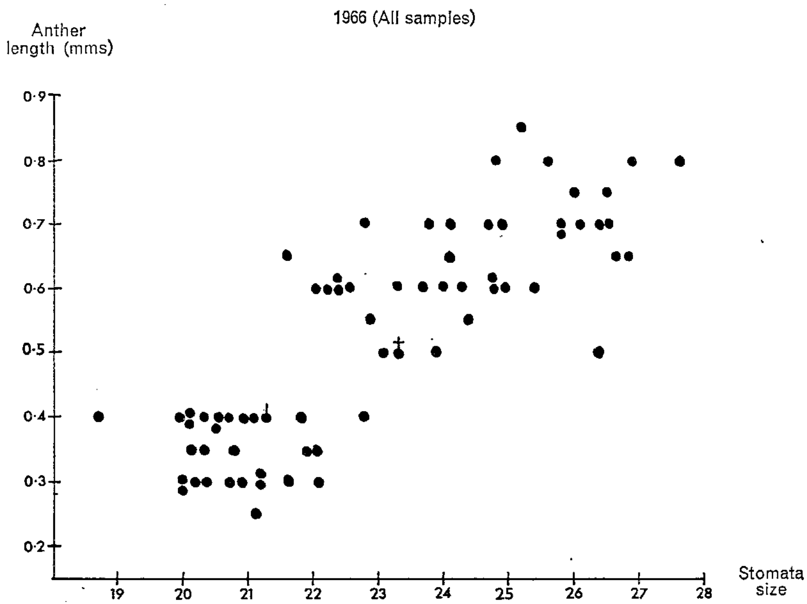


FIGURE 3. For legend see p. 31

FIGURES 3–7. Pictorial scatter diagrams of samples collected in 1966. Stoma size is measured in arbitrary units.

┼ = $2n = 36$ | = $2n = 18$

▲ = Fertile segment shape A (Fig. 2)

△ = Fertile segment shape B (Fig. 2)

× = Fertile segment shape C (Fig. 2)

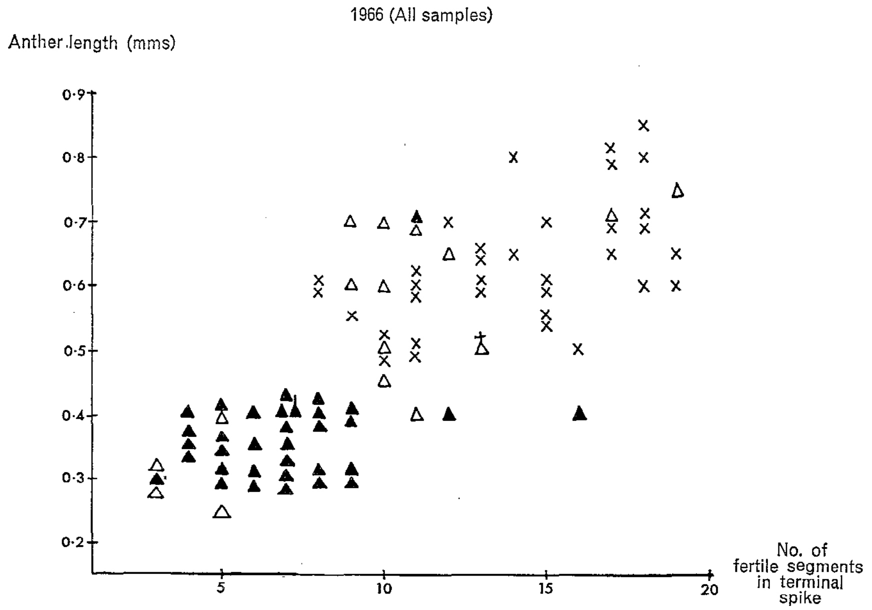
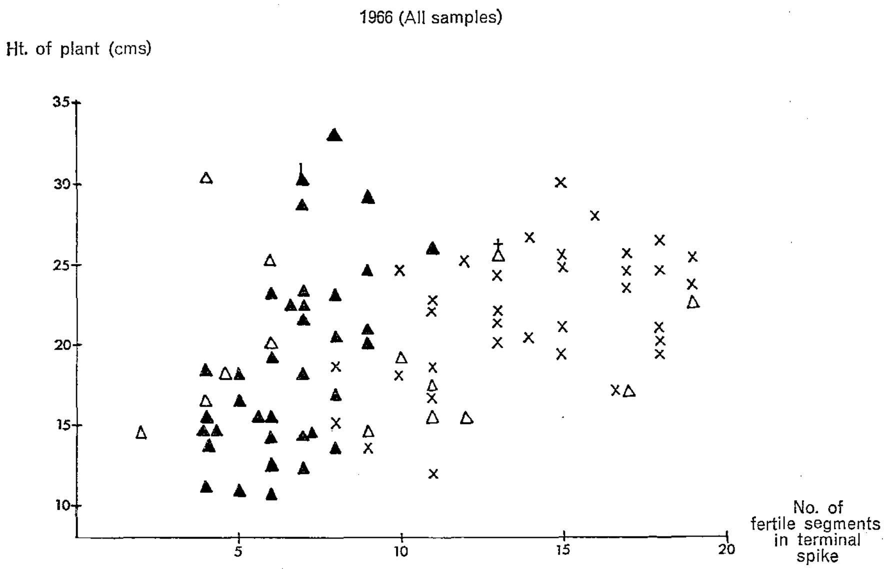


FIGURE 4. For legend see above



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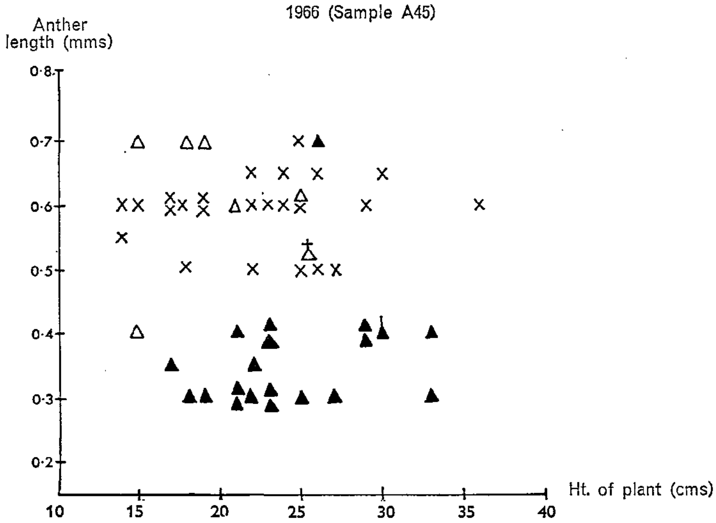

FIGURE 6. For legend see p. 31

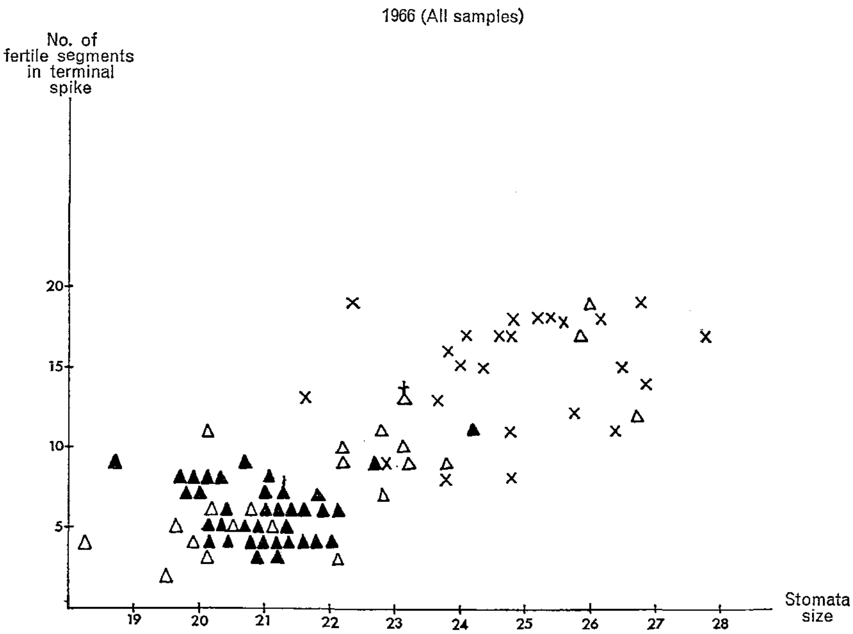

FIGURE 7. For legend see p. 31

It will be seen from these diagrams that the height of plant is not correlated with anther size or fertile segment shape, whilst anther size, stomatal size and fertile segment shape are all strongly positively correlated. There is a weaker positive correlation between these 3 characters and the number of fertile segments in the terminal spike. There is also some correlation between height of plant and the number of fertile segments in the terminal spike although the pattern of variation is different for each species.

Figures 4 and 7 confirm that, by means of a combination of fertile segment shape and the number of fertile segments in the terminal spike, it is possible to identify the majority of individuals in the field. Where any doubt arises this can almost always be resolved by anther length or stomatal size, or a combination of these two measurements. Where anthers were available it was found that the distinction was almost complete, *S. dolichostachya* having anthers (0·45–)0·5 mm. long or more, whereas *S. europaea* had anthers 0·4 mm long or less.

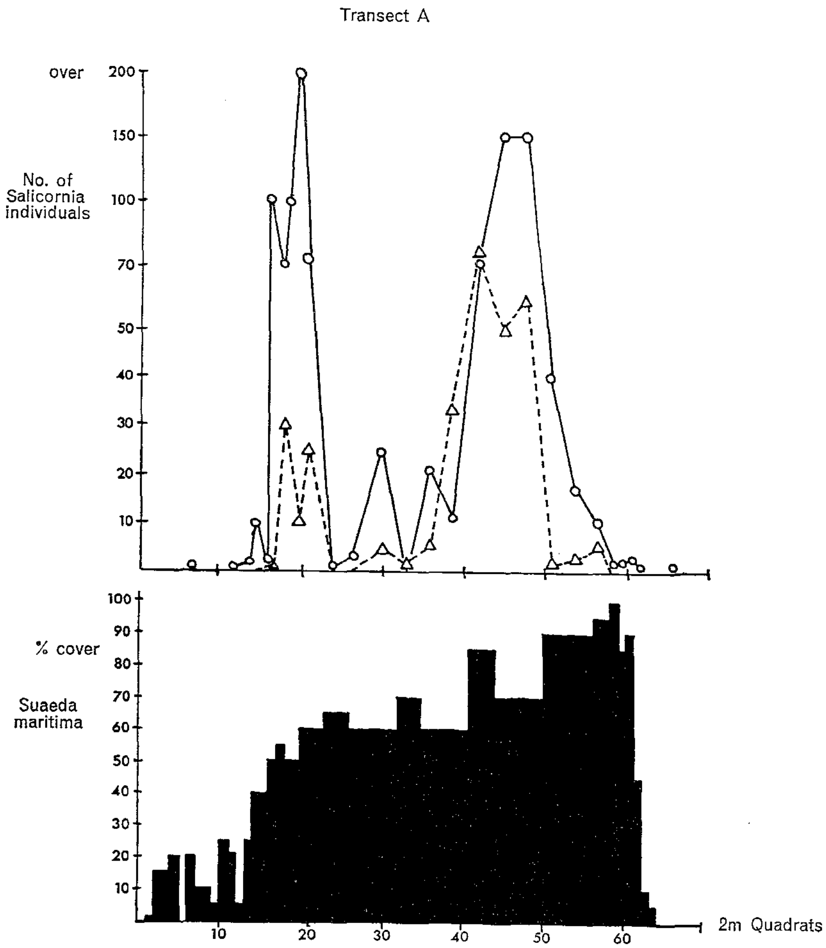

FIGURE 8. % cover of *Suaeda maritima* through Transect A and the frequency of *Salicornia dolichostachya* (O) and *S. europaea* (Δ).

Ecological investigations

Once it had been demonstrated that it was possible to identify the vast majority of individuals in this locality, an attempt was made to compare the detailed distribution of the two species in the areas studied, and to compare their performances in terms of dry weight and seed production. Transects 2 metres wide were taken through Areas A and B; that through A was 120 metres long, running roughly at right angles to the shoreline, and that through B was 22 metres long. (In A the first 21 2-metre quadrats were examined, but after this only every 3rd quadrat was examined; in B every quadrat but one was examined.) The percentage cover of each species was recorded, but for *Salicornia* the total number of individuals of each species was also noted. The results obtained are illustrated in Fig. 8.

In Area A, *Salicornia dolichostachya* occurred throughout. In the part of the transect with large areas of bare ground (quadrats 1–16, 62–end), this and *Suaeda maritima* were the only species present. The density of *Salicornia* and *Suaeda* increased in quadrats 17–21, *S. dolichostachya* still being the commonest species, but *S. europaea* appearing more frequently. In the central region (quadrats 36–48) *S. europaea* became more frequent, both in number of individuals and as a proportion of the total population of *Salicornia*. In those quadrats with very high (*c.* 90 per cent.) *Suaeda* cover the number of individuals of *Salicornia* was extremely low and they were often difficult to find.

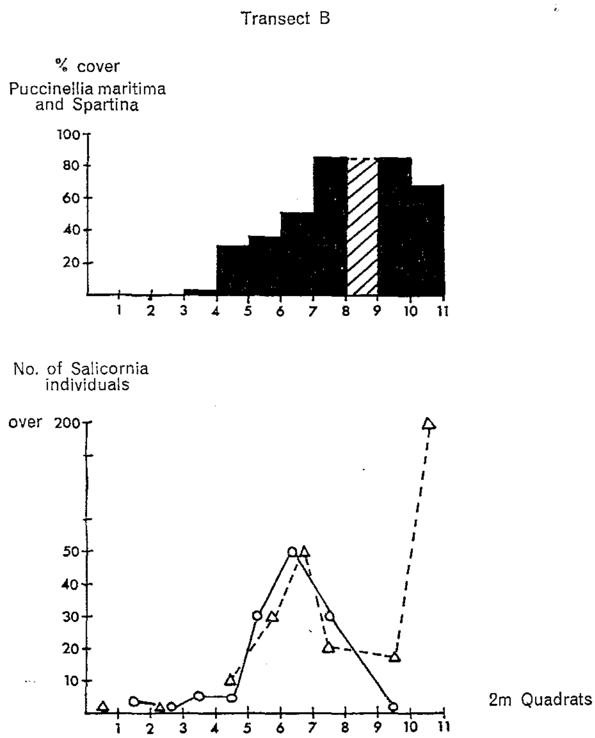

FIGURE 9. Combined % cover of *Puccinellia maritima* and *Spartina* through Transect B and the frequency of *Salicornia dolichostachya* (O) and *S. europaea* (Δ).

Whilst it is impossible to draw any definite conclusions from these data a number of points should be noted. Firstly, *S. dolichostachya* occurred in most parts of the areas sampled; secondly, *S. europaea* did not occur where there was less than 40% *Suaeda* cover; thirdly, the largest number of *Salicornia* individuals occurred in those areas where the *Suaeda* cover was between 40 and 70% (in only one case up to 85 per cent.); fourthly, with *Suaeda* cover in excess of 85%, *Salicornia* virtually disappeared.

Transect B gave a somewhat similar picture, but with some slight variations (Fig. 9). On the open sand and mud the number of individuals was extremely low, there being only 5 plants of *S. dolichostachya* and 2 of *S. europaea* in the first three 2-metre quadrats. A larger sample collected nearby for morphological examination comprised 20 individuals of *S. dolichostachya* and 4 of *S. europaea.* In the quadrats where *Puccinellia maritima* and *Spartina* first appeared, the number of *Salicornia* individuals increased considerably, but where the combined *Puccinellia-Spartina* cover exceeded 50 per cent. the number declined. *S. dolichostachya* showed a more rapid decline than *S. europaea,* and it was noticed that in mid-September many individuals of *S. dolichostachya* in quadrats 6–8 were in a very poor condition and appeared to be dying without producing seed. The last quadrat of this transect contained only *S. europaea.*

Areas C and D were isolated from the main populations of *Salicornia* and both contained only *S. europaea.* In both cases the area containing *Salicornia* did not greatly exceed one 2m quadrat so only the one could be examined in each. In Area C it was found that *Puccinellia maritima* was the dominant species with 80 per cent. cover; in Area D *Festuca rubra* was the dominant species with 75 per cent. cover.

The above information was obtained in mid-September when many *Salicornia* plants were still in flower and very few contained ripe seed. During October some attempt was made to investigate the variation in size and seed production of the two species in different parts of these habitats. Further samples were obtained by means of random 0·5-metre quadrats. All individuals were collected from each quadrat and an estimate of the seed production obtained by counting the total number of fertile segments (Tables 2 and 3). Previously it had been shown that

TABLE 2. VARIATION OF MEAN NO. OF FERTILE SEGMENTS PER *SALICORNIA* PLANT WITH % COVER OF *SUAEDA MARITIMA* IN AREA A.

% cover	Mean no. of fertile segments per plant	
Suaeda maritima	*S. europaea*	*S. dolichostachya*
10	676	967
15	640	118
20	—	394
45	176	83
50	37·5	55
50	40	49
70	58	53

there was no significant difference between the two species in the number of seeds in each fertile segment, the mean ranging from 2·8 to 3·8 seeds per segment. When these samples were taken it was found that all of the *S. dolichostachya* in areas with more than some 50 per cent. *Spartina-Puccinellia* cover had died,

TABLE 3. VARIATION OF MEAN NO. OF FERTILE SEGMENTS PER *SALICORNIA* PLANT WITH % COVER OF *PUCCINELLIA MARITIMA* AND *SPARTINA* IN AREAS B AND C AND WITH *FESTUCA RUBRA* IN AREA D.

% cover *Puccinellia maritima* and *Spartina*	Mean no. of fertile segments per plant *S. europaea*	*S. dolichostachya*
0	245	544
0	—	451
30	187	47
40	27	65
75 (*Festuca rubra*) (D)	53	—
80 (C)	52	—

and it seemed doubtful whether they had produced any seed. Thus, in contrast to *S. europaea*, under these conditions *S. dolichostachya* appeared to fail completely.

The difference in distribution of the two species of *Salicornia* raised a number of problems. On the open sand and mud the individuals of both species were extremely large and well-grown and produced a large quantity of seed. The observations by Wiehe (1935) in the Dovey estuary, Cardiganshire, indicated that in a habitat where only *Salicornia* occurs the density of the individuals was closely related to the frequency of submersion by the tide. This was related to the effect of movement and drag on seedlings and young plants, the critical period being 2–3 days undisturbed by tides. From the photographs published by Wiehe it appears that what is probably *S. dolichostachya* predominated in the area where there was frequent disturbance, while both *S. dolichostachya* and *S. europaea* (or another diploid species) occurred in the dense *Salicornia* community.

This suggested that germination rate and the initial rate of growth of the seedlings might explain the difference in frequency between *S. dolichostachya* and *S. europaea* on the open sand in the Dee estuary.

Germination experiments

Ten plants of each species were selected at random and stored in polythene bags at 2°C for a short period. The spikes were then broken up into small pieces and divided into six parts. These were given different treatments prior to germination as follows:

(a) Frozen for 7 days in a sealed container.
(b) Stored at 10°C for 7 days in a sealed container.
(c) Soaked in 100 ml of distilled water for 7 days at 10°C.
(d) Soaked in 100 ml of 50% filtered seawater (made up with distilled water) at 10°C for 7 days.
(e) Soaked in 100 ml of 100% filtered seawater at 10°C for 7 days.
(f) Seeds extracted from the segment, dried at 25°C and then kept at 10°C for 7 days in a sealed container.

After treatment 25 seeds were placed in vermiculite soaked in distilled water in petri dishes, there being four replicates of each. Daily records were kept of the number of seeds that had germinated. The results obtained are shown in Figure 10.

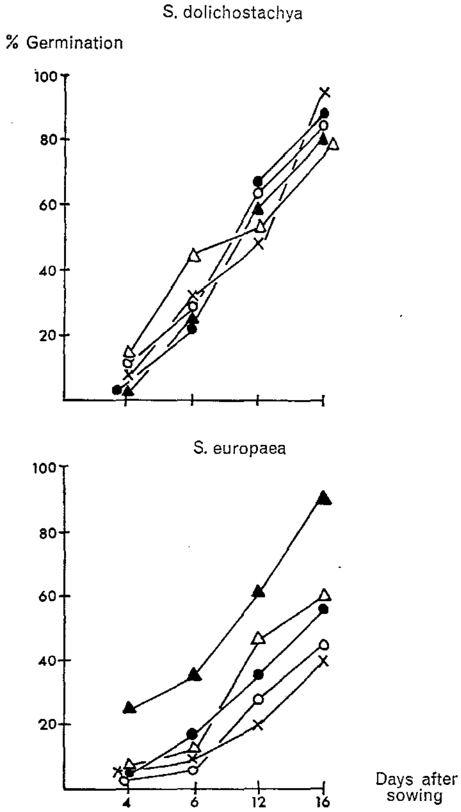

FIGURE 10. Germination of *Salicornia* seeds kept under various conditions.

× = Kept at 10°C (Treatments (b) and (c) combined)
● = Soaked in 100% seawater
Δ = Soaked in 50% seawater
▲ = Extracted and dried at 25°C
O = Frozen for 7 days

In general, the treatments do not affect the rate of germination or the total percentage germination of either species over a period of 16 days. The only exception to this was treatment (f) which with *S. europaea* gave a higher germination rate and a higher percentage total germination than was obtained for the other samples of *S. europaea*. A surprising feature of these results was the consistently lower rate of germination and the lower total germination of *S. europaea* as compared with *S. dolichostachya*, except for treatment (f) in which *S. europaea* was almost identical with *S. dolichostachya*. These experiments were performed in the late autumn of 1966 and it was too late to obtain further seed samples to check these results in the spring of 1967. Plants were therefore collected from Area A in the autumn of 1967 and stored in polythene bags at 2°C until the spring of 1968 before any further experiments were carried out. These experiments, which were primarily concerned with measuring the rate of growth of the newly germinated seedlings, gave much quicker and almost identical rates of germination (87 per cent. for *S. europaea* and 90 per cent. for *S. dolichostachya* after 4 days) for both species. The most likely explanation for the results obtained in the autumn of 1966 is that the 1966 seeds of *S. europaea* were not fully mature. It has been noted by a number of authors, e.g. Ball & Tutin (1959), that *S. dolichostachya* flowers slightly earlier than *S. europaea*, and it is likely therefore that the seeds of *S. dolichostachya* also mature earlier.

Growth of seedlings

A number of plants of both species were collected from Area A in October 1967 and stored in polythene bags at 2°C until the end of February 1968. By this time the fleshy parts of the plants had decayed so it was not possible to mix the broken spikes at random. As far as possible they were cut into pieces containing only one fertile segment and 10 pieces were placed in vermiculite soaked in distilled water in petri dishes. 6 replicates of each species were prepared, and they were placed in a heated greenhouse kept at about 21°C. To avoid confusion only one seedling from each segment was allowed to grow. The day on which a seed germinated was recorded and 4 days later the lengths of the plumule and radicle were recorded separately. The results obtained are shown in Fig. 11. Whilst there is a small difference in the mean length of the plumule of

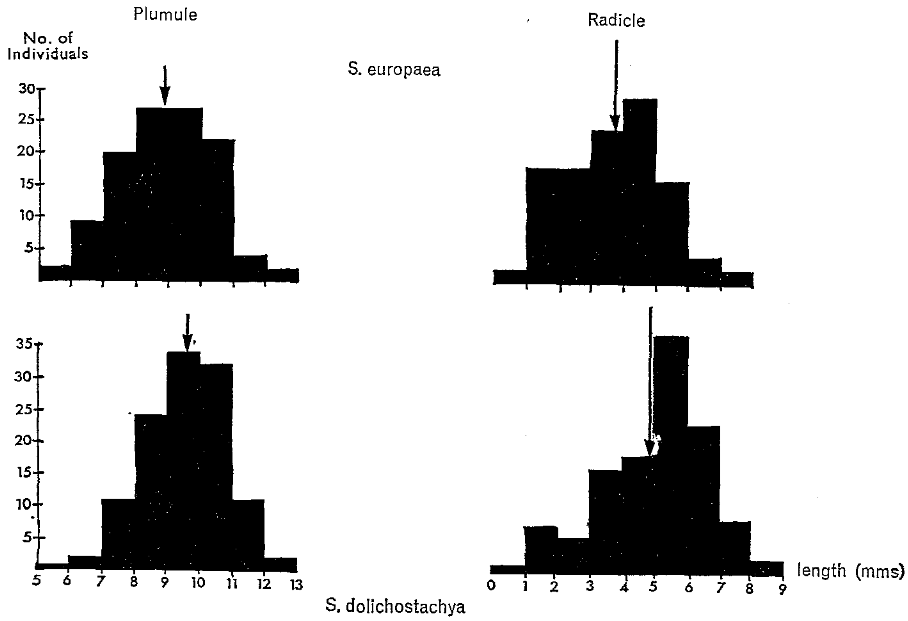

Figure 11. Frequency distribution of the length of the plumule and radicle of *Salicornia* seedlings 4 days after germination.

S. europaea and *S. dolichostachya* (8·9 mm against 9·5 mm), the total range of variation found in the two species is almost identical. The difference in mean radicle length is much more marked (3·7 mm against 4·9 mm). The results obtained from both species were distorted by the fact that in many seedlings the radicle failed to elongate at all or it elongated by a small amount and then shrivelled. Most radicles 2 mm long or less were shrivelled, and so too were some longer radicles. No satisfactory explanation of this phenomenon could be found. Whilst it often occurred in instances where the radicle was exposed to the light, this was not always so. The seedlings were always in direct contact with wet vermiculite and the humidity in the petri dishes was high, there being droplets of water permanently on the lid. In a few cases in which the radicle had shrivelled, adventitious roots were beginning to appear at the base of the stem. However, the results obtained show clearly that in *S. dolichostachya* seedlings the radicle elongates more rapidly than in *S. europaea*, both in absolute length and as a proportion of the total length of the seedlings.

Discussion

It is not proposed to discuss in detail the taxonomic situation in *Salicornia* in the Dee estuary. The main purpose of the systematic part of the present investigation was to show that two species occurred in this locality and that most individuals could be reliably identified. Similar populations were described by König (1939, 1960) from N. W. Germany and by Nannfeldt (1954) from S. Sweden. However, taxonomic conclusions drawn from these populations may not be valid for localities in south and east England, so further discussion is best left until populations from this area have been described.

The results of the ecological study largely confirmed the conclusions from the previous more casual observations. On completely open ground it appears that plants of the diploid *S. europaea* are less able to establish themselves than the tetraploid *S. dolichostachya*. However, once established in this habitat, *S. europaea* is almost as successful as *S. dolichostachya* in terms of the seed production of individual plants. With the increasing stability afforded by plants of other species and by the somewhat flatter ground found in the centre of Area A and in the middle and upper parts of Area B, plants of *S. europaea* are able to establish themselves more readily. The results obtained in the seedling growth experiments indicate that the radicle of seedlings of *S. dolichostachya* grows more rapidly than that of *S. europaea*. In the habitats most exposed to tidal disturbance this could be expected to give *S. dolichostachya* a marked advantage over *S. europaea*. The observations by Wiehe (1935) strongly support the view that establishment of the seedlings is the critical factor in determining whether *Salicornia* can grow in a habitat that is frequently covered by the tide. It is unlikely that the same tidal level will be critical in each locality. Many factors such as the stability of the surface substrate, the slope of the land and the rate at which the water flows over a particular area are likely to play an important part in determining the critical point.

The behaviour of both species of *Salicornia* when growing in competition with other species is not absolutely clear. A very slight difference in tidal level could substantially affect the availability of water during parts of the summer and early autumn and it was not possible to exclude this factor. In Area A, where *Salicornia* was competing with *Suaeda maritima*, another, but more robust, annual, both *Salicornia* species seemed able to survive and to produce seed at approximately the same rate per plant. In area B, where competition was with perennial grasses, *S. europaea* appeared to be rather more successful than

S. dolichostachya. However, in this case it is not possible to ignore the possible effects of tidal level, although there did not appear to be any significant difference between the heights of quadrats 6 and 11. The failure to find any *S. dolichostachya* plants in the areas similar to quadrats 8–11 of transect B in October, combined with the fact that in September many of the small plants of *S. dolichostachya* from this area appeared to be dying without producing seed suggests that, for reasons not determined, this species is less able to compete successfully with perennials than is *S. europaea*. If only the plants that come to maturity are considered, seed production per individual does not show any marked differences in those areas where both species occur in competition with other species. However, no individuals of *S. dolichostachya* were found with less than a total of 6 fertile segments and only 4 (out of 147) with 10 or fewer fertile segments. The corresponding figures for *S. europaea* were 18 and 43 (out of 237) (Fig. 12). This would appear to suggest that the minimum vegetative growth requirement for *S. dolichostachya* to successfully flower and fruit is greater than that for *S. europaea*.

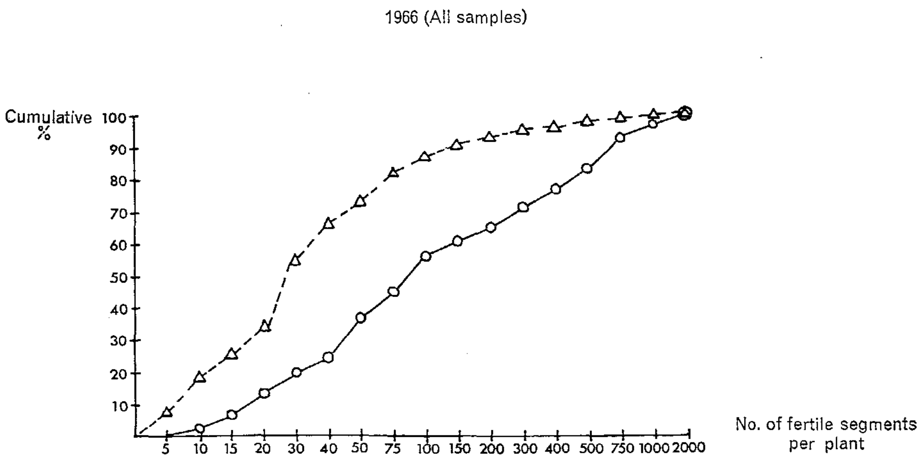

FIGURE 12. Total number of fertile segments in each plant expressed as a cumulative %.
O = *S. dolichostachya* Δ = *S. europaea*

ACKNOWLEDGMENTS

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