Watsonia, **13**, 11–26 (1980)

Variation in *Silene dioica* (L.) Clairv.: numerical analysis of populations from Scotland

H. C. PRENTICE

*The Botany School, University of Cambridge**

ABSTRACT

Numerical analyses (multidimensional scaling and B_k non-hierarchic cluster analysis) of wild populations of *Silene dioica* (L.) Clairv. from Scotland showed a complex pattern of variation, related partly to habitat and partly to geographic location. Subsets of characters—flower/capsule, seed, and vegetative characters—showed discordance, *i.e.* imperfectly correlated patterns of variation.

Material from Shetland, v.c. 112, has previously been treated as a variety (*Melandryum dioicum* Schinz & Thellung var. *zetlandicum* Compton) and, later, as a subspecies (*Melandrium dioicum* (L. emend.) Coss. & Germ. subsp. *zetlandicum* (Compton) Baker), but few individuals from Shetland possess all the character-states that define these taxa. Analyses based on 47 morphological characters from 29 populations showed that Shetland populations form a separate group. The differences between these and many mainland populations were, however, found to be marginal and some mainland populations (especially from sea-cliffs and woodlands) are more distinctive.

INTRODUCTION

Compton (1920) described material of *Silene dioica* (L.) Clairv. from Shetland, v.c. 112, that had large, strikingly deep magenta flowers and robust, densely hairy stems. He treated such plants as a variety, *Melandryum dioicum* Schinz & Thellung var. *zetlandicum*, which Baker (1947) later elevated to the rank of subspecies (as *Melandrium dioicum* (L. emend.) Coss. & Germ. subsp. *zetlandicum*). Clapham (1962) published the new combination *S. dioica* subsp. *zetlandica* for Baker's taxon. Baker (1947, 1948a) amplified Compton's original description, and recognized some features not mentioned by Compton, such as the variability in flower colour (from white to deep magenta) previously noticed in Shetland *S. dioica* by Druce (1922). Pale-flowered Scottish *S. dioica* (Gardiner 1848, Druce 1922, Baker 1948a) may have caused confusion with *S. alba* (Mill.) Krause and with the hybrid *S. alba* × *S. dioica*.

Although Baker (1948a, 1948b) regarded the Shetland subspecies as the British representative of Turesson's coastal ecotype (Turesson 1925), coastal material from elsewhere in Britain (Wright 1933, Murray 1974) possesses only some of the supposedly distinctive features of Shetland material. My own observations in Scotland and elsewhere also suggested that variation in *S. dioica* might be more complex than previously thought, and in particular that striking, atypical variants are misleadingly over-represented in herbaria (e.g. **BM**, **CGE, SLBI**).

This paper describes a numerical study of the pattern of morphological variation among populations of *S. dioica* from Scotland. The numerical analyses were based on 29 wild populations from various habitats and locations in Scotland (including seven populations from Shetland), plus six extra seed samples, and eight wild populations from elsewhere in Britain and Europe, for comparison. Special attention is given to the taxonomic status of Shetland material.

MATERIALS AND METHODS

VARIATION IN SCOTTISH *S. DIOICA*

Character selection, sampling and scoring

Forty-seven flower, capsule, seed and vegetative characters (Table 1) were selected. The same list of

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* Present address: Department of Biology, University of Southampton.

TABLE 1. LIST OF CHARACTERS AND CHARACTER-STATES

	Character	Character-states
1*	pedicel length	
2*	calyx length	
3	calyx shape	cylindrical/constricted-cylindrical/conical/spherical/oval
4	calyx-nerves (anastomosis)	anastomosing/not anastomosing
5	red calyx pigment	present/absent
6	calyx glandular hairs	absent or very sparse/present
7	calyx-hairs (straightness)	straight/flexuous/crispate
8	calyx-hairs (stiffness)	soft[1]
9	calyx-tooth shape	acute/subacute/obtuse
10*	corolla diameter	
11	corolla colour	(18 colour-depth categories, ranging from white to a deep magenta, were distinguished on a home-made colour chart)
12	petal dissection	indented to less than half-way/ indented to half-way or more
13	additional petal-lobes	present/absent
14	coronal scale colour	as petals, pink/not as petals, pink/not as petals, white
15*	petal-claw length	
16*	capsule length	
17	capsule shape	globose/ovoid/pyriform/long-pyriform
18	capsule-tooth orientation	erect/ascending/deflexed/ curled back
19	pedicel orientation[2]	erect[1]
20*	seed length	
21*	seed length/breadth ratio	
22	seed-back shape	convex/flat/concave/rounded
23*	seed-back width	
24	seed-face type	very convex/convex/flat/concavo-convex/concave
25	seed colour	(from Rayner's (1970) colour chart)
26	tubercle-tip colour	black/dark-brown/brown/ginger/chestnut/grey
27*	seed-plate length	
28*	seed-plate length/breadth ratio	
29*	number of suture points per plate	
30*	tubercle length	
31	hylar zone type	prominent/level/recessed
32	seed-surface granulation	coarse/medium/fine/absent
33	suture width	very narrow/narrow/medium/wide
34	suture outline	sinuous/sharply-sinuous/serrate/lobate/stellate/digitate
35	tubercle shape	conical/tall-conical/cylindrical/tall-cylindrical
36*	plant height	
37	stem glandular hairs	absent or very sparse/scattered/dense
38	stem clothing[3]	shortly hairy/with long hairs
39	stem-hairs (straightness)[3]	straight/flexuous/crispate
40	stem-hairs (orientation)[3]	patent/deflexed
41	stem-hairs (softness)[3]	rather stiff/soft
42*	number of internodes below inflorescence[4]	
43*	length of lowest cauline leaf	
44	shape of lowest cauline leaf	lanceolate/ovate-acute/ovate-obtuse/rounded
45	leaf glandular hairs (above)	absent or very sparse/present
46	leaf glandular hairs (below)	absent or very sparse/present
47	proportion of shoot with flowers	less than half/half or more/nearly all

* treated as quantitative. See Prentice (1979) for details of character-handling

[1] invariant in the present data set

[2] when capsule ripe

[3] on an internode in mid-stem

[4] from the ground to the lowest side-shoot bearing visible flower-buds

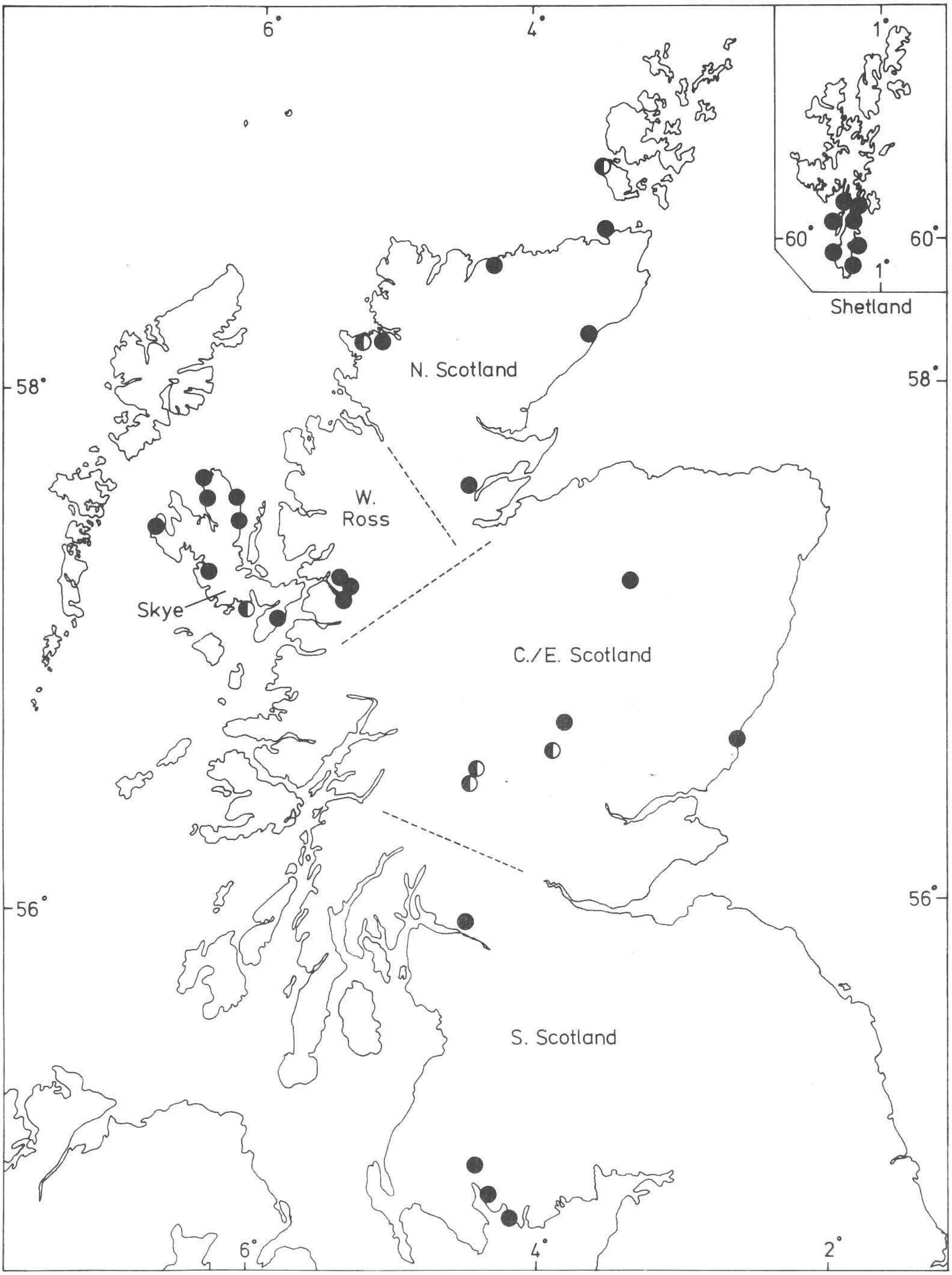

FIGURE 1. Map showing localities of Scottish *S. dioica* populations used for numerical analysis. Half-open circles (◑) represent populations from which only seeds were scored; closed circles (●) represent fully scored populations.

TABLE 2. LOCALITIES AND HABITAT-TYPES FOR POPULATIONS

No.	GR (British populations)	Locality (and vice-county for British populations)	Habitat type
59	41/037.080	Heythorne, Dorset (v.c. 9)	woodland
140	—	Rébénacq, Pyrénées-Atlantiques (France)	woodland
151	28/560.601	Dingwall, E. Ross (v.c. 106)	woodland
153	39/202.768	Dunnet Head, Caithness (v.c. 109)	coastal cliff
154	41/035.037	Whitesheet, Dorset (v.c. 9)	hedgerow
155[1]	57/233.021	Howes of Quoyawa, Hoy, Orkney (v.c. 111)	montane cliff
156	—	Saana, Kilpisjärvi, Enontekiö (Finland)	woodland
157	—	Stokkedalen, Finnmark (Norway)	woodland
158	—	Storfjord, Finnmark (Norway)	woodland
165	—	St Samson-la-Poterie, Oise (France)	woodland
226	25/633.457	Brighouse Bay, Kirkcudbrights. (v.c. 73)	woodland
234	—	Tammisaari (Finland)	woodland
235[1]	27/593.396	Meall nan Tarmachan, Killin, Mid Perth (v.c. 88)	montane cliff
236[1]	27/590.410	Creagan Lochain, Killin, Mid Perth (v.c. 88)	montane cliff
237[1]	27/852.477	Birks o'Aberfeldy, Mid Perth (v.c. 88)	woodland
238	27/916.625	Pass of Killiecrankie, E. Perth (v.c. 89)	woodland
239	18/935.187	Sheil Bridge, W. Ross (v.c. 105)	hedgerow
241	18/915.225	Inverinate, W. Ross (v.c. 105)	woodland
242	18/881.276	Conchra, Dornie, W. Ross (v.c. 105)	saltmarsh
243[1]	18/522.154	Carn Mòr. Elgol, Skye, N. Ebudes (v.c. 104)	coastal cliff
244	18/668.090	Teangue, Sleat, Skye, N. Ebudes (v.c. 104)	hedgerow
245	18/370.331	Fernilea, Carbost, Skye, N. Ebudes (v.c. 104)	woodland
246	18/519.517	Holm, east of Loch Leathan, Skye, N. Ebudes (v.c. 104)	coastal cliff
247	18/468.715	Kildorais, Flodigarry, Skye, N. Ebudes (v.c. 104)	saltmarsh
248	18/368.707	Camas Mòr, Kilmuir, Skye, N. Ebudes (v.c. 104)	coastal cliff
249	18/398.638	Uig, Skye, N. Ebudes (v.c. 104)	woodland
250	18/153.507	Meanish, near Dunvegan Head, Skye, N. Ebudes (v.c. 104)	coastal cliff
251[1]	29/115.327	Drumbe, W. Sutherland (v.c. 108)	hedgerow
252	29/136.320	Nedd, Drumbeg, W. Sutherland (v.c. 108)	woodland
253	29/716.621	Bettyhill, W. Sutherland (v.c 108)	hedgerow
254	39/153.289	Dunbeath, Caithness (v.c. 109)	woodland
256	38/150.197	Tomintoul, Banffs. (v.c. 94)	woodland
257	37/695.488	Ethie Haven, Lunan Bay, Angus (v.c. 90)	coastal cliff
258	68/432.353	East Voe of Quarff, Mainland, Shetland (v.c. 112)	saltmarsh
259	68/369.313	Papil, West Burra, Shetland (v.c. 112)	saltmarsh
260	68/408.396	East Voe of Scalloway, Mainland, Shetland (v.c. 112)	saltmarsh
261	68/397.155	Voe, Mainland, Shetland (v.c. 112)	saltmarsh
262	68/376.185	Bay of Scousburgh, Mainland, Shetland (v.c. 112)	coastal cliff
263	68/435.249	Sand Lodge, Mainland, Shetland (v.c. 112)	saltmarsh
264	68/434.325	Fladdabister, Mainland, Shetland (v.c. 112)	roadside bank
265	26/400.745	Dumbarton Rock, Dunbarton (v.c. 99)	coastal cliff
266	25/430.657	Newton Stewart, Kirkcudbrights. (v.c. 73)	roadside bank
267	25/471.582	Creetown, Kirkcudbrights. (v.c. 73)	saltmarsh

[1] seed sample only

flower, capsule and seed characters was used in the survey of European *S. alba* and *S. dioica* by Prentice (1979); 12 vegetative characters were added for the present survey.

Twenty-nine populations (see Fig. 1 and Table 2 for localities) were scored in August 1975 for all 47 characters. The sampling procedure was as follows. A marker was placed at an arbitrary point within the wild population. I selected for scoring the six flowering males and the six flowering females nearest

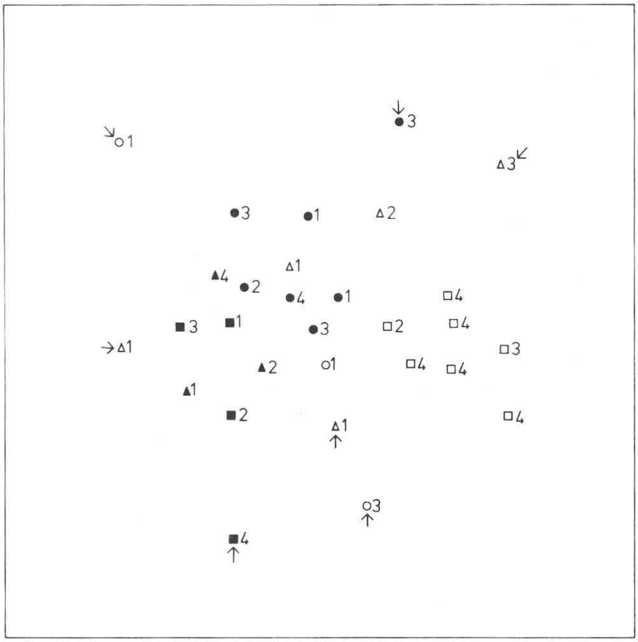

FIGURE 2. Multidimensional scaling of 29 Scottish populations of *S. dioica* with the full character set (characters 1–47 in Table 1). Selected outliers are indicated by arrows. Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C./E. Scotland. Numbers indicate habitat types: 1 woodland, 2 hedgerow or roadside bank, 3 coastal cliff, 4 saltmarsh. Percentage stress = 18·5.

to the marker; then further fruiting females, if necessary, to bring the total of plants with ripe capsules to six. I took one capsule from each of the six fruiting plants; the seed in the capsules was pooled and a random subsample of twelve seeds taken for microscopic examination. For the purposes of analysis, therefore, each of the 29 populations was represented by six observations (one per plant) on males and six on females for the flower and vegetative characters (1–15 and 36–47 in Table 1), six observations for the capsule characters (16–19), and twelve observations for the seed characters (20–35).

I visited a further six populations (Fig. 1, Table 2) that were past flowering (three of them montane); these were scored for seed characters only. A set of eight populations from England, France, Norway and Finland, scored for all 47 characters in 1974-1975 (Table 2), was added to the 29 Scottish populations for analysis.

Populations varied in size from less than ten individuals on a montane ledge in Mid Perth, v.c. 88, to over 1,000 individuals on an upper saltmarsh in Shetland. I included populations from a wide range of localities and habitats: woodlands, hedgerows and roadside banks, upper saltmarshes, sea cliffs and montane cliff ledges in mainland Scotland, Skye (N. Ebudes, v.c. 104), Orkney (v.c. 111) and Shetland (Fig. 1). Skye provided a particularly good range of habitats in a small area (see Birks 1973).

Specimens from each population have been deposited in **CGE**. The complete data on character-state frequencies are available on request.

Numerical analyses of differentiation between populations

Analyses were carried out on the main group of 29 populations with the full set of 47 characters. Variation in separate character subsets—flower and capsule characters (1–19 in Table 1), seed characters (20–35) and vegetative characters (36–47)—was also examined, in case of there being discordance, i.e. differences in the variation patterns shown by different functional groups of characters. Further analyses based on seed characters alone were carried out on an expanded group of

35 populations, i.e. the main group plus the six seed samples. Finally, the relationships of some non-Scottish populations to the Scottish ones were investigated by joint analysis, with all 47 characters, of the main group plus the eight non-Scottish populations.

A résumé of the numerical methods follows. For more details and notes on computation see Prentice (1979).

Each 'block' of populations and characters was used for separate computation of a matrix of dissimilarity coefficient (DC) values between populations. (One block consists of the main group of 29 populations and the full set of 47 characters, another of the same 29 populations and the 19 flower/capsule characters, and so on.) Each DC value expresses the net dissimilarity between two populations, on the basis of all the characters in the block; there is a DC value for every pair of populations in the block. K-dissimilarity (Jardine & Sibson 1971) was used as the DC. This DC works on populations rather than individuals as the operational taxonomic units (OTUs), and can be used with both qualitative and quantitative characters. It automatically gives a high weighting to characters that vary between populations but are constant within populations, and a low weighting to characters that are highly variable within populations. Observations on males and females form separate contributions to the K-dissimilarity values (i.e. the flower and vegetative characters were each treated as two units). Subsequent analysis of the pattern contained in the dissimilarity matrices was by two methods, non-metric multidimensional scaling (MDS) and B_k clustering. Non-metric MDS (Kruskal 1964a, 1964b, Jardine 1971, Sibson 1972, Jardine & Edmonds 1974) represents OTUs as points in a scatter diagram in which the distances between points are related monotonically, or nearly so, to the DC values between the OTUs. B_k clustering (Jardine & Sibson 1968, 1971, Jardine & Edmonds 1974) is a method for non-hierarchic cluster analysis and finds overlapping clusters of OTUs. The maximum number of OTUs permitted to be shared by any two clusters (one less than the value of the parameter k in B_k) can be set as required. B_2 and B_3 can give a better representation of some semi-continuous variation patterns than single-link (hierarchic) cluster analysis, which is equivalent to B_1.

The extent to which the methods succeed in producing undistorted representations of the information held in the dissimilarity matrices, and therefore the confidence with which the representations can be interpreted, is measured by distortion statistics. For MDS, percentage stress quantifies the deviation of interpoint distances from the ideal of monotonicity with the DC values. $\hat{\Delta}_{\frac{1}{2}}$ (Jardine & Sibson 1971) is used to measure the distortion that B_k clustering imposes on the DC values; $\hat{\Delta}_{\frac{1}{2}}$ ranges from zero to one. These distortion statistics can reasonably be compared among analyses of similar data types and with similar numbers of OTUs.

The possibility of discordance between character subsets was investigated for the main group of 29 populations by calculating Δ (Jardine 1971, Jardine & Edmonds 1974) between dissimilarity matrices based on character subsets, and between these and the dissimilarity matrix based on the full character set. Δ ranges from zero to two, a zero Δ value signifying perfect concordance.

MDS diagrams were inspected first for association between MDS-placing and habitat-type for populations from the same general area, then for association between MDS-placing and area for populations from the same habitat type, in order to assess the extent of ecological and geographic components of variation, respectively. I adopted this approach rather than a simple search for relationship with area or habitat, because not all habitats were represented in each area and a simple search would have been biased. B_k diagrams, drawn up at a few convenient clustering levels, were likewise examined for clustering by habitats in populations from the same area and for clustering by areas in populations from similar habitats. (High clustering levels, like the upper levels of a dendrogram in hierarchic cluster analysis, depict broader relationships than lower levels). The MDS diagram derived from joint analysis of Scottish and non-Scottish populations was examined for association between MDS-placings and geographic regions of origin.

THE STATUS OF SHETLAND POPULATIONS

Comparison with mainland populations

The Shetland group of seven populations was compared with a 'standard group', including most of the 'mainland' (including Skye) populations but excluding 'outliers' found by numerical analysis (Fig. 2). Data were not available on all the characters mentioned by Baker (1948a: table 2), but I compared histograms based on pooled character-state frequencies in the two groups for a series of characters related to Baker's: stem-hair stiffness, stem-hair straightness, leaf shape, number of internodes below inflorescence, proportion of shoot with flowers, calyx-hair straightness, corolla diameter, corolla colour, capsule shape, capsule length, and seed length.

Investigation of variation within a Shetland population

I selected a large population (>1,000 individuals) of *S. dioica* at East Voe of Quarff, Mainland, Shetland (GR 68/432.353) for an investigation of within-population variation. This population is typical of the numerous upper saltmarsh *S. dioica* populations in Shetland. The object was to find out whether the various distinctive character-states of Compton's Shetland variety and Baker's Shetland subspecies (Compton 1920, Baker 1947, 1948a) tend to occur together or independently, i.e. to investigate the extent of statistical (within-population) correlation among the relevant characters. Twenty-five plants of each sex were scored for a new set of characters closely related to those given by Baker (1948a) as differentiating the Shetland subspecies. These characters were:

ratio of inflorescence length to plant height
stem diameter (mm, lowest internode)
leaf length/breadth ratio (on median stem-leaf)
corolla diameter (mm)
corolla colour (see Table 1)
capsule length (mm, females only)
mean seed weight (mg for 20 seeds, females only)

The results were (a) represented for immediate visual comparison as polygraphs, and (b) subjected to correspondence analysis (Hill 1974), a numerical technique that summarizes the correlations between characters; males and females were treated separately. Correspondence analysis is closely related to principal components analysis, but takes into account non-linear correlations. The percentage contribution of successive eigenvalues to the total variance depends on the amount of correlation between characters. If all the characters were independent, the eigenvalues would be approximately equal, but if all the characters were highly correlated with one another the first eigenvalue would be much larger than the rest.

RESULTS

ALL-CHARACTER ANALYSES OF DIFFERENTIATION BETWEEN SCOTTISH POPULATIONS

The result of MDS applied to the main group of 29 populations, with the full character set, is shown in Fig. 2. There is no perceptible clumping by habitat in populations from each area, although most of the outliers are from woodlands or coastal cliffs, but there is clumping by area: saltmarsh populations divide into Shetland, Skye/W. Ross, and (with one member) S. Scottish groups; the Shetland populations form a group, irrespective of habitat.

Fig. 3 shows the result of B_2 clustering, pictured at two clustering levels. B_3 is not shown because its $\hat{\Delta}_{\frac{1}{2}}$ value was not appreciably better than that of B_2 (see Table 3). Fig. 3 shows some clustering related to geographic distribution: most Skye populations are interrelated at a low clustering level, regardless of habitat; at the higher clustering level Shetland populations form a loosely linked group consisting of several overlapping two-membered clusters, but some of the Shetland populations are also linked to populations from other parts of Scotland at this level. Fig. 3 also emphasizes that some populations are true outliers, as distinct from one another as from the residue.

ANALYSES BASED ON SUBSETS OF CHARACTERS

Dissimilarity matrices derived from the main group of 29 populations with three subsets of characters (flower/capsule, seed, vegetative) were subjected to MDS and to B_1 (single-link), B_2 and B_3 clustering. Table 3 compares percentage stress and $\hat{\Delta}_{\frac{1}{2}}$ values for analyses based on all 47 characters and on the subsets. B_k clustering gave higher $\hat{\Delta}_{\frac{1}{2}}$ values with each of the subsets than with the full character set. MDS stress values were also higher, except for the vegetative subset. Among the three subsets there was an inverse relationship between B_k and MDS performance. Thus the subset that was most aptly described by a system of overlapping clusters proved least amenable to two-dimensional representation, and *vice versa*.

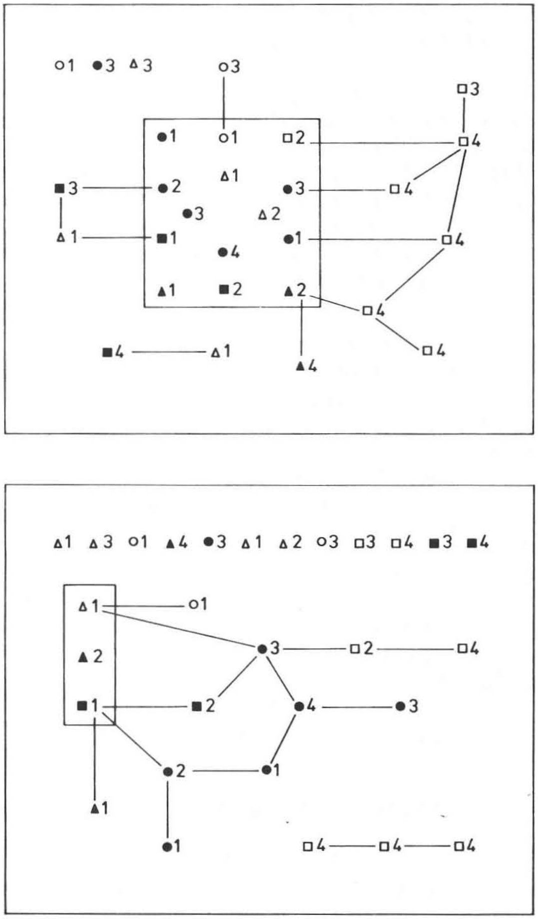

FIGURE 3. B_2 clustering of 29 Scottish populations of *S. dioica* with the full character set (characters 1–47 in Table 1). Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C./E. Scotland. Numbers indicate habitat types: 1 woodland, 2 hedgerow or roadside bank, 3 coastal cliff, 4 saltmarsh. The diagrams show the overlapping clusters formed at two levels. Clusters containing more than two populations are enclosed by solid lines, clusters containing two populations are indicated by a line joining the pair, and single-membered clusters are shown at the top of each diagram. $\hat{\Delta}_{\frac{1}{2}} = 0{\cdot}22$.

TABLE 3. DISTORTION VALUES FOR ANALYSES BASED ON DIFFERENT SETS OF CHARACTERS

	all	flower/capsule	seed	vegetative
$\hat{\Delta}_{\frac{1}{2}}$ (B_1)	0·27	0·33	0·42	0·59
$\hat{\Delta}_{\frac{1}{2}}$ (B_2)	0·22	0·28	0·35	0·55
$\hat{\Delta}_{\frac{1}{2}}$ (B_3)	0·19	0·24	0·32	0·53
percentage stress (MDS)	18·5	20·5	18·8	14·8

TABLE 4. DISCORDANCE VALUES BETWEEN DIFFERENT SETS OF CHARACTERS

flower/capsule	seed	all	
0·35	0·37	0·24	vegetative
	0·29	0·13	flower/capsule
		0·21	seed

Δ values revealed discordance among character subsets and between these and the full character set (Table 4). Values for the comparisons all:vegetative and all:seed at this geographic scale are high compared with those quoted by Prentice (1979) for flower/capsule/seed:seed in studies of variation in *S. alba* and *S. dioica* on a European scale, where seed characters were found to be a reliable guide to the major variation patterns.

MDS results for separate subsets of characters (Figs. 4, 5, 6) differ from Fig. 2 and differ markedly from one another. The patterns in each case can be related in different ways and in differing degrees to geography and ecology.

MDS for flower/capsule characters (Fig. 4) shows slight geographic differentiation, grouping some of the Skye populations, some of the Shetland populations, and all three populations from W. Ross. MDS for seed characters (Fig. 5) shows some habitat-related features, for example within Skye, where sea-cliff populations are separated from woodland populations; the woodland population from Kirkcudbrights. (v.c. 73), S. Scotland, is placed with two other woodland populations (from Skye and N. Scotland), while the Kirkcudbright saltmarsh population is next to one of the saltmarsh populations from Shetland. Geographic features of variation are also detectable: for example, some Shetland populations are adjacent irrespective of habitat, and west-coast populations (Skye, W. Ross, S.

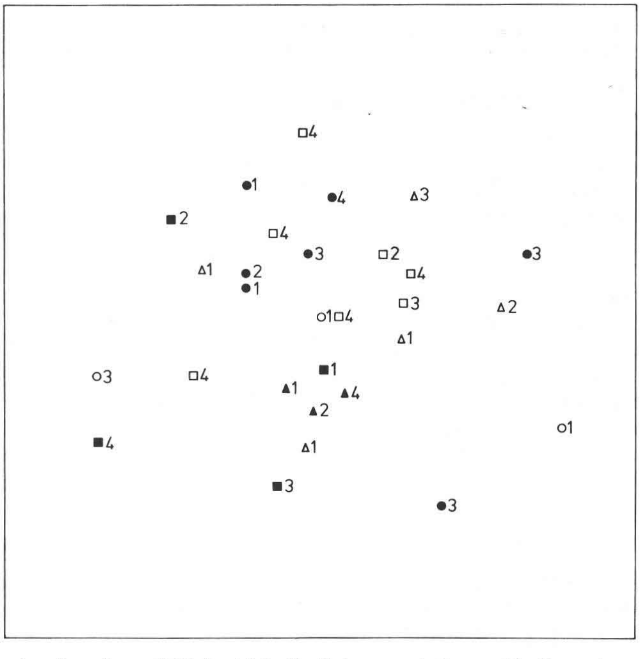

FIGURE 4. Multidimensional scaling of 29 Scottish *S. dioica* populations with flower/capsule characters only (characters 1–19 in Table 1). Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C. & E. Scotland. Numbers indicate habitat types: 1 woodland, 2 hedgerow or roadside bank, 3 coastal cliff, 4 saltmarsh. Percentage stress = 20·5.

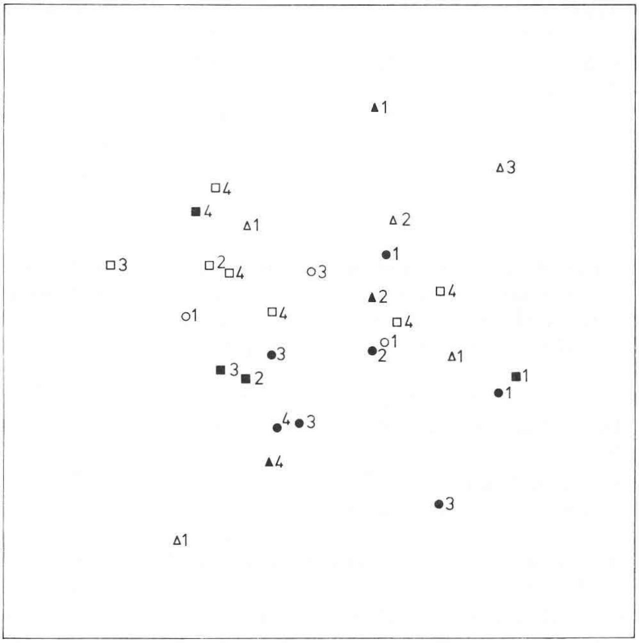

FIGURE 5. Multidimensional scaling of 29 Scottish *S. dioica* populations with seed characters only (characters 20–35 in Table 1). Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C. & E. Scotland. Numbers indicate habitat types: 1 woodland, 2 hedgerow or roadside bank, 3 coastal cliff, 4 saltmarsh. Percentage stress = 18·8.

Scotland) mostly fall in the lower half of the diagram. The influence of habitat type is most obvious in the MDS for vegetative characters (Fig. 6), although this too has a mixture of geographic and ecological features. Skye populations are clumped; woodland populations from outside Skye all fall into one part of the diagram; most of the Shetland populations (those from saltmarshes and coastal cliffs) are placed together, but the single inland roadside bank population from Shetland is placed next to a hedgerow population from W. Sutherland (v.c. 108), well away from its compatriots. The three Kirkcudbright populations are clumped. Hedgerow and bank populations appear in a horizontal band across the centre of the diagram.

Seed-character analysis of the expanded group of 35 OTUs gave distortion values close to those for the former 29 OTUs, as follows: MDS stress 20·6%; $\hat{\Delta}_{\frac{1}{2}}$ values of 0·42, 0·36 and 0·34 respectively for B_1, B_2 and B_3. MDS largely repeated the result for the 29 populations; the three new montane seed samples were placed in the same part of the plot as most of the sea-cliff populations. B_2 showed a relationship (though at a high clustering level) between the montane samples and some sea-cliff populations.

ALL- CHARACTER ANALYSIS OF SCOTTISH AND NON-SCOTTISH POPULATIONS

Fig. 7 shows the result of MDS based on all 47 characters for the 29 Scottish populations plus the eight from elsewhere in Britain and Europe. Stress is low and there is clear geographic grouping, although no overall north-south trend. The Shetland populations form a subgroup of the Scottish group.

STATUS OF SHETLAND POPULATIONS

Comparison with mainland populations

Numerical analysis shows that Shetland populations of *S. dioica* form a local race that is just

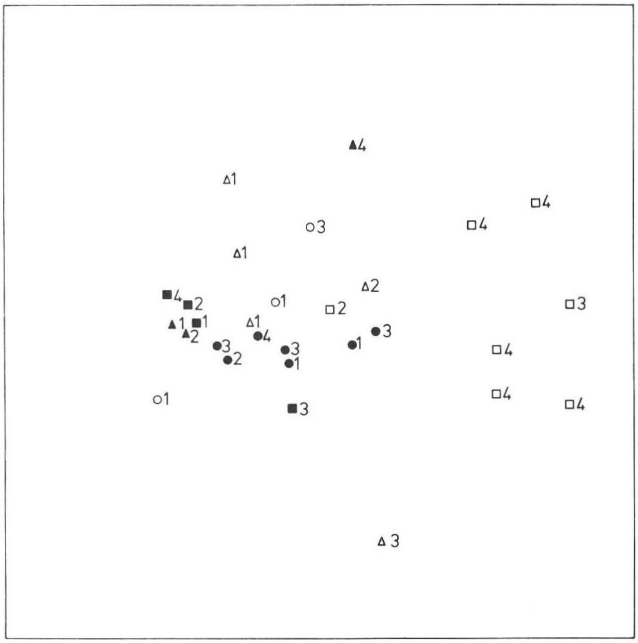

FIGURE 6. Multidimensional scaling of 29 Scottish *S. dioica* populations with vegetative characters only (characters 36–47 in Table 1). Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C. & E. Scotland. Numbers indicate habitat types: 1 woodland, 2 hedgerow or roadside bank, 3 coastal cliff, 4 saltmarsh. Percentage stress = 14·8.

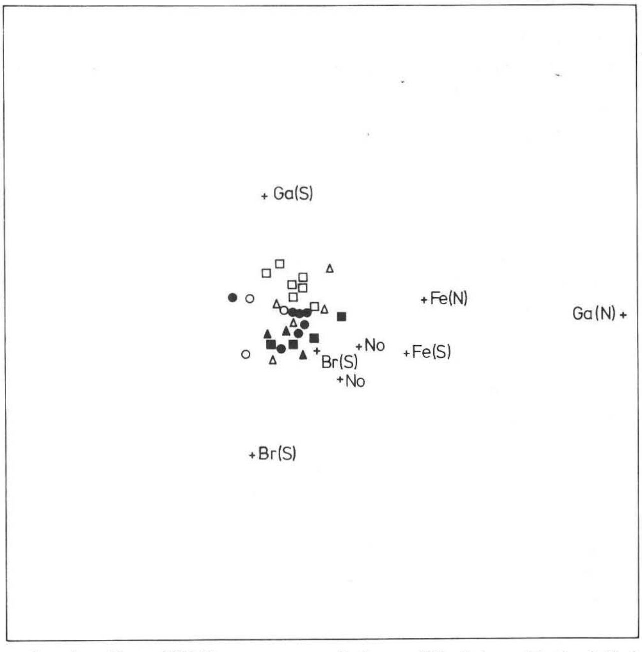

FIGURE 7. Multidimensional scaling of 37 European populations of *S. dioica* with the full character set (characters 1–47 in Table 1). Symbols indicate geographic areas (see Fig. 1): closed squares (■) S. Scotland, closed triangles (▲) W. Ross, closed circles (●) Skye, open squares (□) Shetland, open triangles (△) N. Scotland, open circles (○) C. & E. Scotland, crosses (+): other areas, i.e. Br(S) southern Britain, Ga(N) northern France, Ga(S) southern France, Fe(S) southern Finland, Fe(N) northern Finland, No northern Norway. Percentage stress = 12·4.

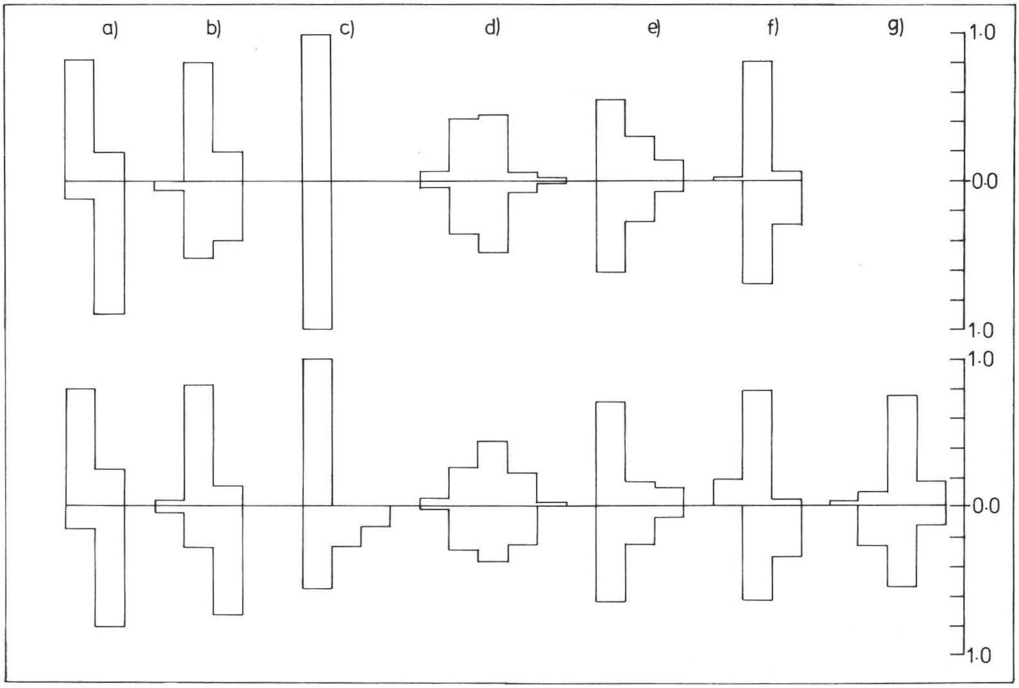

FIGURE 8. Histograms of seven qualitative characters for Shetland populations and a standard group of Scottish populations of *S. dioica*. The lower, inverted histograms are for Shetland populations; the upper pairs of histograms represent males, the lower pairs, females. Characters: (a) stem-hair stiffness (rather stiff/soft), (b) stem-hair straightness (straight/flexuous/crispate), (c) leaf shape (ovate-acute/ovate-obtuse/rounded), (d) number of internodes below inflorescence (1–2/3–4/5–6/7–8/9–10), (e) proportion of shoot with flowers (less than half/half or more/nearly all), (f) calyx-hair straightness (straight/flexuous/crispate), (g) capsule shape (globose/ovoid/pyriform/long-pyriform). Vertical scale: frequency.

distinguishable from others when all characters are examined together. This race is not similar to other coastal populations. Individual subsets of characters fail to separate a definite Shetland race.

Histograms of critical characters (Figs. 8-10)* showed that the differences between Shetland populations and more typical Scottish ones are slight. (The 'standard group' of mainland Scottish populations chosen for these comparisons excludes seven outliers: numbers 151, 153, 238, 248, 252, 257 and 267 in Table 2. These were selected by eye as the outliers from the main group of mainland populations in Fig. 2; they also appear among the outliers at a low level, and some also at a high level, in Fig. 3. All seven were noted as distinctive in the field.) Shetland populations have on average larger flowers, deeper magenta petals and larger seeds (as also observed by Baker (1948a) and Palmer & Scott (1969)), soft, crispate stem-hairs and crispate calyx-hairs. However, no appreciable differences were found between Shetland and non-Shetland populations in capsule size and shape, nor in compactness of the inflorescence (judged from 'proportion of shoot with flowers' and 'number of internodes below inflorescence'), all characters also regarded by Baker as definitive of the Shetland subspecies. The Shetland populations were not found to have the narrow cauline leaves of Baker's material (Baker 1946, 1947, 1948a); on the contrary, some females had unusually rounded leaves, as was also observed by Compton (1920).

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* Bimodality in capsule size (Fig. 10) results from an artefact of sampling: the basal capsule is normally the largest, the others appreciably smaller.

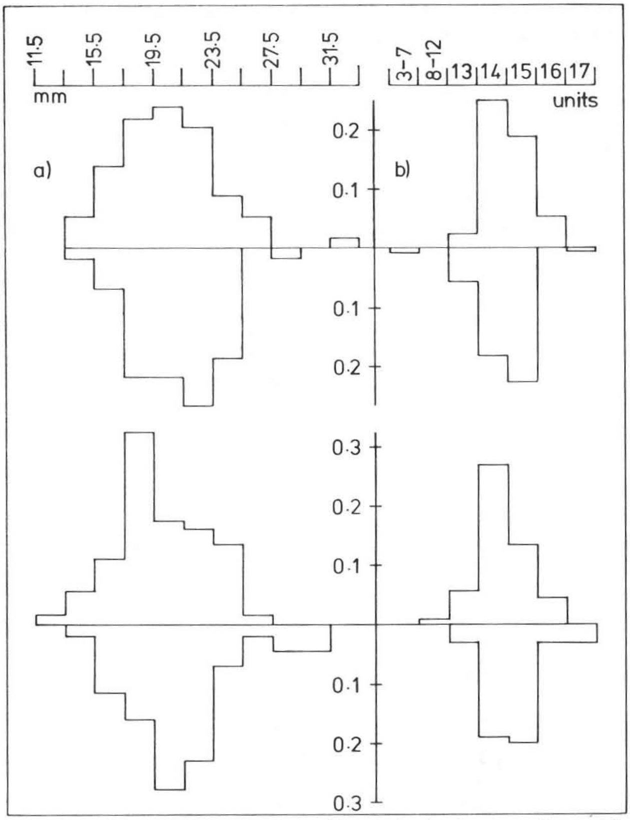

FIGURE 9. Histograms of corolla diameter (a) and colour (b) for Shetland populations and a standard group of Scottish populations of *S. dioica*. The lower, inverted histograms are for Shetland populations; the upper pairs of histograms represent males, the lower pairs, females. Corolla colour is in colour chart units (see Table 1). Vertical scale: frequency.

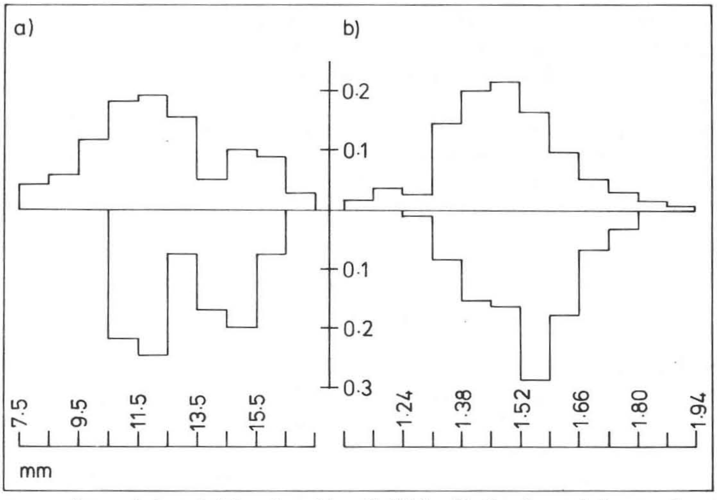

FIGURE 10. Histograms of capsule length (a) and seed length (b) for Shetland populations and a standard group of Scottish populations of *S. dioica*. The lower, inverted histograms are for Shetland populations. Vertical scale: frequency.

TABLE 5. CORRESPONDENCE ANALYSIS OF VARIATION WITHIN THE *S. DIOICA* POPULATION AT EAST VOE OF QUARFF, SHETLAND: TABLE OF EIGENVALUES

	females (25 individuals, 21 character-states):		males (25 individuals, 16 character-states):	
eigen value number	contribution to total variance, %	cumulative contribution, %	contribution to total variance, %	cumulative contribution, %
1	11·6	11·6	13·9	13·9
2	10·5	22·1	12·2	26·1
3	9·4	31·5	11·1	37·2
4	8·9	40·4	10·2	47·4
5	7·6	48·0	8·4	55·8
6	7·0	55·0	6·6	62·3
7	6·5	61·5	6·4	68·8
8	5·4	66·8	5·7	74·5
9	5·0	71·8	5·3	79·7
10	4·6	76·4	4·8	84·5
11	4·3	80·7	4·0	88·5
12	3·4	84·1	3·1	91·6
13	2·9	87·0	2·7	94·3
14	2·7	89·7	2·4	96·6
15	2·1	91·8	1·6	98·2
16	2·0	93·8	1·0	99·2[1]
17	1·7	95·5		
18	1·3	96·8		
19	1·2	98·0		
20	0·9	98·8		
21	0·5	99·3[1]		

[1] 100% not reached because of rounding errors during computation

Variation within a Shetland population

Plants fitting Compton's (1920) varietal description—squat, stout-stemmed and hairy individuals with showy dark magenta flowers—do occur in Shetland populations; I have not seen such plants elsewhere. I estimated from rough counts that such individuals occur only about once in a thousand plants. Most individuals are less spectacular.

Initial examination of polygraphs showed little correlation within the East Voe of Quarff population between the characters that define Compton's variety. Female plants appeared to be more variable than males, more often possessing extreme character-states such as exceptionally large or deeply-coloured flowers. Poor correlation between characters was confirmed by correspondence analysis (Table 5).

DISCUSSION

In another paper (Prentice 1979) I have shown that in Europe *S. dioica* has local, weakly differentiated ecogeographic races, defined at least by seed characters (which were found to vary concordantly with flower/capsule characters). *S. alba* in contrast has a clinal pattern of variation. Analyses described in the present paper gave results that are consistent with the idea of combined ecological and geographic differentiation, but within Scotland different subsets of characters—flower/capsule, seed, vegetative—are discordant. Variation in all characters, and in flower/capsule characters (the subset most concordant with 'all characters'), was found to have a geographic component but no relation to habitat, whereas seed characters and vegetative characters showed a mixture of both types of variation.

Analyses based on seed characters by Prentice (1979) do not substantiate the concepts of homogeneous alpine and subalpine ecotypes in the montane areas of Europe (Turesson 1925, Baker 1948a) but suggest the existence of different races in, for example, the French Alps, N. Fennoscandia and the mountains of Scotland. The present work has also provided some evidence that montane *S. dioica* populations in Scotland are distinctive, at least in seed characters. Shetland populations are not adequately differentiated by seed characters alone.

Baker (1947, 1948a) adopted an approach to variation in *S. dioica* that emphasized vegetative features, and combined an 'ecotype' classification with ordinary taxonomy. My results show that the vegetative subset of characters is the most discordant with others, and MDS based on vegetative characters provided evidence for ecological differentiation. In this MDS an inland population from Shetland was separated from the grouped coastal ones. However, the coastal Shetland populations were not placed with other coastal populations and cannot therefore be regarded as representatives of a coastal ecotype. When the full set of characters was used it became clear that the Shetland populations constitute a local race, including coastal and inland members. B_2 clustering showed that the majority of mainland populations most like the Shetland ones were, in fact, not coastal.

The Shetland populations are not unique in being distinctive. In Fig. 2 seven other populations, all noted in the field as distinctive, appear as outliers. Three of these were from woodlands (151, 238, 252: see Table 2 for localities). Populations 238 and 252 consisted of spindly pale-flowered plants growing in deep shade. Three outliers were from sea-cliffs: population 153 was made up of thick-stemmed, tall, stiffly-hairy individuals with large, thick leaves and little variation in flower colour; plants from population 257 were also unusually robust; population 248 included plants with much-branched inflorescences with numerous large flowers. Population 267 was from an atypical saltmarsh habitat—a dense reed bed—and consisted of tall, weak-stemmed plants. Population 243, scored for seed characters only, had few inflorescence branches, long-pyriform capsules, and the largest seeds of all the populations visited.

Given that the Shetland populations are representatives of a local race rather than a coastal ecotype, should the race be recognized taxonomically? My answer is no, for several reasons. Firstly the race is differentiated by only a few characters. Secondly, it is no more distinctive than a number of other possible taxa: there are more distinctive outliers, and other groupings related to ecology or geography. Thirdly, the race overlaps too much with non-Shetland populations, because of substantial, uncorrelated within-population variation in the critical characters. Many Shetland *S. dioica* plants could not be confidently assigned to the Shetland race on morphological criteria without information on the whole population. Subsp. *zetlandica* on present evidence fails the '75% rule', which is an ultra-minimal criterion for recognizing subspecies (Jardine & Sibson 1971). Compton's (1920) variety might be retained for the occasional extreme individuals of *S. dioica* found in Shetland, but this taxon also makes little biological sense because it merely embodies a chance combination of character-states.

ACKNOWLEDGMENTS

This paper describes work that formed part of my Ph.D. thesis. I am grateful to my supervisor, Dr S. M. Walters, for his help throughout the project, and to S. R. C. for financial support. I would like to thank the following people for allowing me to use their unpublished computer programs: Dr H. J. B. Birks (correspondence analysis), Dr I. C. Prentice (K-dissimilarity, discordance) and Professor R. Sibson (MDS). Dr I. C. Prentice also suggested the use of correspondence analysis. I would also like to thank Drs P. Adam, H. J. B. Birks and N. Jardine and Mr W. Scott for discussions; Dr I. C. Prentice for fieldwork assistance; Mr J. Laughton Johnston and his family, and Mr W. Scott for their hospitality in Shetland; and Drs I. C. Prentice and S. M. Walters for reading and commenting on the manuscript.

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(*Accepted February 1979*)