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The pattern of morphological variation in the *Salicornia dolichostachya* Moss group from different sites in southern England

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SUMMARY

A numerical taxonomic analysis of tetraploid *Salicornia* L. (Chenopodiaceae) plants from four salt marshes in south-eastern England was carried out by minimum variance clustering (Ward's method), a probability clustering procedure (NORMIX) and principal components analysis. The pattern of morphological variation showed a greater correlation between sites than that found in diploid species, providing evidence for the taxonomic recognition of at least two taxa. One variant correlates with *S. fragilis* P. W. Ball & Tutin.

Key-words: population, *Salicornia*, taxonomy, tetraploid.

INTRODUCTION

Salicornia species continue to be described (Wolff and Jeffries 1987). Nevertheless, ideas about the boundaries between species remain vague. Different characters have a passing fashion. The length of the anther is useful for distinguishing tetraploid and diploid species in Holland (Koutstaal *et al.* 1987) and is used to distinguish different diploid variants in America (Wolff & Jeffries 1986). The once valued characters of colour and scarious margin (Ball & Tutin 1959) are shown to be unworkable (Ingrouille & Pearson 1987).

The difficulties arise in part from the breeding system of *Salicornia*. Electrophoretic evidence (Jeffries & Gottlieb 1982) suggests there is little outbreeding in the diploid species. Much of the variation is a pattern of distinct inbreeding microspecies. However, *Salicornia* is not unique in its breeding system. It poses an exceptional problem only because of the difficulty of cultivation of natural-looking specimens and of preserving pressed specimens. The arisal of various 'morphs' in cultivation demonstrates potential problems of phenotypic plasticity, though in practice such 'aberrations' are rarely recorded in nature and are therefore not a serious problem to the field botanist. However, taxonomic names which cannot be applied with confidence are of little value. On the other hand, although it is impossible to preserve adequate specimens in the traditional way, we do have the means of preserving *Salicornia* variants. They can be digitized and stored in a database, recording patterns of within-population variation and variants in different populations.

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Table 1. Site details of sampled populations

Sampled site	Number of plants		Grid reference
	S. europaea agg. 2×	*S. dolichostachya* agg. 4×	
E. Norfolk			
Blakeney Point		75	TG 0146
N. Essex			
Tollesbury	100	70	TL 9710
S. Essex			
Saint Peter's	100		TM 0307
Canvey	74	92	TQ 8283
W. Sussex			
Itchenor	99	100	SU 7801

This paper represents progress towards the identification of a suite of characters for the recognition of *Salicornia* species; it is an attempt to discern the necessary discontinuities in the spectra of morphological variation between species. We have previously described (Ingrouille & Pearson 1987) the pattern of variation within diploid *Salicornia*. Here we report the patterns of variation with tetraploid *Salicornia* and contrast it with that in the diploids.

MATERIALS AND METHODS

We have chosen, as a working hypothesis, to assume that only three obvious variants in the British Isles exist in annual species of *Salicornia*; namely *S. pusilla* Woods (the variant with predominantly one-flowered cymes), *S. europaea* L. agg. (the diploid three-flowered variant) which is probably identical to *S. brachystachya* (G.F.W. Meyer) Konig identified from The Netherlands (Huiskes *et al.* 1985) and *S. dolichostachya* Moss agg., the tetraploid annual variant.

Sampling strategy

S. pusilla Woods with its one-flowered cymes was excluded from the analysis which was based only on plants with three-flowered cymes. Sampling was carried out at the end of the growing season because this represents a well-defined point in the life cycle. The different patterns of colouration which have been recorded as being useful in the identification of taxa are only fully expressed at this time. Plants were collected over a 2-week period in late September 1985 and 1986. We were unable to make use of the anther length to identify different ploidy levels because anthesis was finished, but tetraploids were identified from diploids by their long spike and fertile segment morphology. The efficiency of this preliminary allocation of plants was demonstrated by chromosome counts of a few representative individuals and was backed up by the results of the cluster analysis when all three-flowered plants were analysed together.

Five marshes were sampled (Table 1), three twice. They were chosen to include a wide range of tetraploid and diploid morphologies. Plants were sampled by random walk over the whole range of the marsh from low water to high water mark. Only damaged plants

were excluded. Plants were kept in polythene bags at 4°C until they were scored. Scoring took place over the following 2–3 weeks before any shrinkage or distortion of plants became apparent.

Scoring of characters and data analysis

Cluster analysis with squared euclidean distance as the measure of similarity between plants was carried out using the CLUSTAN package (Wishart 1978). Clustering was carried out by Ward's method, which we, with many other workers, have found to be the most useful, i.e. discerning the most predictive clusters. Plants were scored for the characters in Table 2 and are illustrated in Fig. 1. The only multistate character records colouration; it proved of little value and was excluded from later stages of the analysis. All other characters were metric. Seventy-seven characters were scored with roughly equivalent weight given to spike characters and habit characters. A large number of characters were scored in order to reduce any subjectivity in a priori character choice which would otherwise arise.

Many characters are plastic in development. For example, branching characteristics may be affected by the density of individuals, availability of water and nutrient status (Dalby 1956). The inclusion of many potentially plastic branching characteristics which might obscure any pattern of taxonomic discontinuities requires some comment. First, *Salicornia* plants vary not only in the degree of branching but also in branching pattern, so that different plants have a different 'gestalt'. Such differences in overall appearance are very difficult to measure except by the itemization of all the elements which make up the pattern or gestalt. Secondly, although these characters are plastic there is probably a strong genotypic component in their expression as can be seen by different looking plants growing adjacently in nature. Thirdly, and most importantly, it is impossible by any objective means to exclude such characters except a posteriori, after the first stages of analysis. We adopted the strategy of including all characters in early stages of the analysis and then successively reducing the character set by identifying at each stage of analysis the characters which proved a posteriori to be the worst cluster diagnostics. Characters were standardized by being converted to standard deviation units (Z-scores) (i.e. character value—character mean)/standard deviation, so that all characters were equally weighted.

Most characters proved to be correlated. Correlations may arise from a number of sources, the most important being logical correlations, e.g. the length of a branch, and the sum of the lengths of all the segments of that branch. Logical correlations have been avoided. Ratio characters are not logically correlated to the characters used to construct them. Although in practice shape often changes regularly with size there is no logical necessity for this to occur. Other correlations may arise if different characters are controlled by the same pleiotropic gene, are chromosomally linked, or are taxonomically correlated. Without experimental cultivation of plants, impossible to carry out in *Salicornia*, one can only speculate upon the source of the correlation. It is not possible to eliminate in any objective way some characters on the basis of correlation, but one can carry out a kind of analysis which utilizes the correlations to simplify the data set: a factor analysis. In this case we carried out a principal-components analysis.

It is the comparison of the results from a cluster analysis and a factor analysis which provides useful insights into the pattern of variation in nature. The inclusion of correlated characters in a cluster analysis effectively weights some aspects of the morphology, but in an objective and logical way, so that weighted 'characters' are those scored with increased precision by being measured several times on different parts of the plant.

Table 2. Characters scored for taxometric analysis

Growth form characters

From rooting point
1. Height to apex
2. Height to 1st branch
3. Number of internodes to 1st branch

Length
4. 1st internode
5. 2nd internode
6. Penultimate internode
7. Ultimate internode
8. Longest 1st 1° branch
11. Longest 2nd 1° branch
14. Longest penultimate 1° branch
17. Longest ultimate 1° branch
26. Longest 2° branch
29. Longest 3° branch

Number branch segments
9. Fertile in 1st 1°
10. Sterile in 1st 1°
12. Fertile in 2nd 1°
13. Sterile in 2nd 1°
15. Fertile in penultimate 1°
16. Sterile in penultimate 1°
18. Fertile in ultimate 1°
19. Sterile in ultimate 1°
27. Fertile in longest 2°
28. Sterile in longest 2°

Distance from plant apex to apex
20. Of ultimate 1° branch
21. Of 1st 1° branch

Maximum number of 2° branches
22. On 1st 1° branch
23. On 2nd 1° branch
25. On any 1° branch
24. From branch node

Terminal spike characters

30. Total length
45. Last sterile segment

Number of segments
31. Fertile
32. Sterile

Maximum width or diameter
33. 3rd fertile segment
34. Middle floret
35. Three florets
36. Apex of 2nd fertile segment
38. 2nd fertile segment
44. Scarious margin 2nd fertile segment
46. Penultimate fertile segment

Minimum width
37. 2nd fertile segment
47. Penultimate segment

Distance between
39. Florets 3rd fertile segment
40. Apex 3rd fertile segment and middle floret

Height
41. Middle floret 3rd fertile segment
42. Side floret 3rd fertile segment
43. Triangular apex 2nd fertile segment

Colour, dark green→yellow
48. Sterile segment

Green–yellow/diffuse pink/red
47. Fertile segments
48. Florets

Distribution of colour in whole vegetative plant
51. Basal or even/apical
52. Yellow/not yellow

Ratio characters

53.	1.÷11.	54.	(1.−2.−8.)÷3.	55.	54.÷(4.+5.)
56.	54.÷(6.+7.)	57.	23.÷8.	58.	24.÷(8.+1.−2.)
59.	11.÷14.	60.	11.÷20.	61.	17.÷20.
62.	29.÷11.	63.	29.÷32.	64.	33.÷(40.+41.)
65.	34.÷41.	66.	35.÷42.	67.	37.÷43.
68.	37.÷38.	69.	35.÷39.	70.	45.÷(40.+41.)
71.	38.÷46.	72.	37.÷47.	73.	46.÷47.
74.	36.÷43.	75.	33.÷37.	76.	33.÷38.
77.	45.÷7.	78.	38.÷1.	79.	8.÷20.
80.	9.÷21.				

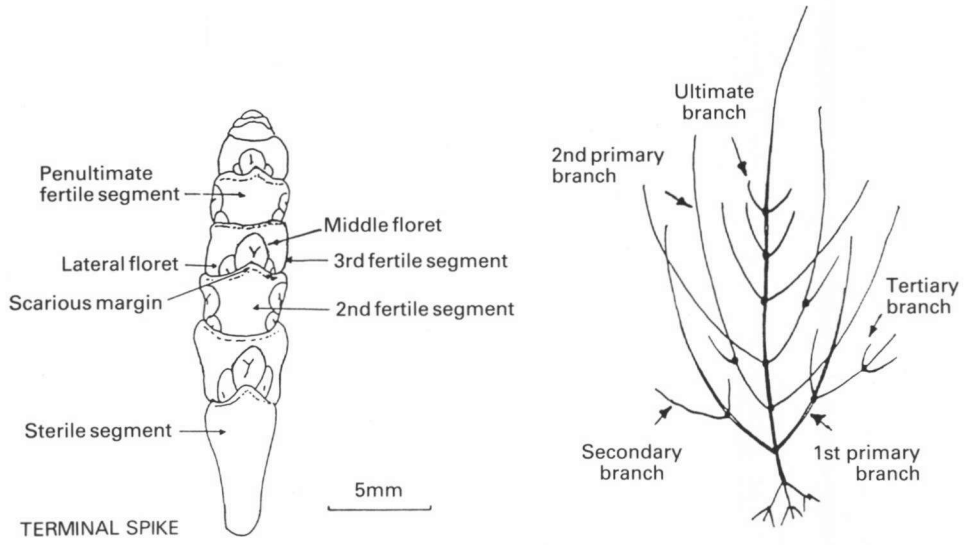

Fig. 1. Characters scored for taxometric analysis.

Table 3. Means (standard errors in parentheses) of diploid and tetraploid variants from sampled sites of characters with high eigenvalues on first two factors

Site	Blakeney	Tollesbury	Saint Peter's	Canvey		Itchenor	
Variant	4×	2×	4×	2×	2×	4×	2×	4×
Characters								
30. Spike length	51·6	29·5	50·0	21·4	25·4	50·4	32·8	53·8
	(2·3)	(0·9)	(1·4)	(0·6)	(0·9)	(1·4)	(0·8)	(1·2)
35. Width of three florets	4·0	2·9	4·1	2·6	3·0	3·7	3·3	3·8
	(0·6)	(0·4)	(0·5)	(0·3)	(0·4)	(0·6)	(0·4)	(0·3)
37. Minimum width of 2nd fertile segment	4·1	3·3	4·4	2·8	3·3	4·1	3·5	3·8
	(0·6)	(0·4)	(0·7)	(0·4)	(0·5)	(0·5)	(0·4)	(0·3)
42. Height of side floret	1·8	1·1	1·7	0·8	1·2	1·7	1·3	1·8
	(0·4)	(0·3)	(0·4)	(0·3)	(0·4)	(0·4)	(0·2)	(0·4)
8. Length of longest 1st 1° branch	86·7	40·0	66·3	69·5	84·3	98·2	61·8	75·1
	(5·6)	(3·2)	(1·2)	(3·4)	(5·9)	(4·3)	(3·5)	(4·4)
22. No. of 2° branches on 1st 1° branch	3·8	0·9	0·7	8·2	9·5	8·5	3·2	3·9
	(0·6)	(0·3)	(0·3)	(0·8)	(1·0)	(0·9)	(0·5)	(0·6)
26. Length of longest 2° branch	19·7	6·6	6·7	21·9	27·5	41·6	11·9	19·3
	(2·2)	(1·3)	(1·8)	(2·1)	(3·0)	(3·2)	(1·3)	(2·5)

Measurements in mm.

RESULTS

Diploids and tetraploids are clearly identified in the cluster analyses of *Salicornia* plants from marshes where all three-flowered annual species were sampled (Table 3). One of the most useful characters for identifying diploids from tetraploids is the distance between the

Table 4. Principal components analysis of all three-flowered plants

Factor		1	2
Percentage variance		21·6	16·2
Characters			
30.	Spike length	0·22	0·00
35.	Width of three florets	0·22	−0·03
37.	Minimum width of 2nd fertile segment	0·21	−0·03
42.	Height of side floret on 3rd fertile segment	0·21	−0·02
8.	Length of longest 1st 1° branch	0·06	−0·22
22.	No. of 2° branches on 1st 1° branch	−0·04	0·24
26.	Length of longest 2°	−0·12	0·25

Percentage variance of the first two factors and eigenvalues of diagnostic characters.

apex of the middle floret and the apex of the segment (character 40). In diploid *Salicornia* this is less than 2 mm and usually less than 1 mm. In tetraploids the distance is about 3 mm. A principal components analysis gives high eigenvalues on the first principal component to many of the same characters which were good cluster diagnostics for separating the ploidy levels (Table 4). The second principal component orders plants on the degree of branching.

Similarly, in an analysis of the complete data set of the tetraploids alone it is the degree of branching which defines the two major groups in a cluster analysis. One cluster has well-branched individuals while the other has individuals with only a few short secondary branches. These clusters are not homogeneous for spike characters so that when an analysis of terminal spike characters alone is carried out, two completely different clusters are identified; one with a long, broad spike and one with a shorter thinner spike.

An examination of the distribution of individuals at the three cluster stage shows a much better agreement between the analyses carried out on the complete and spike data sets of the tetraploids. The same three variants are defined, though the boundaries between them are drawn slightly differently. Characteristics of the three clusters from the complete data set analysis following iterative relocation of individuals to maximize cluster homogeneity are listed in Table 5. The characteristics of taxa are listed in Table 6 for comparison.

Principal components analysis correlates only very poorly with the cluster analysis when it is carried out on the whole data set. When carried out on the spike data alone, factor loadings identify the same characters identified as good cluster diagnostics but there is no clear separation of variants. Scatter diagrams of the principal components illustrate that there is a continuous spectrum of variation, though members of different clusters occupy different portions of the spectrum (Fig. 2).

Overall, the tetraploids show greater variation within marshes and less variation between marshes than the diploids in our previous survey (Ingrouille & Pearson 1987).

Table 5. Character distribution at three cluster stage of analysis of tetraploid *Salicornia*

	Cluster means		
	A ($n=85$)	B ($n=106$)	C ($n=146$)
Character			
1. Height of plant	324 (6·4)	195 (5·4)	219 (4·5)
8. Length of longest basal branch	80 (5·2)	117 (3·8)	58 (2·6)
26. Length of longest 2° branch	11 (1·5)	52 (2·6)	8 (0·8)
30. Spike length	61·8 (1·7)	52·4 (1·3)	45·0 (0·9)
31. No. of fertile segments	13.9 (0·3)	15.1 (0·3)	11.6 (0·2)
37. Minimum width of 2nd fertile segment	4·6 (0·05)	3·7 (0·04)	3·9 (0·04)
42. Height of side floret	2·0 (0·03)	1·7 (0·03)	1·7 (0·02)
71. Spike cylindricality 2nd/penultimate segment width ratio	1·5 (0·02)	1·7 (0·03)	1·4 (0·02)
48. Colour (dark green = 1 →yellow = 4)	2·0 (0·08)	1·8 (0·07)	2·2 (0·07)
Source of cluster members			
Itchenor	4	35	65
Tollesbury	36	3	31
Canvey	19	54	19
Blakeney Point	26	14	—

Measurements in mm (standard errors in parentheses).

The existence of local variants, indicated by the presence of small clusters homogeneous for site, is less pronounced in the tetraploids: 34% of all tetraploids are found in site-homogeneous clusters of eight individuals or more and 52% in clusters of four or more individuals. This compares with the diploid species in which 52% of individuals were in site-homogeneous clusters of eight or more individuals and 71% in clusters of four or more individuals. As a result the rate of increase in total variance in the cluster analysis is greater in the tetraploids than in the diploids (Fig. 3). When clustering is carried out on individuals from a single site the level of the final fusion of clusters by Ward's method indicates the extent of variation at that site. At each site where all three-flowered annual plants were collected, variance for the tetraploid cluster is larger than that for the diploids (Table 7), though the overall variance for all sites is almost exactly equivalent in each case (error sum of squares; tetraploids = 77·7, diploids = 77·9).

DISCUSSION

The tetraploids exhibit a different pattern of variation from the diploids. We have shown (Ingrouille & Pearson 1987) that the difficulty in the diploid *S. europaea* group in the UK

Table 6. Character distribution of named taxa (from Ball and Tutin 1959) for comparison with Table 5

	Species			
	S. fragilis	*S. dolichostachya*	*S. lutescens*	*S. nitens*
Character				
Height	150–350	100–300	100–400	50–250
Degree of branching	Primary branches only	Abundantly branched	Abundantly branched	Primary branches only
Length of lowest branches to plant height	1/4	Equal	2/3	< 1/4
Spike length	30–80	50–120	25–60	12–40
Number of fertile segments	8–16	12–25	8–12	4–9
Width of 2nd fertile segment	3·0–4·5	3·0–6·0	3·5–6·0	2·0–3·5
Height of side floret	2·0–2·5	1·8–3·0	1·8–2·5	1·2–1·8
Spike cylindricality	Tapering	Strongly tapering	Cylindrical	Cylindrical
Colour	Glaucous green	Dark green	Becoming yellow	Green to yellowish-green

Measurements in mm.

arises from the presence of a continuous spectrum of variation without discontinuities and even without obvious variants other than minor ones confined to a single site. There is less evidence for the existence of purely local variants in the tetraploids. Conversely, there is more evidence for the existence of variants which can be identified in several different marshes, though there is a broad overlap in the spectrum of variation between them. The characteristics of the three clusters obtained after iterative relocation of individuals following a standard cluster analysis (Table 5) may be loosely identified with the three named taxa, *S. fragilis, S. dolichostachya* and *S. lutescens* but there are important differences from the published descriptions (Table 6). *S. nitens* does not appear to be present in the sampled marshes or is included within one of the other groups.

Of the sampled sites, the *S. fragilis* variant may be absent from Itchenor and the well-branched *S. dolichostachya* variant may be absent from Tollesbury, or were only present at a very low frequency in the sampled area. Of the three variants, the *S. fragilis* variant is probably the easiest to distinguish (cluster A in Table 5). In part this is due to the best diagnostic characteristics being spike characters. There is the greatest correspondence between cluster boundaries from different analyses for this variant. It is tall, weakly branched with mainly primary branches and with a long stout terminal spike. The importance of overall height and fertile segment diameter has not previously been recognized. Their use will give a high probability of correct identification at least in the sampled marshes.

The *S. dolichostachya* and *S. lutescens* variants in which vegetative characters are important as diagnostics are poorly distinguished, with a broad overlap of individuals.

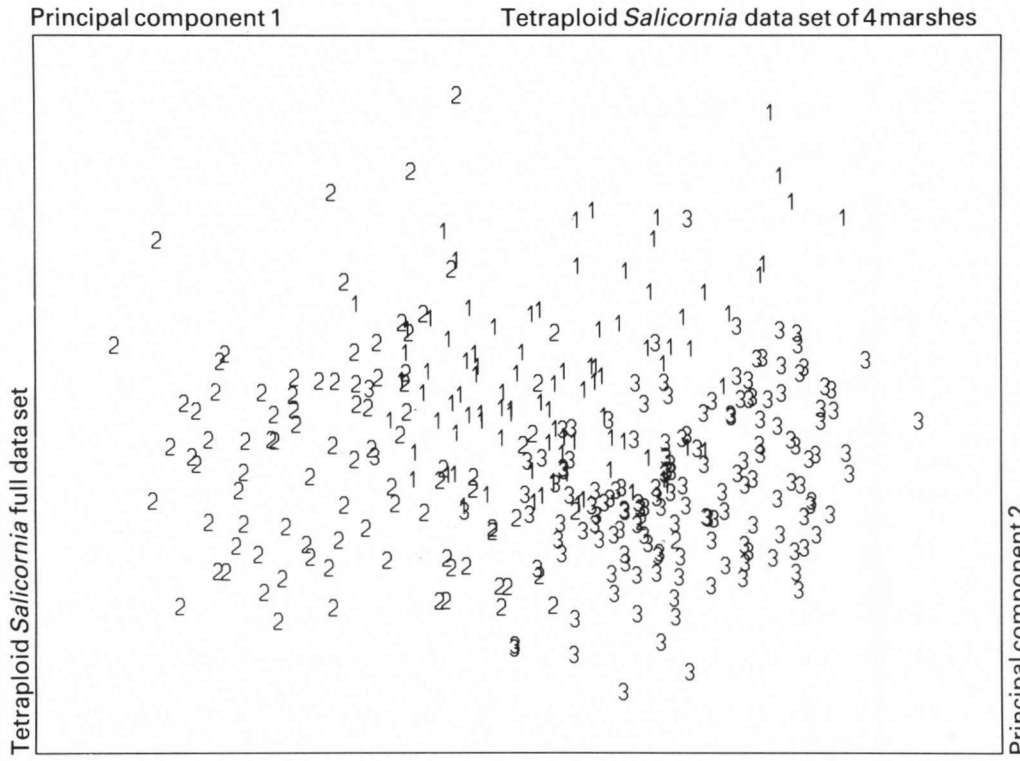

Fig. 2. Principal components scatter plot of the first two components illustrating the separation of members of the three clusters produced by HIERARCHY with iterative relocation in Table 5. Key: 1 = A, 2 = B, 3 = C.

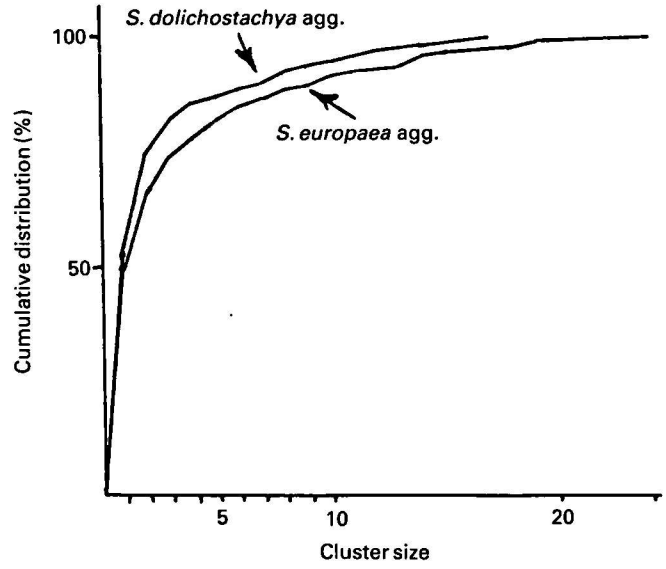

Fig. 3. Cumulative distribution of cluster sizes homogeneous for the site of origin of cluster members, illustrating that *S. europaea* agg. has larger site-homogeneous clusters, i.e. a greater level of local differentiation.

Table 7. Overall variability at sites

	Tollesbury	Canvey	Itchenor	Blakeney	St Peter's
S. dolochostachya agg.	15·95 (70)	30·85 (92)	27·02 (100)	14·78 (75)	
S. europaea agg.	11·90 (100)	11·13 (74)	11·55 (99)		17·93 (100)

Error sum of squares from clustering using squared euclidean distance and Ward's method. Number of plants sampled in parentheses.

Depending on method of analysis, a cluster which has richly branched plants with many secondary branches is sometimes identified. It has a narrower and somewhat shorter tapering spike with shorter segments. This cluster may relate quite closely to the *S. dolichostachya* variant.

The third cluster discovered here is similar in spike characteristics to the *S. dolichostachya* variant but has a slightly more cylindrical spike and is poorly branched, having the habit of the *S. fragilis* variant but not its height. This may represent *S. lutescens* but might also include plants akin to *S. nitens*. The difficulty of identifying any of the clusters listed above with any described taxa is twofold. First, they cannot be precisely delimited. Different clustering procedures draw the boundary between them in different places so that the provision of a definitive set of characteristics would be misleading. Secondly, the characteristics of the clusters do not correspond closely with described taxa, furthermore, these overlap to a considerable degree and are said to vary considerably.

It is the third cluster which correlates most poorly with described taxa. In some respects it is similar to the description of *S. fragilis* (in lack of branching) and in others to *S. lutescens* (in cylindrical shape of spike). It corresponds better to the diagram of *S. lutescens* in Ball and Tutin (1959) than the description. Their diagram of *S. nitens* shares some characteristics with that of *S. lutescens* but many with *S. europaea*. In our analysis any *S. nitens* plants would have been included with the other tetraploids because of the morphology of the fertile segment, especially as the tip of the middle floret is distant from the margin of the next segment.

The difficulty of the absence of useful diagnostic characters was also experienced in the diploids. Especially important is the question of whether a plant is poorly branched because it is growing in a crowded situation. It was for this reason that little emphasis was placed on branch characteristics in our study of the diploid species. However, whole marshes differ in the behaviour of *Salicornia* with respect to branching. At Tollesbury there are few well-branched specimens at either ploidy level. At Itchenor there are few well-branched diploids but many well-branched tetraploids. Does Tollesbury marsh have particular physical characteristics which are inimical to branching for all *Salicornia* species? Possibly the differences are the result of density-dependent phenotypic responses to inter/intraspecific competition. Or is the pattern more easily explained by the distribution of genotypically different variants, well-branched and poorly branched?

It is interesting that Ball & Tutin (1959) and Ferguson (1964) note that diploids may or may not exert their stamens while tetraploids always exert theirs. Tetraploids may then outbreed to a greater extent than the diploids, reducing the potential for the development of local inbreeding variants so that geographically widespread variants may be more

obvious. The existence of more widespread variants makes the recognition of separate taxa in the tetraploids more worthwhile than in the diploids.

However, only four marshes in the south and east of England have been studied so far. No progress to the solution of the *Salicornia* problem will be achieved until a widespread survey of *Salicornia* variation is carried out. Marshes in The Netherlands and western France must be included as well as more sites in the UK. Species such as *S. emerici* Duval-Jouve have been described from France (Lahondère 1985) which may or may not be the same variants as differently named taxa from the UK. In each country 'experts' have defined taxa very narrowly in isolation from workers elsewhere. The time has passed for this narrow nationalism. It would be a relatively easy task to agree a suite of characters and establish a supra-national *Salicornia* database as a kind of numerical herbarium. We would appreciate correspondence from fellow workers in Europe.

Until stable criteria for the confirmation of the existence of taxonomic variants have been established it would be better to use an aggregate name such as *S. dolichostachya* agg. This might be accompanied by an informal description such as 'the poorly branched variant with stout spikes from Blakeney' for increased accuracy when necessary. We suggest that at present it is wise only to give formal taxonomic recognition to four species of *Salicornia* in Britain, namely *S. perennis* Mill., *S. europaea* L. agg., *S. pusilla* Woods and *S. dolichostachya* agg. and suggest that a fifth, *S. fragilis*, may prove in time to be a useful taxon.

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