Variation in sea mayweed (Tripleurospermum maritimum (L.) Koch) in the British Isles

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ABSTRACT

Population samples of sea mayweed (*Tripleurospermum maritimum* (L.) Koch) collected from 32 maritime sites in the British Isles showed a wide range of morphological variation in simultaneous cultivation at Oxford, and remained distinct from scentless mayweed (*T. inodorum* (L.) Schultz Bip.). All were diploid (2n = 18, 18 + B, or 18 + 2B). Plants from beach sites generally had fairly long, branching stems, brush-like or rather fleshy leaves, and strongly inflated achenes; the stems were prostrate in plants from exposed beaches but ascending or erect in plants from more sheltered sites. Plants from cliff sites were generally short-stemmed, with fleshy leaves and less inflated achenes. Most characters were substantially retained in cultivation. Plants from the Atlantic coast of Europe from north Portugal to southern England characterised by strong purple pigmentation and narrower leaf segments are referred to *T. maritimum* subsp. *maritimum* var. salinum (Wallr.) Kay, comb. nov. Natural selection appears to maintain the distinctive characters of some local populations despite gene-flow from other populations and from *T. inodorum*. Local populations are often very small, and genetic drift may be an important factor affecting variation.

INTRODUCTION

The sea mayweed, *Tripleurospermum maritimum* (L.) Koch (Asteraceae-Anthemideae), is a biennial or short-lived perennial herb, with much-divided, tripinnate leaves and large, white-rayed capitula, which is native on the coasts of western and northern Europe from northern Portugal to the Arctic. It is a halophytic plant, and is most frequently found near the highest drift-line on beaches and in the spray-zone on sea-cliffs, typically on rather unstable or moderately disturbed substrata. It also grows in some seabird nesting colonies, where it may be very abundant, and occasionally grows in artificially disturbed ruderal sites near the sea.

T. maritimum is a variable species which has attracted the attention of many taxonomists. A number of nomenclatural solutions, usually based on studies of herbarium material, have been proposed for the twin problems of variation within T. maritimum and the relationship between T. maritimum and scentless mayweed, T. inodorum (L.) Schultz Bip. (an annual weed of arable land and waste places). Many names have been coined for the taxa involved, at the levels of species, subspecies, variety and form, and nomenclatural confusion has been increased by periodic re-allocation of the taxa to a new genus; the genera Matricaria, Chrysanthemum, Pyrethrum, Chamaemelum and Tripleuro-spermum have been favoured at different periods. Studies of achene morphology (Briquet 1916, Kynčlová 1970) and of the chemistry of secondary products, especially polyacetylenes (Sørensen 1963), strongly support the inclusion of the taxa in the genus Tripleurospermum, which is now generally accepted. Opinion is still divided on the question of the status of T. maritimum and the related

species T. inodorum. A number of investigators who have used comparative cultivation and other experimental techniques have concluded that T. maritimum and T. inodorum, although interfertile to some extent, are best regarded as separate species (Nehou 1953, Lövkvist 1963, Kay 1969), but other workers have regarded the taxa as subspecies (Vaarama 1953, Pedersen 1961). The marked ecological and morphological differences between T. maritimum and T. inodorum, the infrequency of hybrid and intermediate populations, and the partial or complete sterility of a proportion of the hybrids do, however, support the view that it is best to treat the taxa as species.

The pattern of variation within T. maritimum sensu stricto is not well understood. Several forms of the species were described by Neuman (1882) from Swedish material, and Lester-Garland (1921) attempted to apply Neuman's classification to British plants, though with limited success; Lester-Garland's translation of Neuman's key to the forms is erroneous at one point, partly reversing Neuman's meaning, and annotations on herbarium specimens show that Neuman's and Lester-Garland's classifications were interpreted very differently by different taxonomists. Transplant experiments carried out during the nineteenth and early twentieth centuries (Lloyd 1844, Drabble & Drabble 1910, Massart 1921) were interpreted as showing that T. maritimum was merely an environmental modification of T. inodorum, with no genetic basis, and, if this view is taken, named varieties of T. maritimum have little significance. However, several more recent studies of T. maritimum in which transplant experiments or comparative cultivation have been used have demonstrated that T. maritimum and T. inodorum remain distinct in cultivation, and have also shown that different populations of T. maritimum retain their differences in cultivation (Turesson 1922, Hüser 1930, Nehou 1953, Rottgardt 1956). These investigators each restricted their studies to a relatively small area and a small number of populations. Most recent taxonomic treatments of T. maritimum sensu stricto divide it into three taxa: southern populations with distinctive purplish-red stems and brush-like leaves are separated as the taxon *salinum*; northern and Arctic populations with distinctive broad, brown-black borders to the involucral bracts are separated as the taxon phaeocephalum ('ambiguum'), which is sometimes regarded as a species, and the remaining geographically intermediate populations are regarded as typical maritimum. Clapham (1962) observed that the British forms of T. maritimum (and T. inodorum) required further study; he regarded T. maritimum and T. inodorum as subspecies of T. maritimum (subsp. maritimum, and subsp. inodorum (L.) Hyland. ex Vaarama) but, rather surprisingly, tentatively allocated the maritime forms of southern British coasts (var. salinum) to subsp. inodorum. In his view, subsp. maritimum was found only on the coasts of western and northern Britain, usually as var. maritimum but with some var. phaeocephalum in the extreme north.

Although the taxonomic status of British *Tripleurospermum* populations clearly merited investigation, the work described in the present paper was not undertaken primarily in the hope that it would provide a neat solution to a taxonomic problem. During an investigation of the biology of the British species of *Anthemis, Matricaria* and *Tripleurospermum* (Kay 1965), I realised that the maritime *Tripleurospermum* populations were unusually interesting, both in their varied and often extreme maritime habitats, and in their population structure: small, fluctuating populations of short-lived perennials with a high reproductive capacity, growing in localities which are often widely separated

from one another and subject to considerable environmental changes from year to year. It soon became apparent from field observations that virtually all these maritime populations, including those of southern Britain, belonged to T. maritimum rather than to T. inodorum both morphologically (notably in the characters of their achenes) and, with some exceptions, ecologically, in their close limitation to the drift-line and spray-zone habitat. It was felt that an investigation of the amount of morphological and genetic variation that existed in these populations would be extremely interesting and would help to elucidate the relationships between the populations and the extent to which each population was adapted to its local environment, and would also help to clarify the relationship between T. maritimum and T. inodorum; preliminary morphological investigations had suggested that some populations of T. maritimum had been affected by introgression from T. inodorum.

T. maritimum is a phenotypically plastic species, especially in size, habit and leaf characters, and comparisons between specimens collected in the field are of limited value because the phenotypic differences between plants growing in different environments may lack a genetic basis. Sample groups of plants from the populations that were to be compared were, therefore, grown simultaneously under identical conditions in order to eliminate environmentally induced, purely phenotypic differences. Most of the morphological comparisons described below were made using these simultaneously cultivated plants. The characters of the achenes, which appeared to be relatively non-plastic, were, however, studied using material collected in the field; comparison of achenes collected in the field with achenes collected from cultivated plants showed that the morphology of the achenes remained fairly constant in plants from the same population, whether they grew in their natural environment or in cultivation.

MATERIALS AND METHODS

Thirty-two populations of T. maritimum (some apparently affected by introgression from T. inodorum) and 4 populations of T. inodorum, collected from various sites in the British Isles, were included in the comparison. The localities of these populations are listed in Table 1 and shown in Fig. 1. A brief description of the habitat of each population, the dates when achenes were collected, and rough estimates of the number of established plants in each population and the approximate distance separating each population from the nearest population of the same species (unusually easy to estimate in T. maritimum, which is very conspicuous when in flower) are also given in Table 1. Ripe achenes were collected from some populations in 1962 and from the rest in 1963. Where possible, single ripe capitula (each containing c 50–180 achenes) were collected from each of 25-30 well-separated plants and the samples bulked. In many cases fewer plants were sampled (most frequently because the population was so small that fewer than 25 plants bore ripe achenes) and in those cases a single capitulum was still taken from each plant, but instead of bulking the achenes equal numbers of achenes were taken from each capitulum so that each original plant had an equal representation in morphological comparisons.

All 36 populations were included in a single comparative-cultivation experiment carried out at Oxford in 1963–1965. Achene samples from all the populations were germinated simultaneously in Petri dishes in October 1963, and

Ref. No.	Site	Grid reference	Habitat	Altitude above EHWS	A	В	С	D	Date of collection
1	T. maritimum			16			1 년 2 월 ²	로 한 일 전 코	88.88
1	Scolt Head, Norfolk	53/80.46	DlSaSh	0–1m	15	2	> 5	18 (2)	16.9.63
2	Orfordness, Suffolk	62/46.55	Dl/Rs	0–1m	80	25-30	> 5	18 (1)	4.10.63
3	Swalecliff, Kent	61/13.67	DlSh	0–1m	100	25-30	>10	18 (1)	3.10.63
4	Pegwell Bay, Kent	61/35.64	DlSaSh	0–1m	200	25-30	>10	18 (2)	3.10.63
5	St Margaret's Bay, Kent	61/37.44	D1/Rs	1–2m	40	20-25	> 5	18 (2)	2.10.63
6	Selsey, Sussex	40/85.92	Dl/CF	0–2m	30	12	>2	18, 18 + 2B	29.9.62
	지금 김 라보 한 것 같 한 무							(4, 1)	
7	Portchester, Hampshire	41/62.05	D1/Rs	0–1m	200	25-30	< 0.5	18 (5)	29.9.62
8	Keyhaven, Hampshire	40/30.90	DlGr	0–1m	150	35-40	>1	18 (2)	18.9.63
9	Lulworth Cove, Dorset	30/82.97	CFGr	1–4m	300	35-40	2	18 (1)	19.9.63
10	Burton Bradstock, Dorset	30/48.88	CFGr	1–5m	100	25-30	> 5	18 (2)	22.9.63
11	Perranuthnoe, Cornwall	10/548.285	Dl/CF	0–3m	50	20-25	0.5	18 (1)	30.7.63
12	Perranuthnoe, Cornwall	10/544.289	EC	10–16m	50	20-25	0.5	18 (1)	30.7.63
13	Tintagel, Cornwall	20/05.89	CGr	35m	2	2	>1	18 (2)	5.10.63
14	Dinham, Cornwall	10/97.74	Dl	0m	12	3	1	18 (1)	5.10.63
15	Constantine Bay, Cornwall	10/85.74	DlSa	0–1m	50	12	<1	18 (1)	3.10.62
16	Port William, Cornwall	20/04.86	CGr	35m	15	6–8	<1	18 (2)	1.10.62
17	St Bride's, Pembroke	12/80.11	DlSh	0–1m	40	12	0.8-2	18 (1)	5.9.63
18	Cemaes Bay, Anglesey	23/37.93	CF	2–8m	30	12	0.2 (3)	18 (1)	27.3.63
19	Llanbadrig, Anglesey	23/37.94	Dl/CF	0–5m	50	10	0.6 (3)	18 (1)	27.3.63

TABLE 1. SITE, HABITAT, POPULATION AND SAMPLE SIZES, AND CHROMOSOME NUMBERS OF SAMPLED POPULATIONS OF T. MARITIMUM AND T. INODORUM

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20	Traeth Bychan, Anglesey	23/51.85	CFGr	2–10m	20	5	0.2 (2)	18 (2)	26.3.63	
21	Ferry Point, Co. Waterford	d — b	DlSh	0–1m		3	_	18 (1)	26.8.63	
22	Cromane, Co. Kerry	-	DlSh	0–1m	50	3		18 (1)	15.8.63	
23	Aughinish Bay, Co. Galwa	y —	DlSh	0–1m	50	3	2	18 (1)	21.8.63	
24	Loch Etive, Argyll	17/89.33	DISh	0m	40	8	0.2	18 (1)	12.9.63	
25	Luing Island, Argyll	17/73.08	DlSh	0–1m	100	8	0.5	18 (1)	9.9.63	
26	Seil Island, Argyll	17/76.19	DlSh	0m	30	6	>0.5	18 (1)	8.9.63	
27	Garvellachs Is., Argyll	17/640.096	С	10–50m	30	4	0.3 (2)	18 (2)	27.7.62	
28	Garvellachs Is., Argyll	17/636.093	DlSa	0–1m	12	3	0.3(2)	18 + 2B(1)	27.7.62	
29	Greg Ness, Aberdeen	38/97.04	С	5–20m	150	20-25	0.1	18 (3)	6.9.63	
30	Doonies, Kincardine	38/96.03	EC	20-25m	400	20-25	0.1	18 (2)	6.9.63	
31	Tentsmuir, Fife	37/50.24	DlSa	0m	20	3	>2	18 (1)	19.7.62	
32	Easter Quarff, Shetland	N 41/43.25	Dl	0–1m		5	_	18 (2)	7.10.62	
	T. inodorum									
33	Manston, Kent	61/34.65	Ar	45m	500	25-30	0.2	18 (2)	3.10.63	
34	Aldeburgh, Suffolk	62/46.56	Rs	3m	40	12	< 0.5	18, 18 + 1B	4.10.63	
								(1, 1)		
35	Besselsleigh, Berkshire	42/45.02	Ar	105m	2000	50	0.3	18 (5)	10.10.62	
36	Tannadice, Angus	37/50.57	Ar	70m	2000	25-30	0.2	18 (1)	23.7.62	

KEY

Habitats: Dl, drift-line (on); Sa, sandy beach; Sh, shingle beach; EC, unstable cliff with soft substratum; C, more stable cliff with rock substratum; Gr, grassy sward; CF, cliff-foot; Rs, roadside; Ar, arable land.

A: estimated number of established plants in the population

B: number of plants from which achenes were collected

C: estimated distance to next population in km (distance to next group of populations in parentheses)

D: chromosome number (2n) from germinated achenes (number of seedlings counted in parentheses)

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FIGURE 1. Locations of the populations of *T. maritimum* and *T. inodorum* included in the comparison.

ten seedlings were taken from each sample and grown under uniform conditions in a cool greenhouse, evenly spaced and uniformly illuminated in identical boxes, $45\text{cm} \times 30\text{cm} \times 8\text{cm}$ deep, containing a single batch of sieved John Innes No. 2 potting compost, with 20 plants in each box. In some cases one or more of the seedlings failed to establish themselves, but in most cases growth was satisfactory and uniform within population samples, although marked differences between different populations in the rate of growth of the seedlings were observed. In early May 1964 five plants (but six from populations 3, 12, 22, and 31, and all ten from populations 25 and 27) were taken from each of these groups of ten plants, and transplanted singly into 9cm plastic pots, again containing a uniform batch of John Innes No. 2 potting compost; the pots were

evenly spaced at 15cm centres in rows 20cm apart (and thus moderately crowded) in a water-retaining bed of horticultural peat on a flat, uniform, concrete surface outdoors. Care was taken at all stages to ensure uniform watering and to avoid damage to the plants. The populations were arranged randomly, not in a geographical sequence, but plants from the same population were grown side by side in a single row to facilitate comparison. In most cases the plants appeared to be healthy and grew to a size within the range observed in normal plants of the species in the field. However, in three cases-Tintagel (13), Port William (16), and Luing (25)-most or all of the cultivated plants were moderately to severely chlorotic during the entire period of cultivation, and consequently lacked vigour and were considerably smaller than their parents. The Garvellachs beach (28) plants, although not chlorotic, were also unusually small and weak. In some other cases the cultivated plants, although healthy and of average size, were either larger (e.g. Orfordness, 2, and Swalecliff, 3) or smaller (e.g. Perranuthnoe beach, 11, and Tentsmuir, 31) than those of the original wild population. The main characters that were studied in simultaneous cultivation were, in the seedlings, the morphology of the fourth true leaf and, in the adult plants, the morphology of the rosette leaves, the colour, habit and length of the stems and the degree of perennation. Leaf characters were recorded by shadow-printing on bromide paper, using a focussed light-source so that the outline of the leaf was recorded accurately. The characters of the achenes were studied using samples from the field collection made from each population; the main achene characters that were investigated were the length, width and mean weight of the achene, the degree of inflation of the ribs on the ventral face, and the shape of the 'oil-glands' at the upper end of the dorsal face of the achene.

MORPHOLOGICAL AND PHYSIOLOGICAL VARIATION

There was (with some exceptions discussed below) relatively little variation within most populations of T. maritimum, both in the characters of the achenes collected in the field and in the characters of the plants grown in simultaneous cultivation, but the differences between different populations were very striking in many cases. Variation was generally irregularly clinal, and populations from the same region usually had several regional characters in common, but in some cases populations from closely adjacent localities showed conspicuous differences in several characters, and in other cases populations resembled others from the same region in most characters but had one or more unusual features. T. maritimum and T. inodorum maintained their differences in cultivation. Some populations of T. maritimum showed fairly clear signs of introgression from T. inodorum. The polygraphs in Fig. 2 summarise, for each population, six characters (degree of inflation of the ribs and shape of the oil-glands of the achene, length and angle to the horizontal of the main stem, and the shape and number of the leaf-divisions) which were among those characters which differed significantly from population to population and showed apparent correlations with regional and local environmental variation.

ACHENE CHARACTERS

Differences in achene morphology are regarded as being among the most reliable and constant characters separating *T. inodorum* from *T. maritimum*



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FIGURE 2. Polygraphs showing the population means for two achene characters (n = 30), two leaf characters (n = 10) and two stem characters (n = 5 or more). The short radial lines are drawn to a length equal to twice the standard error of the mean in each case. The sites of the numbered populations are shown in Fig. 1 and listed in Table 1.





FIGURE 3. Achene-length. The circles show the population means; the thick bars are drawn to a length equal to twice the standard error of the mean, and the thin lines to a length equal to twice the standard deviation.

(Nehou 1953); T. inodorum typically has relatively small achenes with the ventral ribs dense in texture and well separated, and the oil-glands at the apex of the dorsal face roughly isodiametric, while T. maritimum typically has larger achenes with the ventral ribs spongy in texture, inflated, and contiguous or scarcely separated, and the oil-glands longitudinally elongated. The size of the achenes (Fig. 3) was found to show considerable variation among the populations of T. maritimum that were sampled. Scatter-diagrams of achene characters (Fig. 4) suggest that the relatively small mean size of the achenes of

FIGURE 4. Scatter diagrams showing the characters of samples of twenty achenes from five populations of *T. maritimum* and one population (33) of *T. inodorum*. The Orfordness (2) and Portchester (7) populations of *T. maritimum* appear to be strongly introgressed by *T. inodorum* and the Selsey (6) population also shows some signs of introgression. The Perranuthnoe beach (11) population exemplifies 'pure' beach *T. maritimum*, with buoyant, strongly inflated achenes. The achenes of the Garvellachs cliff population probably show the effects of relaxation of selection for coat buoyancy in its cliff habitat, rather than introgression from *T. inodorum*; the latter was absent from the uninhabited Garvellachs.



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some populations from the southern and eastern coasts of England (2, 5, 7) was a consequence of introgression from T. inodorum. If these introgressed populations are disregarded, the remaining, relatively pure populations of T. maritimum show a fairly clear regional pattern of variation in achene-size in Britain—an irregular cline, with the size of the achenes decreasing from east to west along the southern coast of England, reaching a minimum in Cornwall, and then increasing northwards to reach a maximum in western Scotland. More samples would of course be desirable; the three Irish samples suggest that a parallel cline may possibly exist in Ireland, and the very large achenes of the Shetland population (32) may represent a northward extension of the cline. T. inodorum also showed a range of mean achene-size among the four populations that were included in the comparison, from 1.48 mm $\times 0.69$ mm (Aldeburgh, 34) to 2.10 mm × 1.16 mm (Tannadice, 36). The mean size of the achenes also varies clinally in T. inodorum in Britain, increasing from a minimum of c 1.5mm \times 0.7mm in southern and eastern England to a maximum of $c 2.2 \text{mm} \times 1.2 \text{mm}$ in northern Scotland (Kay 1965); and while it is usually possible to distinguish T. maritimum from T. inodorum by achene-size alone in southern England, where the achenes of T. inodorum are much smaller than those of T. maritimum, it is not possible to do so in north-eastern Scotland, where the achenes of the two species are similar in size.

The degree of inflation and separation of the ventral ribs of the achenes were scored by comparison with a set of standards (Fig. 2). The achenes collected from beach populations of T. maritimum had uniformly strongly inflated and contiguous or almost contiguous ribs, with the exception of those collected from a number of populations that had probably or possibly been affected by in rogression from T. inodorum (2, 5, 7, and possibly 21, 22 and 24). The achenes collected from some cliff populations of T. maritimum (e.g. 16 and 27) had ribs which were less strongly inflated and showed some degree of separation, and the oil-glands also were relatively weakly elongated (see below); the achenes resembled therefore those of 'introgressed' populations. In comparative cultivation, plants from these cliff populations retained their achene characters, but also retained extremely fleshy leaves, short, little-branched stems, and other extreme maritimum characters.

The degree of longitudinal elongation of the dorsal oil-glands of the achene was also scored by comparison with a set of standards (Fig. 2). The pattern of variation shown by this character was similar to that shown by the rib characters; some achenes with isodiametric oil-glands, resembling those of T. *inodorum*, were found among the achenes collected from 'introgressed' beach populations, and some cliff populations, which were morphologically very different from T. *inodorum* in all except achene characters, also had achenes with relatively broad or even isodiametric oil-glands. Oil-gland shape and rib inflation were weakly linked in 'introgressed' populations (Fig. 4). Much variation in oil-gland shape was, however, found in T. *maritimum*, both within populations and between populations from the same area, in contrast to the relative uniformity of the rib characters. Although the oil-glands of T. *inodorum* are uniformly isodiametric or broader than long, never longitudinally elongated, it was clear that oil-gland shape alone is an unreliable character for distinguishing T. *maritimum* from T. *inodorum*.

A number of achene characters that were difficult to measure or score precisely also showed some variation from population to population, for example

colour, surface texture, shape, the length of the groove separating the ribs, and the form of the short membranous pappus at the crown of the achene (Fig. 5). Narrow, supernumerary dorsal ribs were frequent in some populations. Achenes with four ventral ribs were a minor component of the achene collections from several populations, and a few achenes with only two ventral ribs were observed among the achenes collected from the unusual Shetland (32) population.



FIGURE 5. Dorsal and ventral views of typical achenes from six populations of T. maritimum and two populations (35, 36) of T. inodorum.

GERMINATION BEHAVIOUR

The germination behaviour of the achenes collected in 1962 was studied in January and March 1963. Preliminary tests had shown that the achenes of both species required both light and alternating temperatures for optimum germination, and the comparative tests were carried out in the regime which had given the most rapid and complete germination (16 hours in darkness at 3°C alternating with 8 hours in light at 20°C). Samples of 50 achenes from each population were tested in January, and the experiment was repeated, with samples of 100 achenes from each population, in March. The results are shown in Table 2. The populations of T. maritimum that were tested showed some differences from one another, but all except the introgressed Portchester (7) population germinated much more rapidly and completely than any of the twelve populations of diploid T. inodorum that were included in this comparison, without leaving the residue of dormant but viable achenes which is characteristic of T. inodorum. Only two of these populations of T. inodorum were included in the later morphological comparison in simultaneous cultivation (Besselsleigh, 35, and Tannadice, 36), but the results of germination tests on three other populations of T. inodorum are given in Table 2, to show the typical germination behaviour of diploid T. inodorum.

LEAF CHARACTERS

The adult rosette leaves of *T. inodorum* and *T. maritimum* are irregularly tripinnately divided into a large number of segments. These leaf-segments are

TABLE 2. GERMINATION OF ACHENES OF T. MARITIMUM AND T. INODORUM

3°C night/20°C day temperature alternations were used, with diffused natural lighting. After 21 days in this régime, the pericarps of the remaining ungerminated achenes were removed, and achenes which lacked embryos, or contained embryos which failed to germinate within 7 days after removal of the pericarp, were regarded as inviable. Germination is expressed as a percentage of the total number of viable achenes.

			% germination						
Reference	Site of		nuary 1	963	M	March 1963			
number	collection		Days			Days			
		7	14	21	7	14	21		
CMC VI	T. maritimum	10		100			0		
6	Selsey	59	98	100	75	100	100		
7	Portchester	16	68	96	46	88	93		
15	Constantine Bay	80	100	100	91	99	100		
16	Port William	79	100	100	77	97	100		
27	Garvellachs cliff	4	98	100	20	99	100		
29	Greg Ness	54	98	100	66	100	100		
	T. inodorum								
	Fareham, Hampshire	12	69	81	40	79	86		
35	Besselsleigh	16	70	85	23	78	90		
TO_SUOTE	Stillington, Yorkshire	4	72	82	21	88	95		
	Dalmeny, West Lothian	nil	33	66	6	60	82		
36	Tannadice	2	35	48	9	69	81		

long, narrow and acute in T. inodorum, but relatively short, broad, obtuse and fleshy in T. maritimum. It was found that there was a close correlation between the characters of the fourth leaf of the seedling and those of the adult rosette leaves on the same plant, and most quantitative measurements and comparisons between populations were made using the fourth leaves of simultaneously cultivated seedlings. In most cases ten plants were sampled from each population. The results are summarised in Fig. 2. Differences in the characters of the leaves of different populations of T. maritimum had of course been observed in the field, but the extent to which these differences had a genotypic basis had been uncertain. In simultaneous cultivation many populations retained very marked differences from one another, and these differences were even more striking when they were observed in plants growing side by side (Figs. 6 & 7). Most of the cliff populations had, both in simultaneous cultivation and in the field, leaves with very short, broad, fleshy segments which were relatively few in number, e.g. Port William (16), Garvellachs cliff (27) and Greg Ness (29). The beach populations showed more variation. Most beach populations from southern England had short but relatively narrow leaf segments, which were very numerous and closely packed in the adult leaves. giving the latter a rather brush-like appearance, but the Swalecliff (3) and Portchester (7) populations had relatively few leaf segments, and the Portchester population also had unusually narrow leaf segments, probably as a consequence of introgression from T. inodorum. The leaves of beach and cliff-foot populations



FIGURE 6. Leaf-prints of typical rosette leaves from plants grown in simultaneous cultivation, May 27th 1964. Each leaf was taken from a separate plant.

from western England and Wales had relatively short and broad segments, which were generally fewer in number than those of southern English populations; the Dinham (14) population was exceptional in having unusually narrow leaf segments. The beach populations from Ireland and north-western Scotland showed most variety in their leaf characters. The two southern Irish populations (Waterford, 21, and Cromane, 22) had relatively elongated leaf segments, which were few in number; the leaf segments of the Loch Etive (24) and Luing (25) populations were also elongated, but numerous; the Aughinish Bay (23, western Ireland) and Seil (26, north-western Scotland) populations resembled

5cm

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FIGURE 7. Leaf-prints of typical rosette leaves from plants grown in simultaneous cultivation, 27th-28th May 1964. The sites of the numbered populations are shown in Fig. 1 and listed in Table 1.

one another in having short, narrow and numerous leaf segments which were bunched in separate groups on long, narrow leaves of distinctive appearance. The Tentsmuir (31, eastern Scotland) population, which grew on a sandy beach, had extremely fleshy leaves with short, broad segments resembling those of the eastern Scottish cliff populations (Greg Ness, 29, and Doonies, 30).

The four populations of T. *inodorum* that were included in the comparison all had long, narrow and acute leaf segments which were relatively few in number, giving the adult leaves an open structure which contrasted with the compact fleshy or brush-like structure of the adult leaves of most populations of T. *maritimum*.

HABIT AND STEM CHARACTERS

Many of the populations of T. maritimum that were included in the comparison had shown marked differences from one another in size, habit, and stem characters in the field, but, as with the leaf characters, the extent to which these differences had a genetic basis had been in considerable doubt. However, in simultaneous cultivation there was still much variation from population to population in the size of the plants and in the lengths, pattern of branching, angle to the horizontal and colour of the main and subsidiary flowering stems, and the differences between plants from different populations growing side by side were very striking. At one extreme, all the plants from Aughinish Bay (23) had completely prostrate stems, with the primary stem only half the length of the basal axillary stems; at the other extreme, most plants from south-eastern English populations had erect primary stems which equalled or exceeded the ascending basal axillary stems. The mean values for the length and angle of the flowering stems in simultaneous cultivation are shown diagrammatically in Fig. 8. Most population samples were fairly homogeneous in habit and stem characters, but there were some exceptions. The most notable was the occurrence of a few plants (one in the Portchester sample, 7, one in the Constantine Bay sample, 15, and three in the Seil sample, 26) which lacked normal elongated flowering stems, but had a large number of very short flowering stems which were concealed by the leaves, giving the plants a distinctive caespitose appearance when in flower. The other plants in these three population samples had elongated flowering stems of normal length. All the plants which originated from populations growing on exposed beaches in the western British Isles, from Dorset to Argyll (9, 10, 15, 17, 23, 26), were prostrate, nearly prostrate. or caespitose in cultivation; the prostrate stems grew to a considerable length in some cases. Plants originating from beach populations in southern and eastern England (2, 3, 4, 5, 7, 8) were generally ascending or erect in cultivation, although some came from exposed habitats in which the parental plants had been dwarf or prostrate (e.g. Swalecliff, 3); the Scolt Head (1) and Selsev (6) plants, which came from the most exposed sites in this group, were only weakly ascending in cultivation. Plants originating from populations growing in relatively sheltered beach and cliff-foot sites in the western British Isles were weakly or distinctly ascending in habit (e.g. 11, 18, 22). Plants from cliff populations varied: those from the sheltered Perranuthnoe cliff (12) resembled those from the nearby sheltered beach population (11) in their ascending habit and fairly long stems, but the plants originating from the exposed cliff sites at Tintagel (13) and Port William (16) were prostrate in cultivation; only about half of the plants from the exposed Scottish cliff sites (27, 29, 30) flowered in cultivation,



FIGURE 8. Perennation and habit of the flowering stems of the population samples of *T. maritimum* and *T. inodorum* in simultaneous cultivation. The lines show the population means for the lengths and angles of the primary stem (in centre) and the longest basal axillary stems. The metroglyphs show the proportion of plants that had formed perennating rosettes, and the mean diameter of the perennating rosettes, on 18th January 1965.

and those that did had short, ascending flowering stems, as did the anomalous Tentsmuir (31) beach population.

The populations of T. *inodorum* that were included in the comparison showed some variation in habit in cultivation, but all had erect or ascending main and axillary stems, with the primary stem exceeding the axillary stems. However some populations of T. *inodorum* from southern England, for example cereal weed populations from the Berkshire Downs and northern Norfolk, can assume a prostrate habit in cultivation, although others, for example the Tannadice (36) cereal weed population, appear to have a fixed erect habit even in well-spaced cultivation (Kay 1965).

The colour of the flowering stems of T. maritimum shows a wide range of variation, from pale green to intense purplish-red; the purplish-red anthocyanin pigmentation may also extend into the bases of the leaves. The colour of the flowering stems of T. inodorum varies less, and is usually pale or medium purplish-red. In simultaneous cultivation, the most intense purplish-red pigmentation was found in plants of T. maritimum from populations on the southern coast of England (2, 4, 6, 7, 8, 9, 10, 11, 12) and no plants from this region lacked pigmentation. Some plants from several populations in western Britain and Ireland (15, 17, 18, 19, 21, 23, 25) showed medium purplish-red pigmentation, but most plants from the west and north had stems with pale purplish-red pigmentation, and some plants lacking pigmentation occurred in the samples from all the Anglesey and Argyll populations (18, 19, 20, 24, 25, 26, 27, 28). All the plants in the Tintagel (13) and Tentsmuir (31) populations lacked anthocyanin pigmentation.

Deep purplish-red stem coloration has been regarded as a character of the southern 'salinum' taxon of T. maritimum. Some such plants occurred in all the cultivated population samples with relatively brush-like 'salinum' leaves, but other plants in most of these samples had stems which did not differ in colour from those of some plants from northern and western populations with no 'salinum' characters. However, the intensity of the pigmentation appeared to increase in dry conditions, and it is possible that southern populations may have relatively darker stems in their rather drier natural environment than they have in cultivation.

PERENNATION

T. maritimum is intermediate between a hemicryptophyte and a rosette chamaephyte in its growth form, perennating rosettes of leaves being formed near to and around the bases of the flowering stems in the autumn. It is usually a rather short-lived perennial, and in the field plants often die after flowering profusely. The extent to which the plants perennated in simultaneous cultivation was estimated by recording the occurrence and average diameter of perennating rosettes in late January 1965 (Fig. 8). None of the plants from populations of T. inodorum perennated, and all were dead by late January. Most of the plants from populations of T. maritimum perennated well, and in the majority of cases all the plants from a population perennated strongly. One plant was lost from populations 5, 7, 13, 15, 16 and 23, two from 10 and 22, three (of ten) from 27, four from 2, 14 and 12, and none survived from 28. The perennating rosettes were exceptionally small (3 cm or less in diameter) on the surviving plants from 2, 12, 22, 23, 24 and 32. Many of the populations which lost plants or perennated weakly (especially Orfordness, 2, Portchester, 7, Dinham, 14, Loch Etive, 24.

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and, to a lesser extent, St Margaret's Bay, 5, Perranuthnoe cliff, 12, Cromane, 22, and perhaps Shetland, 32) were those which deviated towards T. *inodorum* in their morphological and other characters, and thus may have been affected by introgression. The relatively poor perennation of the plants from the Burton Bradstock (10), Tintagel (13), Constantine Bay (15), Port William (16) and Garvellachs beach (28) populations, none of which showed any clear evidence of introgression from T. *inodorum* in their vegetative characters, appeared to result from their unusual habit of growth. All were exceptionally prostrate (Fig. 8) and formed perennating rosettes some distance along their prostrate stems; in the field, these rosettes would probably be able to form adventitious roots and establish themselves, but in pot cultivation they were formed beyond the rim of the pot and tended to die. The plants from the small Tintagel and Garvellachs beach populations, which consisted respectively of two and twelve established plants, were also rather weak in the field (Table 1), perhaps as a consequence of inbreeding depression.

CHROMOSOME NUMBERS

Both diploid (2n = 18) and tetraploid (2n = 36) cytotypes exist in *T. inodorum* (Rottgardt 1956, Kay 1969); all the populations of *T. inodorum* that were included in the comparison were diploid. Most well-authenticated chromosome counts of *T. maritimum* have given 2n = 18, but counts of 2n = 36 have occasionally been reported for the species, for example by Harling (1951). Chromosome counts were made on one or more plants from each of the 32 populations of *T. maritimum* that were included in the comparison: all were diploid (2n = 18). Plants with one or two supernumerary chromosomes occurred in some populations (Table 1).

FERTILITY OF INTERSPECIFIC AND INTERPOPULATION HYBRIDS

Two interspecific (6×35 , 15×35) and two interpopulation crosses (6×27 , 5×29) were made. The interspecific crosses gave a high yield of hybrid seed, with either species as the female parent; the F₁ hybrid plants were vigorous, morphologically intermediate, and of moderate to fairly high (50%-80%) pollen fertility; F₂s and backcrosses showed a wider range of morphology and fertility, and included a few sterile plants. The plants from the interpopulation crosses were also vigorous and morphologically intermediate between their parents; no plants from the 6×27 (Selsey × Garvellachs cliff) cross flowered in cultivation, but five plants from the 5×29 (St Margaret's Bay × Greg Ness) cross flowered; all were of high pollen fertility (more than 90%).

DISCUSSION

The number of populations of *T. maritimum* that was sampled for this investigation was relatively small (32), but their sites covered a wide geographical and ecological range, and they probably included much of the range of genetic variation found in the British Isles. It would have been desirable to have grown a greater number of plants from each population in simultaneous cultivation, but the large size of the plants and the limited area available for experimental cultivation made this impossible. Nevertheless the samples were large enough to demonstrate satisfactorily the pattern of variation within the species; the relatively small amount of variation found within most population samples,

and the consistent and often large differences found between the samples in many characters, were striking, and in most cases experimental sampling error, although it undoubtedly occurred, probably did not affect the validity of the results.

The problem of the relative importance of the various factors-natural selection, gene-flow from other populations, the number of plants in the population, and introgression from T. inodorum-which may originate and maintain the genetic differences between different populations of T. maritimum. is of great interest. The overall pattern of variation has already been described. Marked differences were found between adjacent populations and among populations growing in the same area in a number of instances. In the case of the Garvellachs beach and cliff populations, considerable differences were found between populations growing in strongly contrasted habitats (shell-sand beach and exposed vertical cliffs) within 300m of one another, on a small uninhabited island 8km from the nearest cultivated island and 11km from the mainland. The Perranuthnoe beach and cliff populations, which were separated by about 500m, grew in less contrasted habitats (cliff-foot and sloping earthy cliffs, both with a southerly aspect) and showed few differences; the differences that were observed were mainly in achene characters and degree of perennation, and may well have been a consequence of introgression into the cliff population from T. inodorum, which grew as a weed of neighbouring farmland. Both the north Cornish (13–16) and the Argyll (24–28) populations showed considerable diversity, much of it apparently adaptive, among populations separated from one another by distances of a few kilometres; only the Dinham (14) and Loch Etive (24) populations showed clear signs of introgression from T. inodorum.

NATURAL SELECTION

Many of the morphological characters that were investigated in simultaneous cultivation appeared to be of some adaptive importance, and a number of the differences between different populations in these characters can be tentatively correlated with differences in the environments of the original populations. In comparative cultivation, plants from exposed cliff populations generally had relatively short and little-branched stems, fleshy leaves with relatively few divisions, showed greater variation from population to population in the date of first flowering (perhaps correlated with the differing aspects of their habitats) and had achenes with ribs less strongly inflated than did plants from beach populations; the latter usually had longer, branched stems, which were extremely prostrate in plants from some exposed localities but ascending in plants from more sheltered localities, and had less fleshy and often muchdivided leaves; the strongly inflated ribs of the achenes of plants from beach sites appear to be an adaptation for dispersal by water (see below). These apparently adaptive morphological differences were retained in cultivation and presumably resulted from genotypic differences between the populations. However, T. maritimum is a phenotypically plastic species, and it was evident that genetic assimilation of apparently adaptive phenotypic characters which were observed in the field had been incomplete in some cases. For example, the Tentsmuir (31) beach population closely resembled the apparently welladapted cliff populations from the same region (29 and 30) in cultivation (short little-branched stems, fleshy leaves, late-flowering), but differed from them

in the field, where the Tentsmuir plants were tall and much-branched, with less fleshy leaves. Conversely, and less unexpectedly, the Swalecliff (3) and Pegwell Bay (4) beach populations were prostrate or short-stemmed in their rather exposed natural habitats, but were tall and erect in cultivation. It could be argued that the relative loss of phenotypic plasticity shown by many of the other investigated populations of T. maritimum, which retained in garden cultivation characters more suited to a windswept beach or spray-washed cliff, was unadaptive because they would be unable to take advantage of locally or temporarily more favourable conditions in the field, but perhaps it is selectively advantageous in their natural habitats to be prepared for unfavourable conditions.

Gene-flow between genetically different populations of *T. maritimum*, and even between *T. maritimum* and *T. inodorum*, is probably fairly free in many cases (see below) and it seems that continuous natural selection must play a very large part in maintaining the genetic differences between different populations of *T. maritimum* growing in different habitats, especially when they are closely adjacent to one another.

GENE-FLOW AND ACHENE DISPERSAL

T. maritimum is self-incompatible (Kay 1965), and is visited and cross-pollinated mainly by flies; few bees visit its flowers, although those that do (e.g. Andrena spp.) may be of some local and seasonal importance. Pollinating flies are, however, abundant and active during most of the flowering season, and some strong-flying species (e.g. Eristalis spp.) are able to fly several hundred metres with ease; other, weaker-flying species may be blown for similar distances and then return to the capitula of T. maritimum, especially in the linear coastal habitat in which coastwise winds may be frequent for topographical reasons. Thus gene-flow by cross-pollination probably occurs freely, both within populations and between closely adjacent populations. Ecological barriers may reduce cross-pollination between neighbouring beach and cliff populations to some extent, but intermediate and transitional habitats are common.

Local populations are often spatially isolated from one another because areas of beach or cliff which are suitable for T. maritimum may be separated by long stretches of unsuitable coastline. Thus, as for example on the coast of south-eastern England where unfavourable chalk cliffs or sea-walls separate occasional suitable drift-line sites, a local population or group of neighbouring populations may be separated from the next population or group of populations by a distance of several kilometres. The same is true of some other coastal species, for example Crambe maritima, Lavatera arborea and Raphanus maritimus. Populations of T. maritimum growing on islands may also, of course, be separated from the next island or mainland population by a considerable distance. Such populations may therefore be separated from one another by too great a distance for inter-population pollen transfer to occur. However, there may still be some gene-flow between the populations. T. maritimum is probably dispersed over medium and long ranges quite effectively by its floating achenes. Achenes collected from the Selsey (6) population were found to remain afloat in sea-water for at least eight months, meanwhile retaining high viability (Table 3); and the highest drift-line, where floating achenes may be deposited by winter storms, is a common habitat of beach populations of T. maritimum. Thus beach populations may be in genetic contact with one another by floating achenes,

TABLE 3. FLOATING AND SURVIVAL OF ACHENES OF T. MARITIMUM AND T. INODORUM IN SEA WATER

Replicates of 50 achenes were used. The containers were stored at 20° C and periodically shaken. After the 40 day and 220 day periods, the achenes from one replicate of each sample were removed from the sea water and washed in distilled water; the pericarps were removed from the achenes and the embryos were placed on moist filter-paper in petri dishes. The embryos which failed to germinate within two weeks appeared to be dead, and were regarded as inviable.

	2 days		40 d	ays	220 days		
	% floating	% viable	% floating	% viable	% floating	% viable	
T. maritimum (Selsey, 6)	100	n.d.	98	84	96	88	
T. inodorum (Besselsleigh, 35)	20	n.d.	16	84	double 4	74	

even though they may be separated by distances of many kilometres. This mode of dispersal will be less effective as a means of genetically linking cliff populations with one another and with beach populations, because many cliff populations do not extend down to the level of the storm drift-line. However, cliff populations which lack suitable cliff-foot habitats may interpollinate with neighbouring beach populations, and may thus be in indirect genetic contact with other cliff populations through the floating achenes of intermediary beach populations. Direct genetic contact between spatially isolated cliff populations may occasionally take place as a consequence of achene-dispersal by seabirds or man.

INTROGRESSION FROM TRIPLEUROSPERMUM INODORUM

Intogression from T. *inodorum* into T. *maritimum* is probably common. Hybrids between the species are vigorous and moderately to fairly highly fertile, and can often be found, sometimes in considerable numbers, in places where the parental species meet and suitable intermediate habitats occur. Populations of hybrid origin are locally well-established as weeds of some ruderal habitats in western Britain (see below).

Many isolated populations of T. maritimum in southern England, and probably also elsewhere, grow in sites where T. inodorum is abundant in nearby farmland, but are separated from the nearest population of T. maritimum by distances of some kilometres. Such populations may cross-pollinate freely with T. inodorum, while they are in contact with other populations of T. maritimum only by drifted achenes. Field observations suggested that this was the case with the Keyhaven (8), St Margaret's Bay (5) and Pegwell Bay (4) populations; the Orfordness (2), Swalecliff (3) and Portchester (7) populations were close to fairly large roadside populations of T. inodorum, and the Perranuthnoe (11, 12) and possibly also the Selsey (6) and Lulworth (9) populations were fairly close to smaller populations of T. inodorum. However, the populations in this southern English group that clearly deviated towards T. inodorum in their morphological characters in cultivation (2, 5, 7, 12) all grew in habitats

that were to some extent intermediate between the arable land and roadside habitats of T. inodorum and the maritime habitat of T. maritimum. The Orfordness and Portchester sites were both disturbed roadsides which sloped down to the beach and were within reach of winter high tides, the St Margaret's Bay plants grew on a shingle-ridge which was enclosed by a low sea-wall and used as a car-park but was still within reach of spray and occasional waves during winter storms, and the Perranuthnoe cliff site was an unstable sloping earthy cliff below the edge of a ploughed field. Natural selection may have favoured the intermediate characters provided by introgression from T. inodorum in these intermediate habitats. Introgression from T. inodorum may also have affected the Swalecliff and Pegwell Bay populations to some extent; although these populations had extremely inflated achenes and other unmistakable characters of T. maritimum, they also had some unusual features, in leaf characters, habit, and perhaps increased plasticity, which may have resulted from some gene-flow from T. inodorum. The Lulworth, Keyhaven, and Selsey populations, which showed scarcely any morphological signs of introgression from T. inodorum, grew in typical maritime sites; the Keyhaven population, which grew on the seaward side of a grassy sea-wall enclosing a cultivated field in which a large population of typical T. inodorum grew as a field weed, must have been particularly subject to cross-pollination by T. inodorum.

This evidence strongly suggests that substantial introgression from T. *inodorum* into a population of T. *maritimum* can only take place when a fairly large population of T. *inodorum* is present and when the habitat of the T. *maritimum* population has been modified by artificial disturbance.

POPULATION SIZE

The population structure of T. maritimum is unusual in several ways: in the small number of plants in a typical population (populations of less than 50 established plants, separated by distances of 1km or more from the next population, are the rule rather than the exception in some areas), in the temporary and unstable nature of the cliff and drift-line habitat, in the fairly wide range of shore habitats in which the species can grow, and in its effective means of long-distance dispersal by floating achenes. It is difficult to see how the founder effect (incomplete representation of the range of genetic variation of the species in the small number of plants founding a new population) and genetic drift (random fluctuations leading to loss of alleles in small populations) can fail to affect the genetic nature of some populations of T. maritimum. The plants that were grown from the achenes collected from the two smallest populations that were sampled (Tintagel, 13, and Garvellachs beach, 28, the former consisting of two established plants and the latter population of about twelve) were relatively weak in cultivation and appeared to suffer from inbreeding depression, presumably as a consequence of the operation of these two virtually indistinguishable factors. However, the small number of adult plants in an apparently isolated population of T. maritimum may be to some extent misleading; many more plants may be seasonally present at the seedling stage, perhaps regularly including some growing from achenes drifted from other populations, and there may thus be opportunities both for competition among a variety of genotypes and for recruitment of new alleles into the gene-pool of the population. On the other hand, not all the established plants may flower in any one year, and those that do flower may have differing success, so that the

majority of the achenes will be produced by a much smaller number of plants than is present in the whole population.

One way to demonstrate the extent to which small populations of T. maritimum may have lost normally widespread alleles would be to determine the number of incompatibility alleles occurring in the population. T. inodorum has a sporophytic self-incompatibility system of the type found in other members of the Asteraceae (Kay 1965), and T. maritimum presumably has the same system. Large numbers of alleles must occur at the single self-incompatibility locus for this system to be fully effective. A population composed of, or solely descended from, a small number of plants will possess a limited number of alleles; if, for example, an isolated population has at some stage reached a minimum of three plants, a maximum of six self-incompatibility alleles will be present in the population.

THE CLASSIFICATION OF TRIPLEUROSPERMUM IN THE BRITISH ISLES

It is difficult to fit the patterns of variation of variable outbreeders like *Tripleurospermum maritimum* and *T. inodorum* into the classical taxonomic categories, and any attempt to do this, and particularly to divide differentiated local populations into varieties, is inevitably unsatisfactory and to some extent misleading in that it superimposes a discontinuous classification on a pattern of variation which is essentially continuous. The most appropriate formal classification of the taxa of *Tripleurospermum* found in the British Isles is given below together with a key.

T. INODORUM (L.) Schultz Bip. $(2n = 18, 36; \text{ annual weeds of arable land and waste places; mainly diploid in western Europe, tetraploid in eastern and northern Europe, tetraploids very rare in the British Isles. Populations 33–36.)$

T. MARITIMUM (L.) Koch (2n = 18; short-lived perennials of maritime habitats and some inland ruderal sites.)

Subsp. MARITIMUM

var. MARITIMUM (Coasts of British Isles, North Sea and the Baltic. Populations 1–3, 13–31.)

var. SALINUM (Wallr.) Kay, comb. nov.

Pyrethrum inodorum var. salinum Wallr., Sched. Crit., 485 (1822) (Atlantic coast of western Europe from northern Portugal to northern France and southern England. Populations 4–12.)

Subsp. PHAEOCEPHALUM (Rupr.) Hämet-Ahti (Coasts of northern Scotland, Shetland Islands, Faroe Islands, Iceland, Greenland, Arctic coasts of N. America, Scandinavia and the U.S.S.R. Population 32.)

3 Flowering stems purplish-red to at least half-way; rosette leaves brush-like distally, with segments 0.5–0.6mm wide

T. maritimum subsp. *maritimum* var. *salinum* Flowering stems with red pigmentation confined to bases of main and axillary stems or absent; rosette leaves not brush-like, with segments 0.6–1.0mm wide ... *T. maritimum* subsp. *maritimum* var. *maritimum*

Some local populations and groups of populations included in var. maritimum in this classification are very distinct morphologically and might well be distinguished as separate varieties (e.g. populations 23 and 26, 27 and 29–31). Each of these groups, like var. salinum and var. maritimum sensu stricto, has a genetic basis and is morphologically distinct and identifiable in its typical form. It must however be clearly realised that within subsp. maritimum all the state either certainly or probably intergrade with some or all of the others both morphologically and genetically; plants of more than one taxon may be found in the same population and many plants and populations are morphologically intermediate between taxa. The same considerations apply to subsp. phaeocephalum and subsp. maritimum; from herbarium specimens it appears that these subspecies probably hybridise and intergrade in northern Scotland as they do in Scandinavia (Hämet-Ahti 1969).

Extensive hybridisation between T. maritimum and T. inodorum, leading to the local establishment of variable but generally intermediate populations, appears to be a relatively recent phenomenon in the British Isles. Morphologically intermediate populations have been observed on areas of industrial waste land with unstable soils within a few miles of the sea in several parts of western Britain. Suitable habitats may be created and maintained by industrial activity (especially smelting and quarrying) and also occur near railways and main roads but are often impermanent (e.g. on construction sites). Habitats of this type have existed only since the mid-eighteenth century in the British Isles. These intermediate populations, which usually include a proportion of morphologically abnormal and sterile plants, require further study. Interspecific hybrids have also been seen by the author at a number of localities where farmland, with T. inodorum as a weed, adjoins drift-line or cliff sites with natural populations of T. maritimum, for example near the Keyhaven (8) and Perranuthnoe cliff (12) populations. These hybrids were, however, few in number and mainly restricted to narrow strips of intermediate habitat. Opportunities for hybridisation between the species must have been present for a much longer time in these seaside farmland habitats than in the industrial wasteland habitats described above.

Much work remains to be done on the problems of micro-evolution and variation in the sea mayweed. More work on the effective size of populations and on fluctuations in their size and genetic composition, and on the interrelationships and degree of differentiation of neighbouring local populations would probably be most rewarding.

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