PART IV

FURTHER ASPECTS OF VARIATION IN THE MATURE PLANT

CHAPTER 10. MORPHOLOGICAL VARIATION.

This chapter contains descriptions of the variation in certain morphological characters which have not been considered thus far. The data on which these descriptions are based have been collected from measurements of the population samples under a range of cultivation conditions. In many cases the within-population variation is considerable and, where it has been tested, the plastic response high. For this reason only the statistics relating to those characters which appears to vary in a (statistically) significant way on general inspection have been further analysed. (It is hoped at a future date to apply to this data the numerical techniques recently developed by the use of computers in taxonomic studies).

Many of the characters have been measured on young plants (i.e. less than 1 year old) and variation in the mature plants is a result of a minimum of 2 and a maximum of 3 years cultivation. (In exceptional cases plants were grown for 5 years).

I Growth Habit.

Variation between populations in general habit of growth, which was often very marked, was easier to recognise and describe than to quantify. Notes were made on certain characteristics, such as the development of basal leaves and the degree of branching, and these are summarised in Table 10.1. In addition to this table, further discussed below, photographs of typical plants from a selection of populations have been included below to give an indication of the general range of variation in growth habit.

Growth habit was found to be related to other characters, such as life-cycle, fruit production, and earliness of flowering, referred to in earlier chapters. A general summary of the between-population variation for all the characters measured is given in Chapter 12.

An attempt to quantify the variation in general habit was made by the measurements of prostrateness in a number of young plants grown from fruit collected in the wild (and thus representing a non-selected range of variation - see Discussion). This is described under (b) below. (a) contains a comparative descriptive account of growth habit in which an attempt to quantify the variation has been made by distinguishing three leaf 'types' and regarding 'branching' and 'woodiness' as characters in the normal taxomonic sense.

(a) Vegetative development. It is possible to recognise three distinct types of leaf in mature A. tripolium plants. These may be described as 'basal', 'sub-basal', and 'stem' leaves respectively (see Fig. 10.1a). The basal leaves are those which first develop after the cotyledons and form the initial basal rosette. They are generally oblanceolate to obovate (but see II below) and may persist for only a short time. The sub-basal leaves develop later below the rosette of basal leaves and are generally borne on a secondarily thickened swollen stem (or rhizome). The

Fig 10.1(a) Leaf types

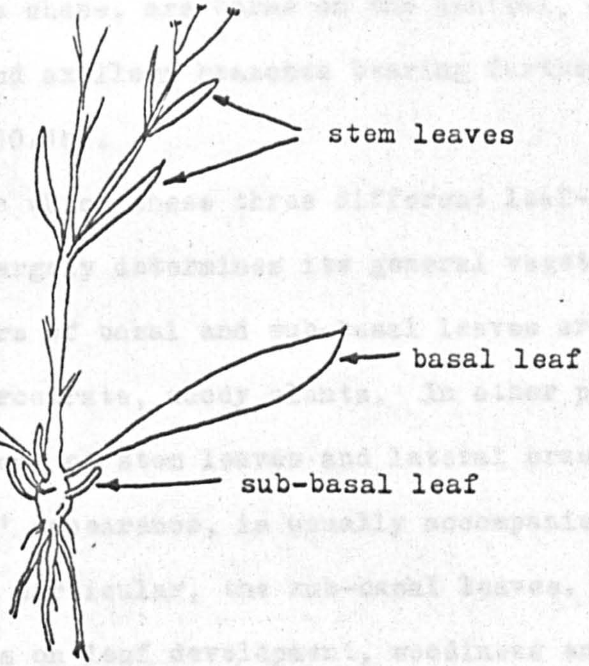
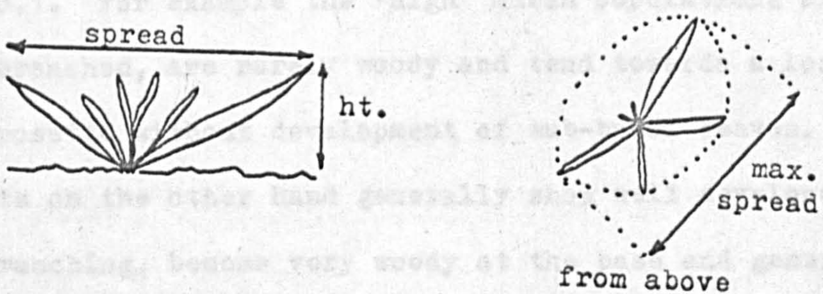


Fig 10.1(b) Measurement of habit index.



$$\text{habit index} = \frac{\text{max. ht.}}{\text{max. spread}}$$

stem leaves which, like the sub-basal leaves, are generally narrowly oblong to linear in shape, are borne on the central, generally erect, stem and may subtend axillary branches bearing further similar stem leaves (Fig. 10.1a).

The extent to which these three different leaf-types develop in a given plant largely determines its general vegetative appearance. Large numbers of basal and sub-basal leaves are developed in the generally prostrate, woody plants. In other plants, extensive development of stem leaves and lateral branches, giving the plant a 'bushy' appearance, is usually accompanied by poor development of, in particular, the sub-basal leaves.

General notes on leaf development, woodiness and degree of branching in those populations measured are given in Table 10.1. The populations are listed in approximate descending order of marsh height (as Table 3.3). Representative plants are shown in Figs. 10.2 to 10.13.

Although there are a number of exceptions, discussed below, in general certain patterns of growth habit emerge from the data in Table 10.1. For example the 'high' marsh populations are largely unbranched, are rarely woody and tend towards a loss of the basal rosette without development of sub-basal leaves. 'Mid' marsh plants on the other hand generally show well developed axillary branching, become very woody at the base and generally develop sub-basal leaves irrespective of whether the basal leaves persist or not. 'Low' marsh plants show little branching, a certain amount of woody basal growth, an almost entire lack of

TABLE 10.1 GENERAL GROWTH HABIT

Population	Treatment	Basal leaves	Sub-basal leaves	Basal development	Degree of branching	Fig. (photograph of representative plant(s))
Gib. Agr.	H	Generally lost	Never develop	Rare	Generally unbranched occas. several leaders	10.2a 10.2b
"	P	Occasionally persist	"	Some thickening	Rarely branched	10.2c
"	G	Usually lost	Never develop	"	Often several leaders	–
"	F	Occasionally persist	"	"	Rarely branched	–
Cley	H	Persist	Present in some plants	"	Unbranched single leader	10.3
Parkgate 1	H	Usually lost	Rarely present	"	Rarely branched	–
Anglesey A	H	Generally lost	Occas. develop	"	Rarely branched but sometimes several leaders	10.7
Scolt Srl.	H	Usually lost	Often present	Occ. woody	Little branching several leaders	10.5
"	G	"	"	"	Tall often much branded	–
Gib. Lim.	H	"	Occ. develop	"	Often spreading much branched	10.6
Naze	H	Persistent	Always develop	Generally v.woody	Few branches many leaders	10.23a
"	G	Occ. lost	"	"	"	–
"	P	"	"	"	"	10.13b

continued..........

Table 10.1 continued.......

Population	Treatment	Basal leaves	Sub-basal leaves	Basal development	Degree of branching	Fig. (photograph of representative plant(s))
Gib. Ast.	H	Generally persist	Generally develop	Most plants woody	Often much branched	10.9
"	G	Often lost	"	"	Often much less bushy	-
Tetney old marsh	H	Generally lost	Often develop	Variable usually thickened	Generally branched with few leaders.	-
"	F	"	"	"	"	-
R. Lune	H	Usually persistent	Always develop	Very wood	Branched	10.17a
Knott End	H	Persistent	"	"	"	9.5b
"	G	Often lost	"	"	Several leaders occ. branched	-
"	F	Occas. lost	"	"	"	10.8
R. Wyre	H	Persistent	Many develop	"	Spreading and bushy but little axill. branching.	-
Anglesey B.	H	Persistent	Some present	Often woody	Some branching	10.4
Beach Pt. Scolt	H	Generally persist	Rarely develop	Generally woody	May be several leaders generally unbranched	10.10 10.17b
"	G	Often lost	"	"	Occas. branched	-
"	F	"	"	"	"	-

continued ....

Table 10.1 continued ....

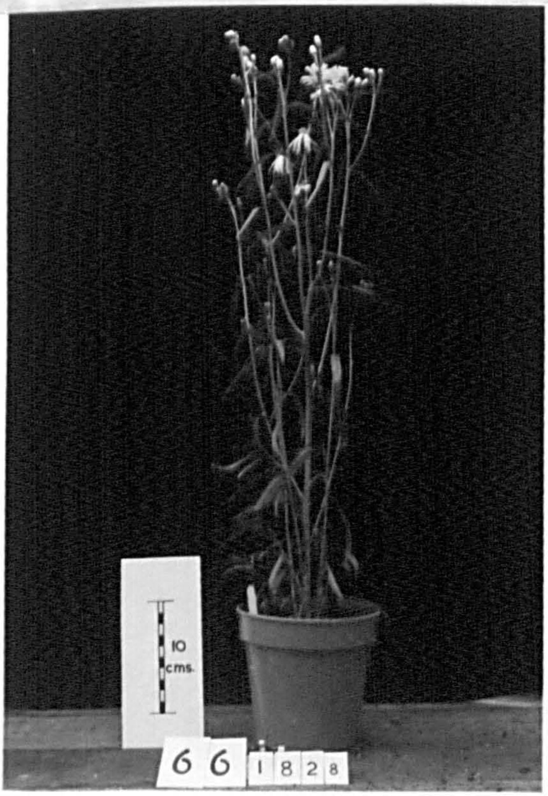
Population	Treatment	Basal leaves	Sub-basal leaves	Basal development	Degree of branching	Fig. (photograph of representative plant(s)).
Beach Pt. Scolt	P	Generally lost	Rarely develop	Generally woody	Rarely branched	–
Beach Pt. 1965	H	Generally persist	"	Occas. woody		9.5a
"	G	Generally lost	"	"	Rarely branched	–
Parkgate 4	H	Usually persist	Rarely develop	Some thickening	rarely branched	–
Gib. Spa.	H	Always lost later	Never develop	Stout at base	Occas. branched	10.11
"	P	"	Rarely develop	"	Rarely branched	–
"	G	"	"	"	Generally some branching	–
Scolt Cob.	H	Generally lost	"	Stout base	Unbranched	10.12
"	G	"	"	"	Occas. branched	–
"	F	"	"	"	Rarely branched	–

The double lines separate marshes of different type (i.e. high, mid and low).

Key to treatments

H – cold house
G – experimental garden
P – poor soil
F – open frame

Fig 10.2 Gib. Agropyron marsh plants. (a) above; cold house from fruit, (b) below left; cold house from wild collected seedling, (c) below right; poor soil treatment.



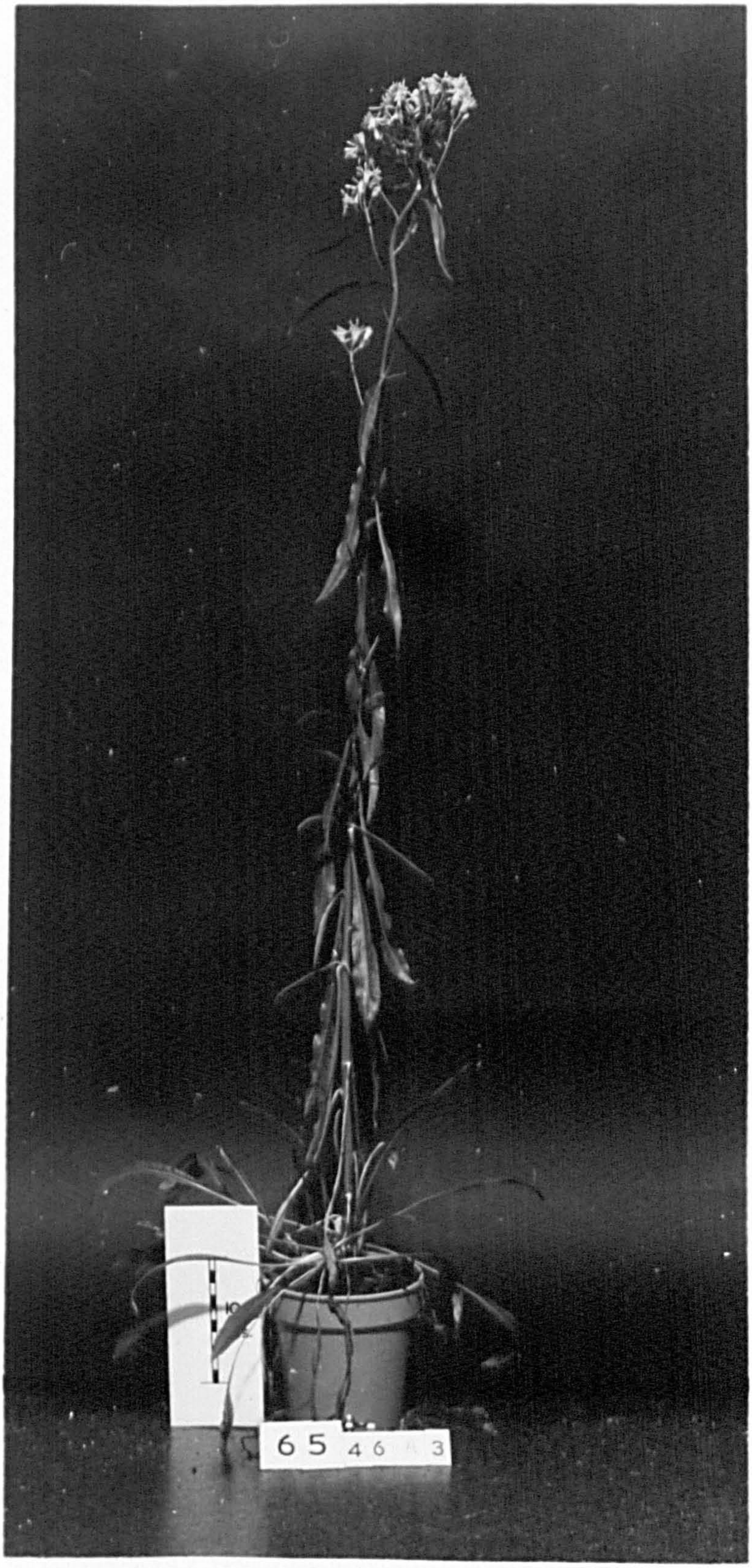


Fig 10.3 Cley - cold house from fruit.

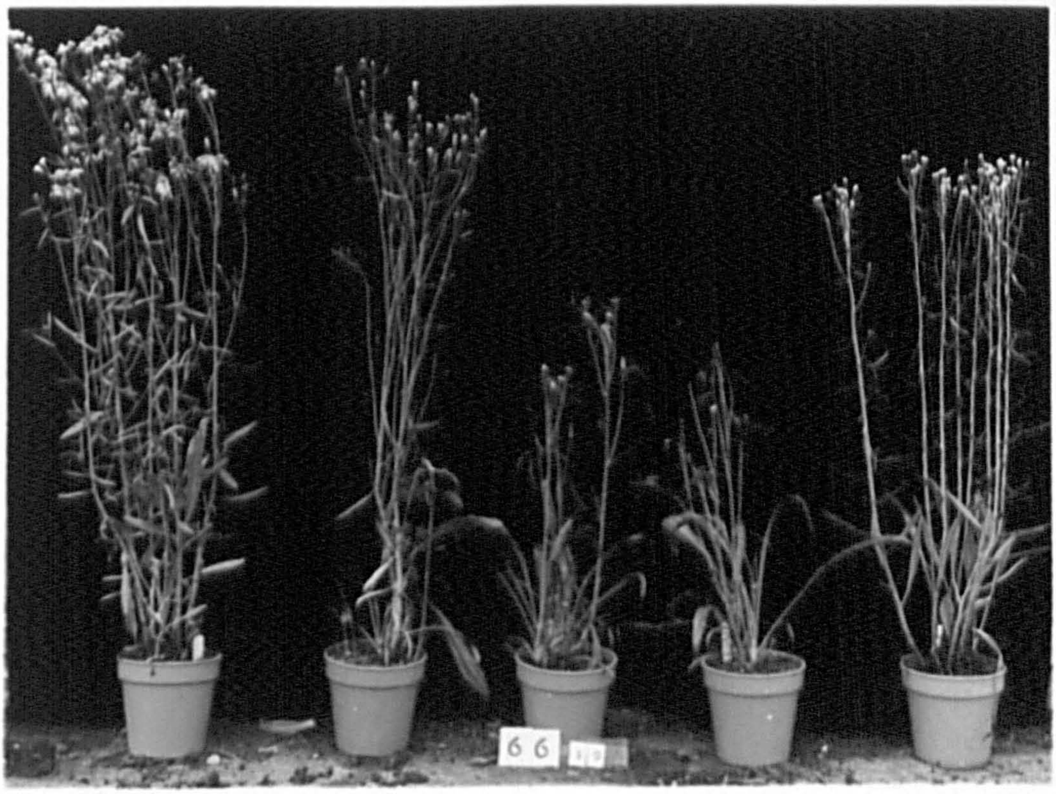


Fig 10.6 Gib. Limonium marsh - cold house from fruit.

Fig 10.7 Anglesey A - cold house from seedlings.

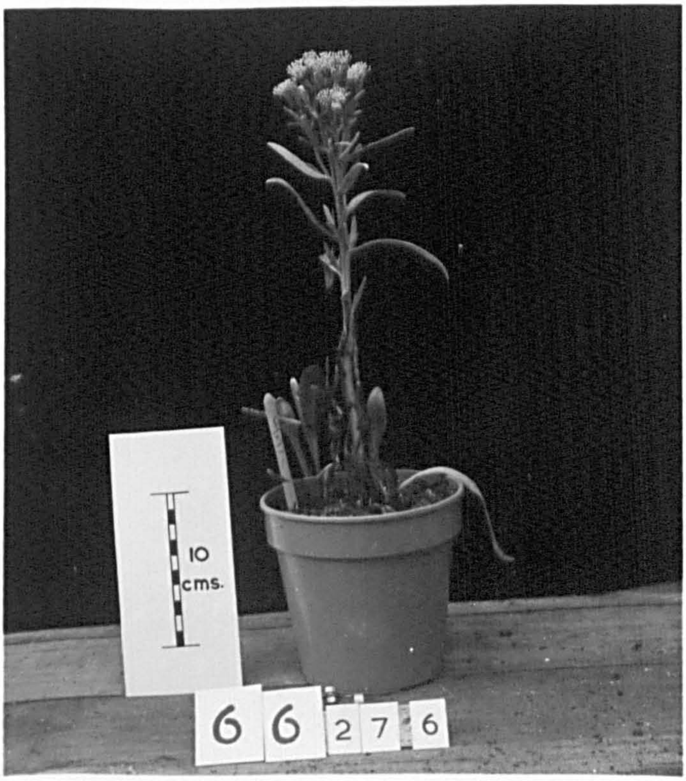


Fig 10.10 Scolt Beach Point - cold house from seedlings.

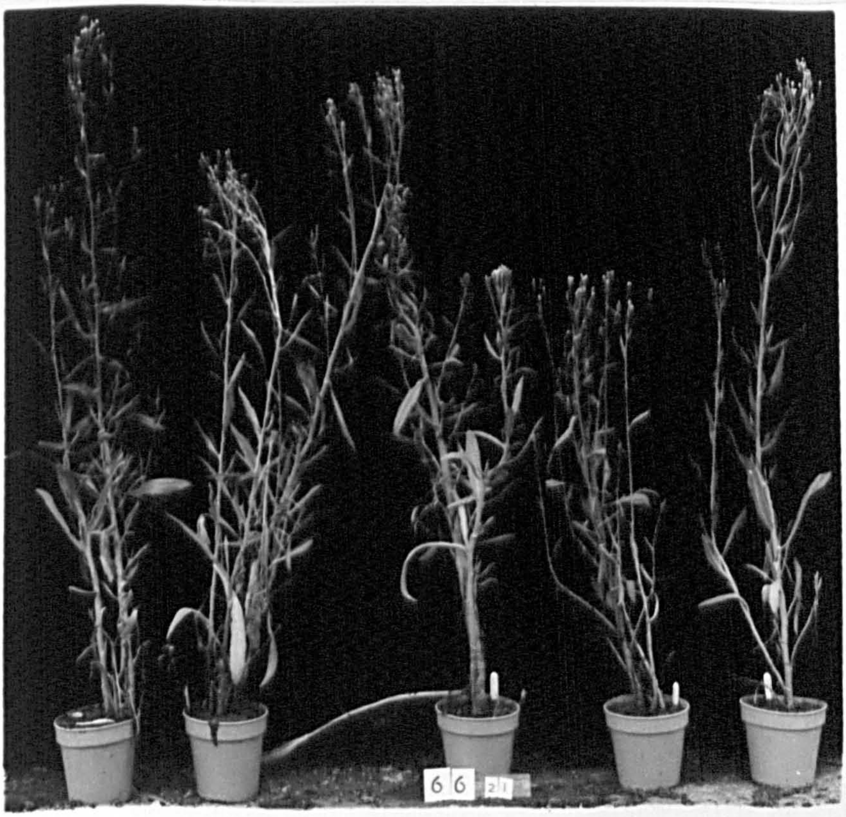


Fig 10.11 Gib. Spartina marsh - cold house from seedlings.

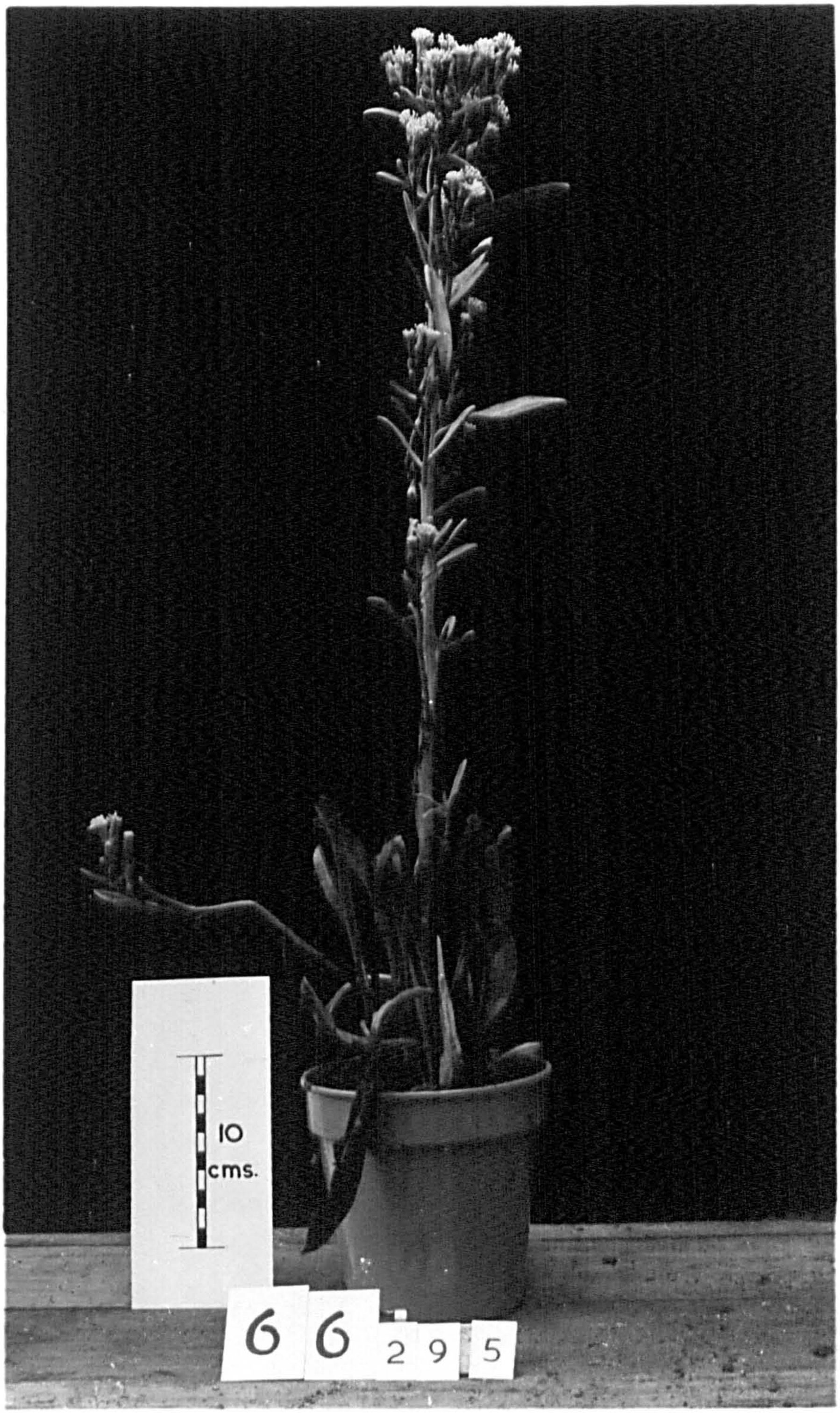


Fig 10.12 Scolt Cockle Bight - cold house from seedling.

sub-basal leaves and a tendency to lose the initial rosette. (Compare for example mid and low marsh plants in Figs. 9.5, a and b respectively).

It can be seen, however, from those populations tested under a range of conditions that growth habit characters are highly variable and can be affected by environment. Branching is an especially variable character. In a number of cases there is an increase in the amount of branching under experimental garden conditions as compared with cold house conditions (e.g. G. Spa., S. Bch., S. Cob.). This may be due to early damage of the leader, possibly by slugs. Although often unbranched in the field the high marsh plants show a propensity for developing the full, ultimately cymose, branched habit. Their plasticity in this respect is illustrated by an examination of Fig. 10.2. Fig. 10.2a shows Gib. Agropyron marsh plants as grown from fruit (collected in the field) under cold house conditions where they resemble those plants found in the field in their tall erect, unbranched, non woody habit (see Fig. IV.8a). Under poor soil conditions too, although considerably reduced in height the plants are generally unbranched (Fig. 10.2c and also Fig. 5.1B). However under cold house conditions certain plants show an ability to develop axillary branches - as did a number of the plants collected as seedlings from the wild (Fig. 10.2b). In some cases where, exceptionally, Gib. Agr. plants overwintered, the branching in the second year was often very extensive (see Chapter 5, especially Fig. 5.1A).

Thus the variation in branching may be a result of both environmental modification and genetic polymorphism.

There is clearly a need to test the products of controlled crosses under a range of conditions of spacing and soil fertility in order to establish the total range of plastic response in such a variable character as branching. Branching which occurs in some genotypes when the plants are artificially thinned, as in cultivation, may indicate that the unbranched appearance in the field of populations such as Scolt Cockle Bight may be related to their presence as close stands.

The tendency to lose the initial basal rosette also varies between treatments in a number of populations. In general the leaves tend to be lost in the garden or open frame to a greater extent than in greenhouse conditions.

Woodiness and the development of sub-basal leaves are apparently less subject to modification by cultivation conditions and are more clearly related to life cycle. Mid marsh plants, which develop extensive woody, often spreading, rhizomes bearing sub-basal leaves do so irrespective of conditions. Typical of these forms are the plants from Knott End (Fig. 9.5b and Fig. 10.8), Gib. Aster marsh (Fig. 10.9) and the R. Lune (Fig. 10.17a). In this respect it is interesting that the only marsh classified as 'high' marsh by the association analysis (Ch. 3) which did not contain pauciennial biotypes, namely Naze, was the only high marsh population to show characteristic mid marsh woodiness. This woodiness was common to plants grown in the cold house and in poor soil conditions (Figs. 10.13a and b).

By contrast 'woodiness' in low marsh plants is rarely accompanied by the extensive development of sub-basal leaves, at least during the first season of growth. The secondary thickening which occurs in low marsh plants is accompanied by the production of perennating buds at or below ground level around the base of the stout stem, and where rhizomes develop these are rarely spreading (see Fig. 10.10., 10.11., and 10.12).

With the exception of Naze plants, and to a lesser extent those from Spiral marsh, the high marsh plants show no tendency to develop thickened basal stems or overwintering organs of any kind. Even in the few plants which overwinter in cold house conditions the perennating bud is held several centimetres above the ground in a curious 'palm-tree' like rosette.

The vegetative appearance of plants in the field is clearly the result of genotype interaction with a large number of factors which require a closer examination. Aster is often grazed by rabbits and even by rats (Drummond 1960) and the amount of branching may thus be affected by loss of erect stems.

In addition, the extent to which a given plant is succulent or not affects its general vegetative appearance. A number of workers have been concerned with the phenomenon of succulence in maritime species (Chapman 1960) but no attempt to measure this has been made here. Although the general 'fleshiness' of the leaves varied somewhat in cultivation cursory observations would suggest that in Aster it is a direct physiological response to sodic environments. Succulent plants apparently fail to retain this characteristic in ordinary soils. However it is clearly a subject for specialised investigation.

(b) Rosette 'shape'. A fundamental aspect of growth habit is the degree of prostrateness or erectness of a given plant. This rather vague and difficult-to-quantify feature has proved to be an adequate basis for delimiting ecotypes in a number of species. The well-known work of Gregor on Plantago maritima is an example of the attempt to quantify the general 'shape' of a plant on the basis of a subjectively defined set of habit grades ranging from decumbent to erect (Gregor 1938).

The variation in the angle at which the basal leaves were held from the main stem was a striking feature of the seedlings being cultivated in seed trays (before pricking out into pots), (see Fig. 10.14). This variation persisted in all populations prior to the growth of a central flowering stem - as can be seen by contrasting Fig. 9.5a with Fig. 9.5b - and it was decided to measure it in some detail.

Initially the actual angle between the imagined vertical extension of the stem and individual leaves was measured but this was later abandoned in favour of the measurement of the parameter 'habit index'. 'Habit index' was defined as the maximum plant height divided by the maximum spread. Its measurement is indicated

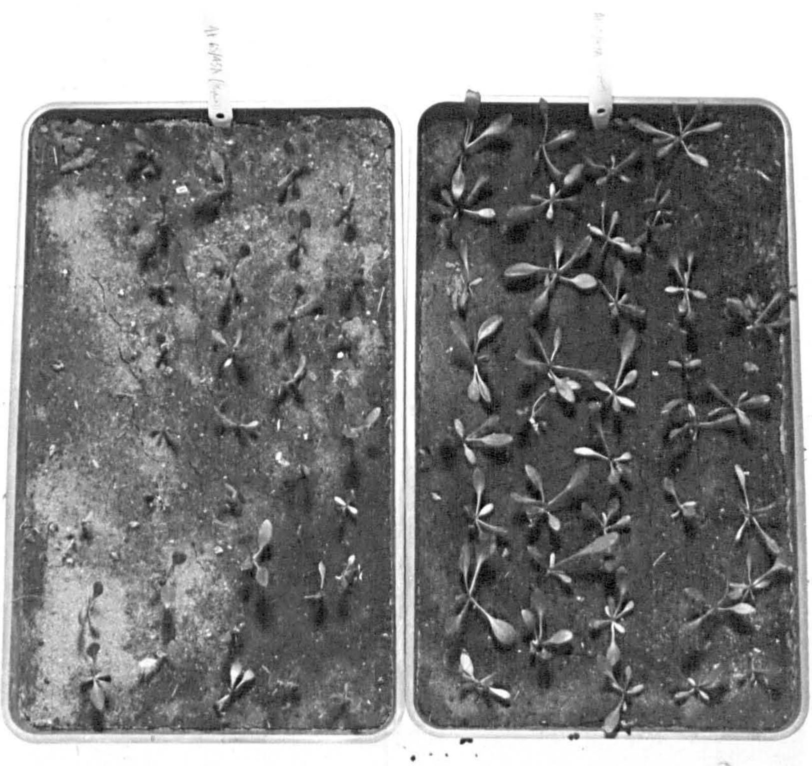


Fig 10.14 Seedlings of Knott End (right) and Beach Point (left) populations viewed from above - note the contrast in the prostrateness of the plants.

in Fig. 10.1(b). The ease with which this character could be measured enable large numbers of young plants to be measured. A total of 13 populations were measured in this way and the data are given in Table 10.2 and plotted in Fig. 10.15.

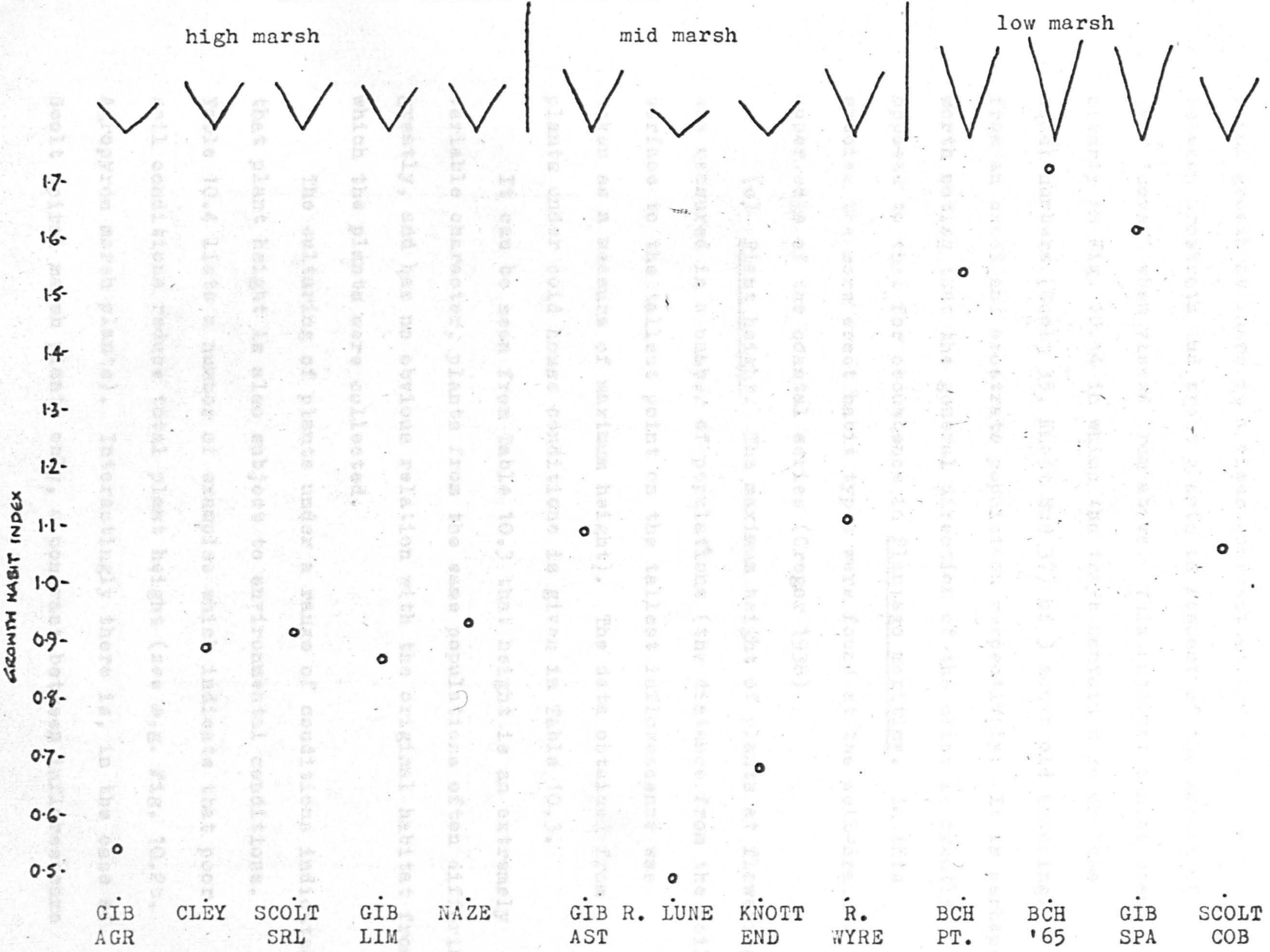
These data suggest that high marsh plants are more decumbent than those from low marshes and that mid marsh plants are variable in this respect. The possible advantage to high marsh plants of a spreading habit (or to low marsh plants of an erect habit) at the seedling rosette stage is not clear and it is not possible to

Table 10.2 'Habit index' in selected populations (listed in order of descending marsh height).

Popn.	n	$\underline{X}$ habit index	variance	
Gib. Agr.	21	0.54	0.02	HIGH
Cley	5	0.89	0.17	
Scolt Srl.	43	0.91	0.12	
Gib. Lim.	29	0.87	0.09	
Naze	53	0.93	0.10	
Gib. Ast.	30	1.09	0.12	MID
R. Lune	30	0.49	0.19	
Knott End	86	0.68	0.05	
R. Wyre	49	1.11	0.19	
Bch. Pt.	37	1.54	0.31	LOW
Bch. Pt.'65	84	1.72	0.37	
Gib. Spa.	33	1.61	0.45	
Scolt Cob.	28	1.06	0.11	

advance an hypothesis at this stage to account for the variation pattern. The variation is likely to have a significant effect on

Fig 10.15 Growth habit index.



plant growth as there is a clear contrast at the extreme ends between prostrate and erect plants in respect of the amount of leaf 'cover' when viewed from above. This contrast can be seen clearly in Fig. 10.14 in which the trays contain more or less equal numbers (Scolt 35, Knott End 37) of 3 month old seedlings from an erect and prostrate population respectively. It is perhaps worth noting that the general direction of the cline is exactly opposed to that for decumbence in Plantago maritima. In this species the more erect habit types were found at the well-drained upper edge of the coastal series (Gregor 1938).

(c) Plant height. The maximum height of plants at flowering was measured in a number of populations (the distance from the soil surface to the tallest point on the tallest inflorescence was taken as a measure of maximum height). The data obtained from plants under cold house conditions is given in Table 10.3.

It can be seen from Table 10.3 that height is an extremely variable character, plants from the same populations often differing greatly, and has no obvious relation with the original habitat from which the plants were collected.

The culturing of plants under a range of conditions indicates that plant height is also subject to environmental conditions. Table 10.4 lists a number of examples which indicate that poor soil conditions reduce total plant height (see e.g. Fig. 10.2b. Agropyron marsh plants). Interestingly there is, in the case of Scolt Spiral marsh plants only, a contrast between inflorescence

Table 10.3	Maximum plant height in selected populations grown under cold house conditions, (in descending order of marsh height). Measurements in cms.		
Population	no measured	mean ht.	range
Gib. Agr.	23	77.6	43 - 104
Cley	4	102.2	95 - 112
Anglesey A	8	37.7	23 - 54
Scolt Srl.	14	13.4	10 - 17
Gib. Lim.	16	65.8	41 - 88
Gib. Aster	17	48.9	31 - 70
Plover (Scolt	10	27.6	14 - 37
R. Wyre	10	56.2	28 - 97
Anglesey B	10	15.2	6 - 24
Scolt Bch.	8	33.5	28 - 39
Gib. Spa	16	81.9	67 - 103
Scolt Cob.	13	42.3	25 - 56
Winsford A	7	19.6	13 - 27
" B	2	21.0	14 - 28
" C	10	41.5	15 - 66
" D	3	57.0	56 - 57
Var. Pannonicus (Vienna)	7	98.6	56 - 115
Var. Longicaulis (Portugal)	3	86.0	70 - 100

Table 10.4 Maximum plant height in selected populations grown under a range of conditions.

Popn.	Treatment	no measured	mean ht.cms.	range.
Gib. Agr.	cold house	23	77.6	43 - 104
"	" (from fruit)	13	79.3	60 - 114
"	poor soil	10	28.4	14 - 49
"	open frame (pots)	4	41.3	29 - 62
Scolt Srl.	cold house collected as plants	14	13.4	10 - 17
"	cold house (from fruit)	3	75.3	42 - 98
"	Botanic garden	5	59.0	50 - 77
Gib. Lim.	Cold house (collected as plants)	16	65.8	41 - 88
"	Cold house (from fruit)	13	69.4	42 - 92
Naze	Cold house (pots)	3	50.1	41 - 66
"	Botanic garden	4	49.3	44 - 55
"	Poor soil	8	9.8	4 - 14
Scolt Bch.	Cold house (plants)	8	33.5	28 - 39
"	" (from fruit)	3	39.3	28 - 52
"	Open frame	5	31.0	23 - 48

height in plants grown from wild-collected plants prior to flowering and those grown from wild-collected fruits. This does not hold for any other populations and may indicate that the small plants on Spiral marsh are 'stunted' by habitat factors such as soil depth or competition (Spiral marsh has a shallow soil on a shingle base). As with the branching character (above) and fruit production (Ch. 5) the conditions under which early growth occurred may be important in determining ultimate plant height.

It is clear, however, that populations may contain plants which are genetically small. Only two such plants were discovered among those grown in the course of this work. One of these was from the Winsford A site in inland Cheshire (this plant remained only 6 cms. high at flowering and a maximum of 4 cms. high during its vegetative phase for 3 season's growth under cold house conditions, whereas all other plants collected from this site (Fig. IV2a and b) showed an increase in both height and leaf length under cold house cultivation when compared to that in the field). The other apparent genetic dwarf was a single plant from the Orkneys which remained small and prostrate, without flowering, for three years in cold house conditions. This plant is shown in Fig. 10.16a together with an environmentally induced dwarf collected from the quay wall at Parkgate (Fig. 10.16b). This latter plant (technically a 'phenocopy') which had not flowered, has, under cold house conditions, become tall and bushy and developed sub-basal leaves up to 10 cms. long. This type of response was typical of all other

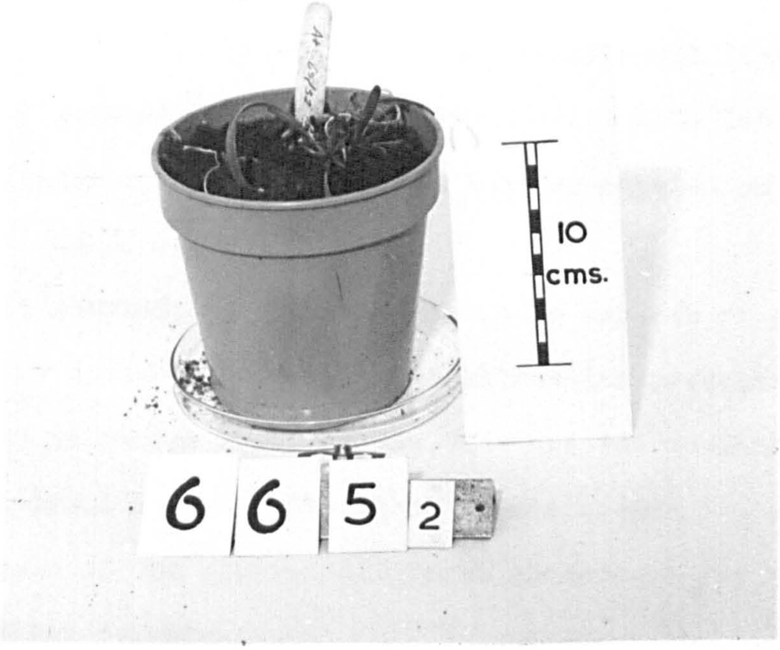
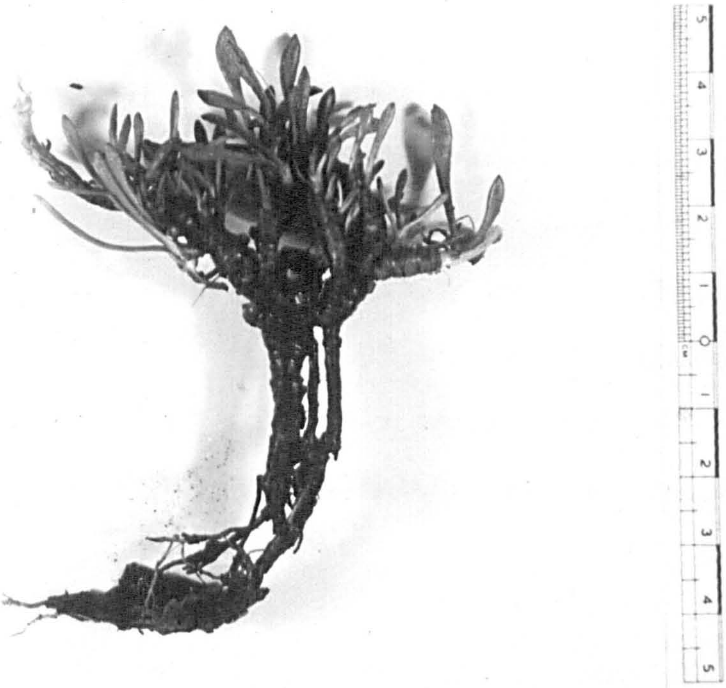


Fig 10.16 Dwarf plants (a) above; from the Orkney Islands (see text), (b) below; a phenotypic dwarf from the quay wall at Parkgate.



dwarf plants collected in the field.

(d) Summary. The difficulty with which growth habit characters can be quantified, the high within-population variation, and the high general level of phenotypic plasticity for characters such as tallness and branching, make between-population comparison less easy to draw.

Within populations the least variable aspects of growth habit are the decumbence of the initial rosette produced from fruit, the tendency to become woody at the base and the tendency to develop sub-basal leaves. The last two characters are related to the life cycle of the plant. All these characters can be correlated with marsh height.

Populations from high, mid and low marshes may contain a proportion of branched plants although mid marsh plants in particular tend to be both well branched and have more than one flowering stem per plant. The extent to which the initial rosette leaves persist after the flowering stems develop varies within populations as does the height of the plant at flowering. This latter character has a particularly high level of plasticity in those populations tested under a range of conditions. Of the many dwarf plants collected from various field sites only two retained this character after cultivation in conditions of plentiful nutrient supply.

II Leaf shape.

Observations of plants in culture suggested that the shape of the rosette or 'basal' leaves varied consistently between populations. The extremes of 'narrow' and 'broad' were easy to recognise and an example of each type is given in Fig. 10.17. Fig. 10.17a depicts representative plants of the narrow-leaved population from the R. Lune; a 'mid' marsh, and Fig. 10.17b depicts representative plants of the broad-leaved population from Scolt Beach Pt., a 'low' marsh.

In view of this variation it was decided to measure leaf shape in plants from two east coast series - the four populations at Gibraltar Point and three at Scolt Head Island. Leaf shape was measured as the ratio of maximum leaf length to maximum leaf width. Maximum length was taken as the length of the lamina from the point where the petiole began to widen to the leaf tip. (Original measurements in mms.). Three leaves per plant were measured where possible (very young leaves were ignored) and only the basal leaves were measured. The data are given in Table 10.5. Subsamples of 50 leaves per population were subjected to an analysis of variance and the Gibraltar Point populations were found to have statistically significantly different leaf ratios (among themselves) at the 0.05 level of p.; the Scolt Head populations were significantly different at the 0.01 level.

An examination of these reveals a pattern of variation consistent to both areas. The basal leaves of the high marsh plants are significantly more lanceolate than those of the low marsh areas, with the plants from the marshes intermediate in height having

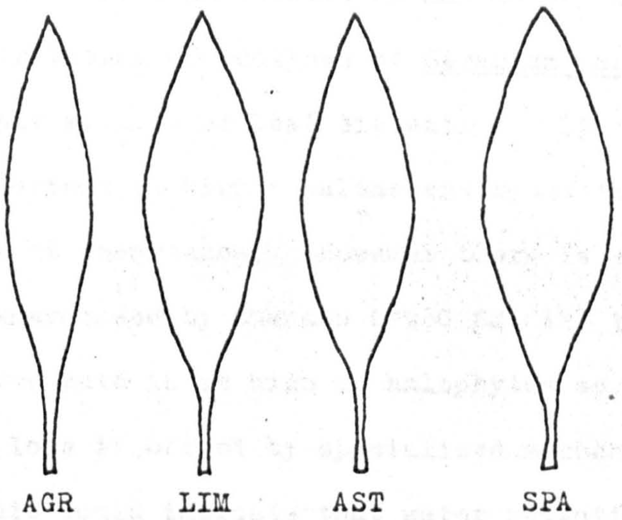
Fig 10.17 A contrast in leaf shapes½ (a) above; narrow-leaved plants from the R. Lune,(b) below; broad-leaved plants from Beach Point, Scolt Head Island.

Table 10.5	Ratio leaf length : width in selected populations.		
Population	no of leaves measured	mean ratio	standard error
Gib.			
Agr.	103	4.610	± 0.191
Lim.	78	3.195	± 0.112
Ast.	92	3.427	± 0.145
Spa.	99	2.992	± 0.125
Scolt			
Srl.	128	4.218	± 0.157
Bch.	102	3.293	± 0.197
Cob.	86	2.770	± 0.118

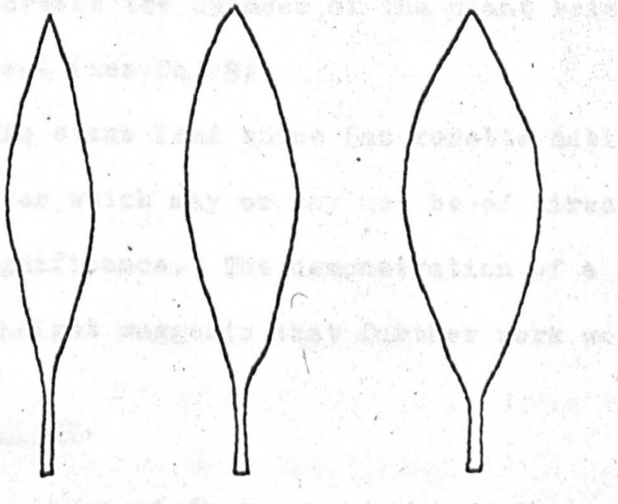
leaves intermediate in shape (the positions of the Gib. Lim. and Gib. Ast. marshes are reversed, however, upsetting the true cline for that series). These differences in shape are expressed in Fig. 10.18 in which leaves of the same length have been drawn to compare their relative widths, and thus shapes.

The possible significance of this pattern of variation is obscure. As in the case of the character 'decumbence', the leaf shape is likely to affect the physiology of the young plant. It may be important in terms of transpiration rate, for example; evaporation from a surface is more rapid at the edges than in the centre and thus rate of evaporation is inversely proportional to the radius or width of a surface but not its area. Therefore under equal conditions (of vapour pressure and density) a broad

Fig 10.18 Leaf shape. (Relative leaf shapes based on mean values see Table 10.5).



Gibraltar Point populations



Scolt Head populations

leaf would lose less water from its surface by evaporation than say an equal area of narrow leaf. Lewis (personal correspondence) has suggested that this phenomenon may be an important factor in the distribution of ecotypes of <u>Geranium sanguineum</u> which vary in their amounts of leaf dissection. If the reduction of water loss is important in highly saline environments the width of a leaf may be of importance. (However there is a good deal of evidence, summarised by Chapman (1960 Ch. XI) to suggest that transpiration rate is as high in halophytes as in other plants and that water loss is offset by specialised mechanisms for water uptake. This would indicate that water retention may not be a critical factor). On the other hand the more obovate leaf of the low marsh plants will offer more resistance to water flow and possibly increase the chances of the plant being dislodged by tidal movement (see Ch. 9).

At this stage leaf shape (as rosette habit) must be regarded as a character which may or may not be of direct or indirect adaptive significance. The demonstration of a cline correlated with marsh height suggests that further work would be of interest.

III Leaf colour.

It was observed that, among the seedlings being cultured in the cold house prior to transplant to single pots, there was a considerable variation in the depth of colour of the rosette leaves. This variation, which persisted for some time, was consistent in that seedlings from low marsh populations had paler leaves than those from mid and high marsh populations. The differences in colour had generally become less noticeable by the time the flowering stem was forming and, with the possible exception of one low marsh population, eventually disappeared. Under intensive high light conditions (to induce flowering, see Ch. 4) the differences did not persist beyond the cotyledon stage.

Leaves from 3 high marsh (Gib. Agr., Cley and Anglesey A) and 3 low marsh (Gib. Spa., Scolt Bch., and Cob.) seedling populations were sampled and solutions prepared for chromatographic separation by grinding with fine sand and separating in acetone, petroleum and water. Both paper and thin-layer chromatography was used, the solvent being a 30:70 mixture of chloroform:pet. ether. The chromatograms were viewed after each run by ultra violet light and the component pigments marked.

Four spots were identified in every case which were thought to be chlorophyll A, chlorophyll B, xanthopyll and carotene. Any differences between the plastid contents of the low and high marsh plants appeared to be quantitative. The xanthophyll spot appeared larger in the Scolt Head populations than in the others but these differences were not further investigated.

CHAPTER 11. THE RAY FLORET CHARACTER.

The so-called '_var discoideus_' differs from the type species in lacking the ray florets present in the normal heterogamous capitulum. The original description by Reichenbach (£)could not be traced but _Eurybia maritima var flosculosa_ (S.F. Gray 1822) may be a prior epithet. Most national and local floras refer to the occasional absence of ray florets in _Aster tripolium_ in the manner typified by Clapham _et al_ (1962) who refer to 'ray florets spreading, blue-purple or whitish or 0 (var discoideus Rchb.)'.

I Distribution of the rayless form.

The existence of the rayless form of _Aster tripolium_ has been known for well over a century. The earliest record traced was of a specimen in the Lincoln Museum Herbarium collected by Dodsworth around Boston in 1838. Other early records of the form in Lincolnshire include Wainfleet Haven, 1879 and 1885, Frieston Shore 1881 (coll. Fowler), South Butterwich (Boston) 1896, South Ferriby 1896 and Holbeach 1896 (coll. Fowler) (Ex. Herb. Linc. Mus. and Mason 1925). A series of paintings by Burgess (1880-90), at present in Lincoln Museum, include one labelled _Inula crithmoides_ which is almost certainly the rayless form of _Aster tripolium_.

Nineteenth century records from other countries include Cheshire (the Dee Shore and Parkgate-de Tabley 1899), West Yorks.

(near Goole-Lees 1888), and Kent (Woolwich. ex. herb. J. F. Bigge-B.S.B.I. records 1846).

At the present day the rayless form is frequent in many English and Welsh localities south of a line from Morecambe, Lancashire to the Humber Estuary. Fig. 11.1 gives its distribution in the British Isles. (This figure is based on a survey of the country floras, correspondence, herbaria (Lincoln, Cambridge and Liverpool), personal observations and information collected as part of the B.S.B.I. Atlas of the British Flora scheme. Dr. F. Perring, who kindly supplied the cards collected as part of this latter scheme, has agreed to the publication of the map in the supplement to the Atlas of the British Flora (Perring 1968 (p. 72)).

As can be seen from Fig. 11.1 the rayless form is particularly frequent on the south and south-east coasts, in Lincolnshire, Norfolk, Suffolk, Sussex and Essex. There is a good deal of evidence to suggest that the spread of the form in these areas may have been a relatively recent phenomenon (and this is presented below). In fact the rayless form may be more generally widespread than an examination of the literature would suggest.

Despite the existence of only one continental record in the Biological Flora account (1942) (a German record-Knuth 1908?) several floras refer to rayless plants of the species. Coste (1903) describes French populations as having 'ligules, (manquant parfois par avortement) violettes', and Hegi (1906) refers to 'eine strahlenlose form (f. discoideus auct.)' which 'kommt gelegentlich

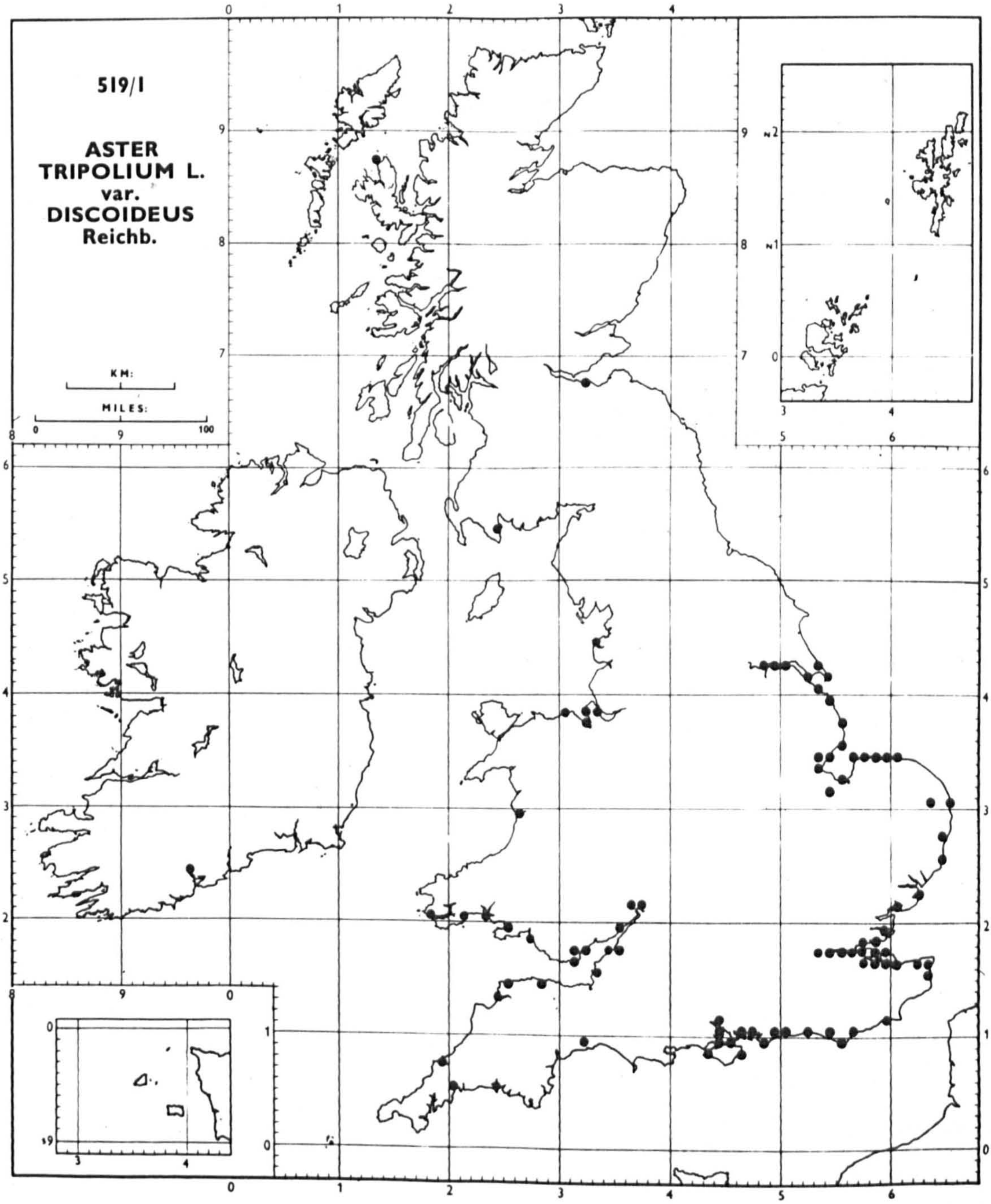


Fig 11.1 Distribution of the rayless form (after Perring 1968).

zwischen der Normalform vor' in German populations. In B.E.C. Plant Notes 1923, p. 37, there is a reference to Belgian records of the variant as a prevailing form in flooded areas, and Beeftink (personal correspondence) has observed large populations of the rayless form in pure stands on the borders of euhaline and polyhaline waters in the south-west Netherlands.

Two most recent of these reports from continental Europe refer to large populations of the rayless form - a fact which is particularly interesting in the light of evidence which suggests that the numbers of this form have recently increased in this country. Most of this evidence relates to populations in S.E. England and is largely anecdotal in nature.

When Chapman was working on the north Norfolk marshes (the 1930s) the rayless form was 'so much less frequent that one tended to treat it as a casual' (Chapman personal correspondence 1965). Nicholson (1914) gives only one Norfolk record of the variant - Hunstanton 1902. At the present day, however, the rayless form is noticeably the most common form in many Norfolk marshes. Swann (personal correspondence 1965) revised the statement in Petch and Swann (1962) that the rayless form was 'a little less common than the typical plant' in Norfolk, stating that 'during the past four or five years he had found it more widespread and abundant; for example on the salt marsh at Burnham Overy Staithe the rayed plant is now noticeably less common'. Ellis (personal correspondence 1966) reports that the rayless form is now more plentiful than the type everywhere on the Norfolk coast e.g. Brancaster, Wells and Gt. Yarmouth. Of Blakeney Point Ellis says 'the rayed form is quite rare and one finds only an occasional specimen now, whereas the reverse was the case less than 50 years ago'. White (personal correspondence) confirms this and dates the increase in the rayless form from earlier than 1946 when he first started to visit the area (interestingly the Aster on the mainland marshes near Morston has remained predominantly rayed since that time). Bingley too reports a possible increase in the rayless form in some Essex marshes, e.g. the Stour estuary, (personal correspondence) and information from local naturalists about both the north and south Lincolnshire marshes suggests that the pattern has been repeated here.

The exact timing of the spread of the rayless form is difficult to fix. Although infrequent in Norfolk in the 1930s a report by Clarke in 1902 from Essex suggests that the variant was common in parts of that country at the turn of the century (Clarke 1902 p. 237). Petch also observed the rayless form in some numbers on the Humber estuary in 1905. The local spread of the rayless form may have depended on a number of factors, which are discussed later. These factors could have arisen independantly in different areas at different times.

II The inheritance of the ray floret character. (See also Appendix VI).

A breeding programme (started in 1963) was undertaken to determine the mode of inheritance of the character responsible for the presence of ray florets in the species. The method of crossing used in the controlled pollinations was described in Chapter 4. The results of crosses are described in Appendix VII and an interpretation of these follows below.

The original cross pollinations were performed in the field in September 1963, some of the parent stocks being transplanted to Keele after the fruits were collected. The fruits from these crosses were grown to maturity and the F_1 plants flowered in 1964 after a period of growth under intense lighting conditions (see Chapter 4). After scoring, some of these were cut back and reflowered in 1965 when they were either selfed or back-crossed with one of the parents. F_2 plants, planted out in April 1966, flowered in 1967 and 1968. The fruits from F_2 plants selfed in 1967 have produced only one plant in flower to date. The original rayed x rayless crosses were repeated in 1965, 1966 and 1967. Full details of the breeding (including unsuccessful crossings), programme are given in Appendix VII, Table 2 of which lists the number of rays of the plant involved.

Unlike the rayed v. rayless cross in Senecio vulgaris which produces an F_1 bearing rays intermediate in size and of a characteristic shape (Trow 1912) the hybrid variation in Aster tripolium is meristic in nature. Fig. 11.2 gives photographs of the two parents and one of the F_1 plants in one of the crosses. (Exp. 7. 66/6/1 X 65/45/8. See Appendix VII).

Fig 11.2 Parents and F1 plant of ray X rayless cross. Top left : parent (66/6/1 mean 15 rays). Top right: parent (65/45/8 - rayless). Below: F1 plant (mean 2 rays, range 0 - 10).

An examination of Appendix VII, Table 2 reveals that the pattern of ray number in the F_1 is variable and that its later segregation is confusing. Not only is there considerable between-plant variation in ray number but also heads on the same plant may carry very different numbers of rays. An attempt to quantify the considerable variation in ray numbers has been made by counting the rays on as many heads as possible. From this the following general observations can be made:(expt. nos. refer to Table 2. App. VII).

(1) Crosses between rayless and fully rayed plants produce a partially-rayed F_1 generation with an overall lower mean numbers of rays/head than the rayed parent (apart from one case - expt. 3. F.3). Both between-plants and between-head variation in ray number is considerable. The reciprocal cross (only made in the earlier experiments in which disc florets were emasculated) produces an equally variable F_1.

(2) Segregation and recombination in the F_2 produces in some cases plants which may be classified as parental types although the within-plant variation makes such types difficult to circumscribe. (See Expt. 3 and Expt. 5 - F_2 plants). Fig. 11.3 shows three F_2 plants from Expt. 5 (plants a, c and d), two of which resemble the original parents in ray number.

(3) Crosses between rayless plants produce an F_1 which

Fig 11.3 F2 plants of a ray x rayless cross. The two outside plants closely resemble the original parents in appearance. The middle plant is clearly intermediate.

remains largely discoid. The occurence in F_1 plants of an occasional head bearing one or two rays (Exp. 8, 9, 10) is recorded.

(4) Not all plants produced as a result of crosses between fully rayed plants appear to retain the full ray number. Although tending to a reduced number of ray florets such plants had overall a mean number of rays greater than the progeny from either reciprocal ray v. rayless cross. This tendency to reduce the mean number of rays in these crosses and on selfing rayed plants was in some cases very pronounced. For example plant 65/16/1, which had a range of 17 - 20 rays/head, on selfing produced a virtually rayless plant, 3 being the maximum number of rays on any head and the majority of heads being rayless.

The conclusions which can be drawn from these results are somewhat limited. The number of plants produced as a result of any one cross are insufficient to analyse statistically the puzzling range of variation in F_1 and F_2 plants. However it is clear that the ray floret character is under genetic control and that the rayless and fully rayed plants are homozygous for this character. Neither gene (or genes) is completely dominant, the heterozygote showing a wide range in the number of ray florets. The number of genes involved is not known. (A possible hypothesis is that 2 genes are responsible for the production of ray florets (say RRṘṘ for rayed, DDḊḊ for rayless), the F_1 being intermediate in character (ṘḊRD) and the F_2 recombining to give one rayed (RRṘṘ): 14 intermediate (4 RRRD, 4 RDDD, 6 RRDD): 1 rayless (DDḊḊ). However the numbers of plants scored are too small to support this hypothesis, and the within-plant variation requires further explanation).

The striking within-plant variation in ray florets number in the F_1 plants may have one of at least four possible explanations. (1) The inheritance of ray florets may be governed by a large number of genes. The developmental processes involved in their production may even be controlled by more than one group of multiple genes with different modes of action. In this case the scale of the breeding programme described here might be insufficient to detect this even were it not modified by the environment. (2) The inheritance of rays may be governed by a relatively small number of genes, which vary in their expressivity and/or penetrance. In this case the hybrid plants may be genetically unbalanced and the phenotypic expression of the genes highly variable due to their general instability. (3) As for (2) with the additional possible modification of phenotypic expression by factors such as the age of the plant and/or external environmental factors, and (4) The numbers of ray florets may be determined by a number of gene controlled processes masked by 'switch genes' which appear to be simply inherited. The penetrance of the genes covered by such switch genes could still vary with the environment.

The first explanation appears unlikely. Although meristic variation may commonly be under polygenic control any method for quantifying the ray floret numbers of the hybrids would leave unaccounted for the juxtaposition on the same plant of rayless and almost fully-rayed heads. There is not enough evidence to support exclusively any one of the alternative possible explanations. Evidence is available however which suggests that ray number may vary with the age of the plant. Table 11.1 lists the ray numbers of plants on separate scoring occasions. The numbers follow the sequence of order of counting and not necessarily of flowering on each scoring occasion. However on each occasion those heads were scored which were easy to score i.e. the ray floret ligules were extended at right angles to the head, and thus the heads scored in each occasion were relatively more mature than those scored at a later date. The time between scoring varied from plant to plant and is not recorded here.

Not all the plants in which ray numbers were scored on different occasions showed a pattern of variation such as that described below. In many cases (including sister hybrids of the F_1 plant listed in Table 11.1), there appeared to be no significant difference between either the mean number or range of rays counted at different dates. Only those plants in which the differences appear to be significant have been included in the Table. Most of these observations were made on plants collected from the wild.

Table 11.1 Rayfloret number on separate scoring occasions

Plant	Source	1st DATE			2nd DATE			3rd DATE		
		no.hds counted	mean	range	no. hds.	mean	range	no.hds	mean	range
65/4/1	F1.DXR	6	5	1- 8	5	15	12-20			
64/4(10)a	F2 DXR	13	5	1- 6	10	9	5-15			
66/21/12	Gib.Spa.	20	0	0- 4	9	4	0- 8	6	1	0- 3
66/21/15	"	5	0	0- 2	18	5	0- 8	9	4	0- 8
66/20/1	Gib.Ast.	9	0	0	11	4	0-10			
66/20/15	"	6	5	1- 8	5	15	12-20			
66/20/25	"	2	1	0- 2	9	4	0- 8			
66/20/29	"	5	16	12-18	6	19	15-23			
66/19/14	Gib.lim.	3	0	0- 1	12	3	0- 7			
66/22/3	Anglesey A	12	25	22-28	3	18	17-19			
66/22/5	"	3	14	12-15	2	15	-	1	3	-
66/24/2	Winsford B	4	22	21-24	2	22	-	4	20	15-21
65/46A/3	Cley	4	24	21-28	1	30	-	1	18	- *
65/54/5	E.Germany	15	22	19-26	3	30	27-32			
65/54/10	"	7	22	19-25	3	25	20-28			
65/53/10	"	3	27	26-29	6	32	30-34	2	20	19-20
65/41A/1	Gib.Agr.	9	2	0- 9	6	2	2- 2	9	3	0- 9
65/41A/2	"	3	13	-	5	9	1-17	3	10	7-14
66/18/28	"	3	22	21-23	6	30	28-32			
65/48A/2	R.Wyre	12	12	6-14	10	18	15-19	9	16	15-19
65/48A/7	"	4	19	15-22	6	19	14-21	9	13	12-14
65/48A/14	"	4	16	15-20	5	15	14-16	3	15	8-22

* reflowering in 2nd yr. 1 count (Aug. 1967) 7 hds. mean 25 range 21-27

The general impression gained from the date in Table 11.1 and from general observation is that the first heads to open on any plant may carry a range of ray numbers but have a generally lower average than those produced during the main period of flowering when mean ray number increases and the dispersion about this mean decreases. As the plant ages the range of ray number increases greatly and the mean, which may shift either upwards or downwards, becomes a virtually meaningless figure in view of the large variance. For example a plant from Gib. Pt. Limonium marsh (66/19/23 - not listed in Table 11.1), in which the sequence of opening was followed, produced the following ray numbers: The first heads, scored on the 14/9/66 had 0,12,20 and 15 rays; those scored on 25/9/66 had 21,24,21,21,20 and 23 rays; and those scored on the 14/10/66 had 21,14,0,0,0 and 2 rays. Variation of this sort may be due either to a seasonal effect of the environment or to ageing within the plant.

A number of parallel cases of 'seasonal' variation in the production of sexual structures can be found in the literature. Gajewski (1963) records such variation in the F_1 hybrids of the cross between <u>Geum rivale</u> and <u>G. montanum</u>, in which the structure of the styles on the same plant and even on the same receptacle may be straight as <u>G. montanum</u> or curved and hooked similar to <u>G. rivale</u>. He reports that 'in general, the flowers that develop later in the season bear more achenes that have the <u>rivale</u> type of appendage. In some F_1 plants nearly all styles of the early flowers are straight, long and pinnately haired, whereas in the last flowers of the season the curved and hooked rivale type dominates' (Gajewski 1963 p. 426). A detailed study in the variation in petal numbers of flowers of Nyctanthes arbor-tristis revealed that not only did the variances and the means of different trees differ significantly but also the variance increased greatly during the season. (Roy 1963). Similar increases in variance of petal number were observed in other species by the same author whose general explanation of the phenomenon is a breakdown of 'canalisation'

Other parallel cases include the production of an increased proportion of trigonous nuts (as opposed to those biconvex in shape) in Polygonum persicaria as the plant becomes senescent (Timson 1965), the formation of exserted fruits (as opposed to those included within the perianth) later in the year in Polygonum aviculare (Styles 1962), and the seasonal variation in corolla diameter, petal width and calyx tooth length in Primula vulgaris described by Woodell (1965). Numerous other examples could probably be found in the literature. The work of Clausen et al (1947) on Layia glandulosa ray floret variation is particularly apposite and is referred to below.

Superimposed on the 'seasonal' variation in A. tripolium is possible variation due to factors such as the position of an individual head on the plant. No accurate information on this is available from the present data, but it has often been observed that different flowering stems of the same plant may bear heads with very different ray floret numbers. (See for example Appendix VII, Table 2, Expt. 15, plant no 66/6/4). Petch, whose early detailed notes on the species are the only accurate field observations of the variation in ray florets, says of the normal form and the var discoideus, 'the two 'varieties' may be gathered from the same plant. On a plant which possessed thirteen main flowering shoots eleven bore discoid heads only, while the heads of the other two had from 0 to 8 rays. Conversely those plants on which the majority of the flowers are rayed may have two or three stems of the discoid heads only'. (Petch 1905 p. 51). (His further observation that 'the well-rayed flowers were less variable than the intermediate form' is interesting in the light of the breeding experiments described above).

Of the 22 plants listed in Table 11.1, 9 are from populations, on the west coast or from continental Europe, in which the rayless form is totally absent. This suggests that ray floret number is intrinsically variable in those plants which are always full-rayed in appearance. The average number of ray florets in plants from totally rayed populations also varied, as can be seen from Table 11.2. The var pannonicus had the largest number of ray florets and the figure of 49 rays/head was the highest recorded (in a normal plant, that is; 55 ray florets were counted on a plant from Gibraltar Point but this appeared to be fasciated).

Such variation in ray floret number, even in isolated, purely rayed populations, is in contrast to other observations made on

TABLE 11.2 Ray floret number in pure-rayed populations

Population	no. plants counted.	no. heads counted	mean no ray florets/hd	(highest)	mid range	(lowest)
Anglesey A	8	44	17.18	(3)	14-25	(28)
Anglesey B	7	26	15.43	(12)	14-16	(21)
R. Wyre	10	63	15.31	(6)	12-19	(23)
Winsford A	7	28	14.10	(10)	13-16	(21)
Winsford B	2	9	19.60	(15)	18-21	(24)
Winsford C	10	65	20.83	(6)	18-24	(31)
Winsford D	3	17	17.36	(15)	16-18.	(23)
Rostock E. Germany	6	60	23.04	(13)	19-26	(32)
Sachsen-Anhalt E. Germany	8	30	27.45	(19)	27-31	(34)
Var. longicaulis (Portugal)	5	21	16.71	(12)	13-17	(18)
Var. pannonicus (Vienna)	7	35	40.33	(33)	35-45	(49)

radiate composite species. Both Senecio jacobeae, cursorarily examined at Gibraltar Point and Southport, and Senecio squalidus, examined at Keele, vary little (in the case of S. squalidus not at all) from the Fibonnaci number of 13 rays. A Lapsana communis population counted near Market Rasen in Lincolnshire also had a common number of 13 ligulate florets/head. However species both variable and relatively uniform with respect to ray number exist within the genus Aster. A. novae-angliae, with a mean of 65 rays/head, varies from 50-68 rays per head whilst A. multiflorus has an invariable 13 rays/head. Their hybrid varies in ray number from 30 - 33 rays/head. (Wetmore and Delisle, 1939). Anderson (1929) presents evidence to suggest that the variable ray numbers in A. anomalus (within the range 19 - 32) may be affected by garden culture.

In addition to their variation in number the ray florets in Aster tripolium also vary considerably in size, shape and colour. Although this variation is generally between-plant, many populations contain plants which differ markedly in these respects. Fig. 11.4 shows a range of ray types collected from plants in culture the variation in which was limited largely by the number of plants in flower on the day of collection. The length of the ray florets may vary from about 4 mms. to 20 mms., their width from 1 mm. to 3 mms., and their shape from long and narrow to short and broad. A number of plants were found in which the ligules were 2 or even 3 pronged at their outermost tips. These bi-and trifid rays resemble

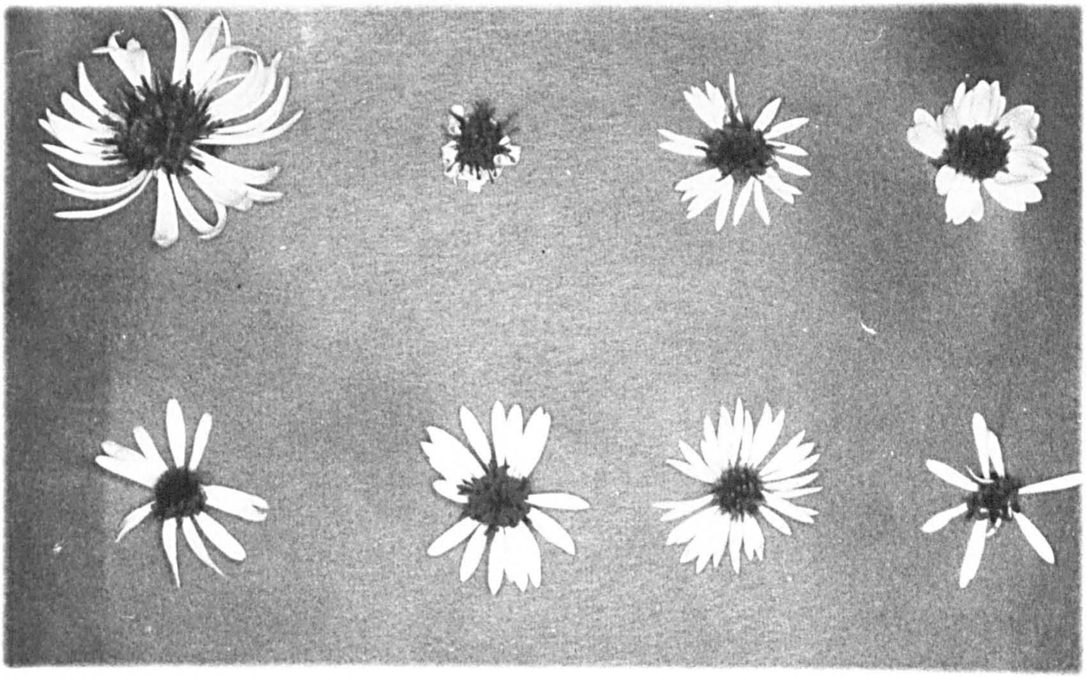


Fig 11.4 Variation in ray floret shape and size. Top row: long, curved (var pannonicus); strongly reflexed from first flowering (R. Wyre); short, narrow (Morston); short, broad (Morston). Bottom row: blunt tipped (Humberstone); white rayed form - typical shape (Morston); bifid and trifid rays (Tetney); narrow pointed (Morston).

the types described by Trow (1912) in Senecio vulgaris as 'fimbriate' rayed. An experiment to determine the mode of inheritance of this type in Aster was thwarted by the highly polymorphic ray shapes of the F_1 plants which contained a mixture of simple, bifid and trifid rays on the same head (see Appendix VII. Table 2, expt. 6). It is not known whether all the rays on the parent plant were fimbriate, but only about 30% (90 of 301) of the rays in the only F_1 plant to flower were of this type.

According to De Vries (1901) the white ray colour in this species is recessive to the normal lilac. An attempt to verify this was unsuccessful. Plants collected in the field showed considerable variation in colour from white through pink to deep mauve. Populations varied in their uniformity with respect to ray colour some, such as at Morston, showing a range of colours, others being uniformly pale lilac.

In summary it may be said that the inheritance of the ray floret character in A. tripolium is complex. In this respect it resembles the inheritance of ray florets in, for example Layia glandulosa rather than, for example, Senecio vulgaris. In the former species, the discovery of a relict rayless form (Roxira serpentina) enabled Clausen, Keck and Heisey to study the inheritance of ray florets. They concluded that two pairs of genes determine whether the plant is rayed, other genes the number of rays, three pairs govern the pappus length and several more control ray colour. (Clausen et al 1947 p. 243-4). The F_1 hybrid also varied in ray number, and they state that 'plants having 3 to 5 rays per head early in the flowering season later developed rayless heads' (op cit. p. 243). (Clausen (1962) Fig. 33, p. 83, gives the pattern of segregation for this character in Layia glandulosa). The exact number(s) of genes involved in the mechanism of ray floret inheritance in A. tripolium can not be determined from the evidence thus far obtained. There is a strong possibility that these genes vary in their penetrance and may be subject to environmental modification. For the present the plants may be regarded as having a certain genotypically fixed 'propensity' to develop ray florets which is variable and which may or may not be influenced by the presence of other genes or by the environment. Cases of variation in the penetrance of genes due to both differential genetic milieu and differential genotype/environmental interaction are not uncommon. The question of their possible association with other floral characters (disc fruit size and number) is returned to later in this chapter.

III The nature of the polymorphism

The existence of large numbers of rayless form in many populations, particularly on the East coast, allows the rayed/rayless variation to be approached theoretically as an example of polymorphism in the sense of Ford in that 'genetic variants* coexist in temporary or permanent balance within a single interbreeding population in a single spatial region, and in such

---

* Footnote on following page.

frequencies that the rarer cannot be solely due to (recurrent) mutation, or the spread of selectively neutral mutants' (Ford 1945 p. 73). It has been established that the variation is genetic and that the two forms can interbreed.

Examples of Fordian polymorphism need to be defined in relation to the answers to a number of questions, the most important of which are probably:- (a) Is the variation clearly discontinuous?, (b) Do any factors operate either externally or internally which tend to isolate the two forms in nature?, (c) Do the two forms have a detectable differential ecological distribution?, (d) Is the variation associated with other genetic characters which may be responsible for reinforcing the polymorphism?, and (e) Is the polymorphism balanced or transient?. Research on the ray floret character is described below under five general headings which correspond to attempts to provide answers to questions (a)-(e).

(a) <u>The continuity of variation</u>. Question (a) above may appear superfluous in the case of a character which is an apparently qualitative one, involving only the criterion of presence or absence. However, as indicated in an earlier section, a large range of intermediate, partially-rayed types result from crossing of the two forms, fully rayed and rayless. Such intermediates are commonly found in the field and represent a large proportion of the types in a number of populations.

The main difficulty in assigning plants to one form or

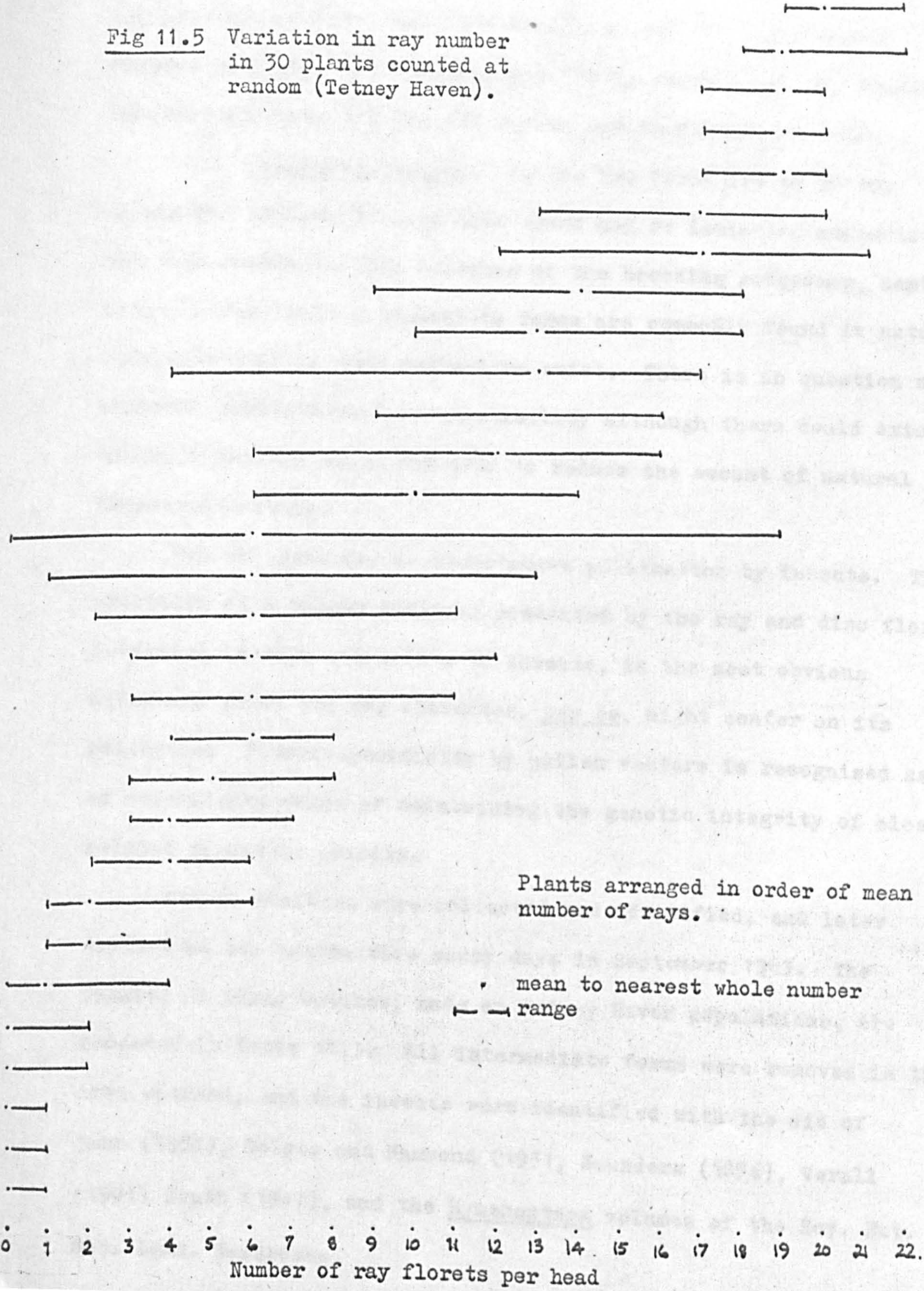
---

* Other versions include the words 'two or more <u>discontinuous</u> forms' as part of the definition (Ford 1940, 1964).

another is the within-plant variation in ray number which is as great in the wild as in plants produced by controlled pollinations. For example a plant collected from Tetney Haven salt marshes in 1964 had the following numbers of ray florets per head: 0.7.11.17.1.4.5. 14.4.4.2.3.13.6.19.0.0.3.4.0.11.0.0.3.0.6. and 0. In 1963, 30 plants on Tetney Haven 'old' marsh were counted at random and the numbers of ray florets on these plants scored. (A cane was thrown at points some distance apart). The data is recorded in Fig. 11.5 in which individuals are arranged in order of the mean number of florets per head. In terms of their means there appears to be at least three 'classes' of rayed plant, those possessing at least 1 ray and with a mean no greater than 6, those with a mean greater than 6 and no greater than 14, and those with a mean greater than 14. (The existence of 4 apparent classes, rayless, fully rayed and two intermediates may provide evidence for the 'two gene' hypothesis advanced earlier). In practice the discontinuities in mean number were not easy to see in the field. The following three classes of rayed plant were generally recognised:- (1) Plants with a high number of rayless heads and with a maximum no more than 4 or 5 rays on any head. (2) Plants with relatively few rayless heads and having a large range of ray numbers and (3) plants with no rayless heads and having a consistently high number of rays with a minimum rarely below 15/head.

The question as to whether tha variation is discontinuous or not is, in view of this range, largely academic, and for the

Fig 11.5 Variation in ray number in 30 plants counted at random (Tetney Haven).



purposes of studying the distribution of the two forms three classes of plant were recognised:- Fully rayed (i.e. (3) above), intermediate i.e. (1) and (2) above, and completely rayless.

(b) Isolating factors. As the two forms are in no way allopatric the possibility that there may be isolating mechanisms has been examined. The evidence of the breeding programme, combined with the fact that intermediate forms are commonly found in nature, indicates that no such mechanisms exist. There is no question of internal physiological incompatibility although there could exist external factors which may tend to reduce the amount of natural cross-pollination.

One of these may be assortative pollination by insects. The provision of a colour contrast presented by the ray and disc florets, rendering it more attractive to insects, is the most obvious advantage which the ray character, per se, might confer on its possessor. Flower-specificity by pollen vectors is recognised as an established means of maintaining the genetic integrity of closely related sympatric species.

Insect visitors were collected and identified, and later watched on two consequtive sunny days in September 1963. The results of these watches, made on Tetney Haven populations, are recorded in Table 11.3. All intermediate forms were removed in the area watched, and the insects were identified with the aid of Imms (1951), Colyer and Hammond (1951, Saunders (1896), Verall (1901) South (1947), and the *Hymenoptera* volumes of the Roy. Ent. Soc. Lond. Handbooks.

Table 11.3. Insect visitors - Tetney Haven salt marsh

Area 1. Mature marsh community (4/9/63)

Diptera		
Syrphidae	Syrphus ribesii	lll/rrr/lrr/rlll/rlllrrr/l.
	Heliophilus pendulus	r/lllrrl/rrllr/llll/rllrllr/rrrllr.
	Eristalis tenax	lll/llll/lll/lllrr/rrr/lll.
	Eristalis arbustorium	rrllr/lrlr/rrr
Muscidae	Graphomya maculata	rllr/ll
Hymenoptera Apidae	Bombus terrestris	rrrl/llll/rrlll/rllrrlr/lrr.
	Bombus agrorum	rll/rll/rrr/rrrrrr/rllr/rlllll/ll
	Bombus lapidarius	rrrr/rrrrr/llrllr/llllrr/rrl.
	Apis mellifera	rllr/llr/rrll/rr/lllrlrlrlrr/rllrr
Lepidoptera	Pieris brassica	rllrl.

Area 2. Halosere - upper region (5/9/63)

Syrphidae	Syrphus ribesii	rl
	Heliophilus pendulus	rrr/lrrr/rrr/rlll/ll/l.
	Eristalis arbustorium	rr/rlllr/llll/lllr/lllll/lll.
Muscidae	Scatophaga stercorarium	rr/llll/rrrr/lllr/llll.
Apidae	Bombus terrestris	lll/lll/lll/lllrlrlll/llr/rrr.
	Bombus agrorum	lllr/rrr/llr/lllrllrrl/rrl/rlrlr/r/r/lll.
	Bombus lapidarius	llrllr/llllr/lllrllrlrl/l/rl/llll.
	Apis mellifera	lllr/lll/llll/llll/lllrllrlr/rr
Lepidoptera	Aglais urticae	rrr

Area 3. Halosere - lower region (5/9/63)

Syrphidae	Syrphus ribesii	lllr/rrlll/llr/lllll.
	Heliophilus pendulus	lll/rr/lll/lllll/ll.
	Eristalis arbustorium	rll/lll.
Apidae	Bombus terrestris	lllr/lllr/lllr/lllll/r/ll.
	Bombus lapidarius	lllr/rl/r/r/rlllr/rll
	Apis mellifera	rlll/l/l/rll/rlllrl.

The region between two strokes (/) marks the visiting flight of a single insect - the same insect may be recorded more than once if it re-entered the area. 'r' marks a visit to the rayed head and 'l' to the rayless. Any contact, even alighting for a moment, was scored as a 'visit' as theoretically pollen could have been transfered although not all the species were pollen collectors e.g. Graphomya maculata is recorded as carniverous in Colyer and Hammond (1951). In addition a number of aphids and a small unidentified black coleopteran were taken from heads of both types.

Although some insect species may be limited ecologically, not visiting the lower marsh, there is random visitation by pollen vectors and no evidence for assortative pollination as an isolating mechanism.

Rayed and rayless forms may be isolated because their flowering periods are not identical. Although they have been observed in flower together in mixed populations the majority of rayless plants occur in the lower zones of salt marshes (see below) where they flower on the whole earlier than the rayed form in the upper zone. In addition, a positive observation of early flowering of the rayless plant in a mixed population was made near Blakeney Point on Aug. 14th 1967, at which date rayless plants fringing 'pans' on a mid marsh were in flower. The majority of the plants in the same zone of this marsh were rayed and were only in bud at that date.

(c) <u>Differential ecological distribution</u>. The distribution of the rayed and rayless forms has been examined by scoring the numbers of rayed, rayless and intermediate plants on a number of E. coast marshes. Only those populations were scored in which the rayless genome could at least in theory be present because of the small distance to the nearest population containing a rayless plant. Thus all the west coast populations which, with minor exceptions, were full rayed, were excluded. The results of these counts are presented in Table 11.4.

The data in Table 11.4 has been rearranged so that the percentage of rayless plants is plotted against the populations ranked in their approximate order of marsh height. This plot is given as Fig. 11.6 which reveals a striking relationship between marsh height and the proportion of rayless plants. This relationship confirms the clear impression gained in the field at Gibraltar Point and Scolt Head Island that the lower populations on salt marshes are practically always rayless and vice versa. A previous analysis of the distribution of the forms at these two areas enabled (in both cases) the null hypothesis that they were distributed at random throughout the individual populations to be rejected. ($\chi^2 = 51.766$ for 3 marshes at Gibraltar Point, p less than 0.001, $\chi^2 = 252.72$ for 5 marshes at Scolt Head, p less than 0.001).

A study of the tidal relations along the area known as the 'Halosere' at Tetney Haven (see Ch. 3 and Appendix VI) enabled the levels in relation to the tide to be plotted on this marsh. The area was sampled by throwing three 1 metre quadrats at random along 3 transects within each of four tidal zones and counting the ray florets on <u>Aster</u> plants occuring within each quadrat. The plants in this case were classified into four types, rayed, rayless and the two intermediate classes described in (a) above and Fig. 11.5. The results are given in Table 11.5 and the data summarised in Fig. 11.7 in which the two intermediate forms have been included in the same class.

The distribution of the three types in this region of the Tetney Haven marshes has a striking resemblance to a morph ratio-cline

Table 11.4	Proportions of rayed, intermediate and rayless plants in some E. coast populations.				
Population	(Yr. of count)	Nos counted	% rayed	% inter.	% rayless
Gibraltar Point					
Agr.	(1963)	50	88	10	2
	(1965)	86	100	0	0
Lim.	(1965)	100	← 83 →		17
Ast.	(1963)	50	20	26	64
	(1965)	80	← 38 →		62
Spa.	(1963)	50	8	40	52
	(1965)	100	← 4 →		96
Scolt Head					
Srl.	(1965)	50	← 70 →		30
Plover	(1965)	582	20	23	57
Missel	(1965)	359	26	26	48
Bch.	(1964)	1302	0.3	4	95.7
	(1965)	50	← 4 →		96
Cob.	(1965)	0	0	0	100
Morston	(1967)	100	72	10	18
Cley	(1965)	20	100	0	0
Tetney Haven					
Old marsh	(1963)	187	5	48	47
Halosere	See Table 11.5.				

(Huxley 1955) in which the ratio of the types varies as one goes from high to low marsh. The population is probably a hybrid swarm recombining in various degrees the differentiating character of the parent as a result of repeated segregation and recombination of parental gene complexes. The implications of this cline-like

Fig 11.6 Percentage rayless plants and marsh type. (Populations ranked in approximate order of marsh height - low to high = top to bottom).

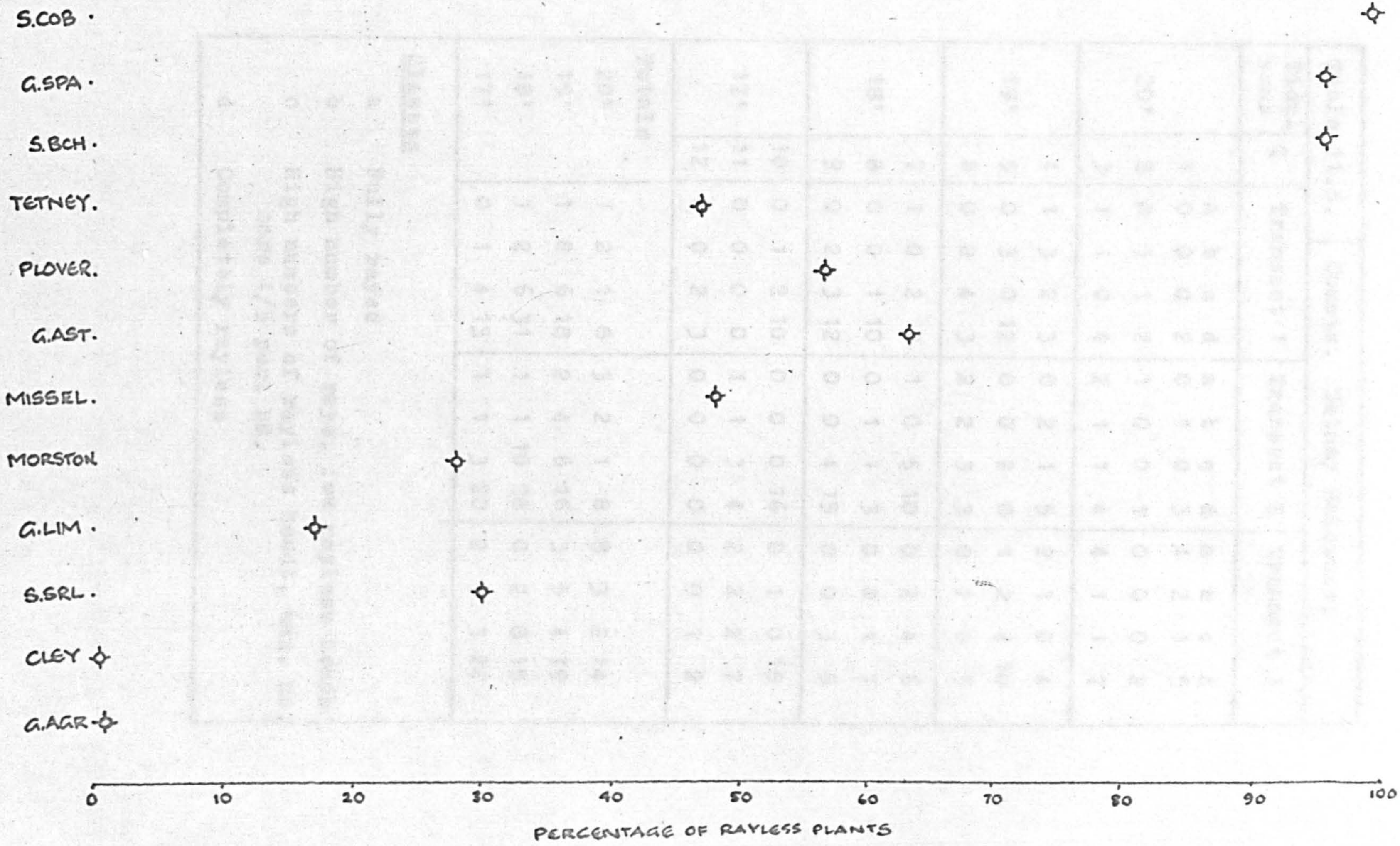


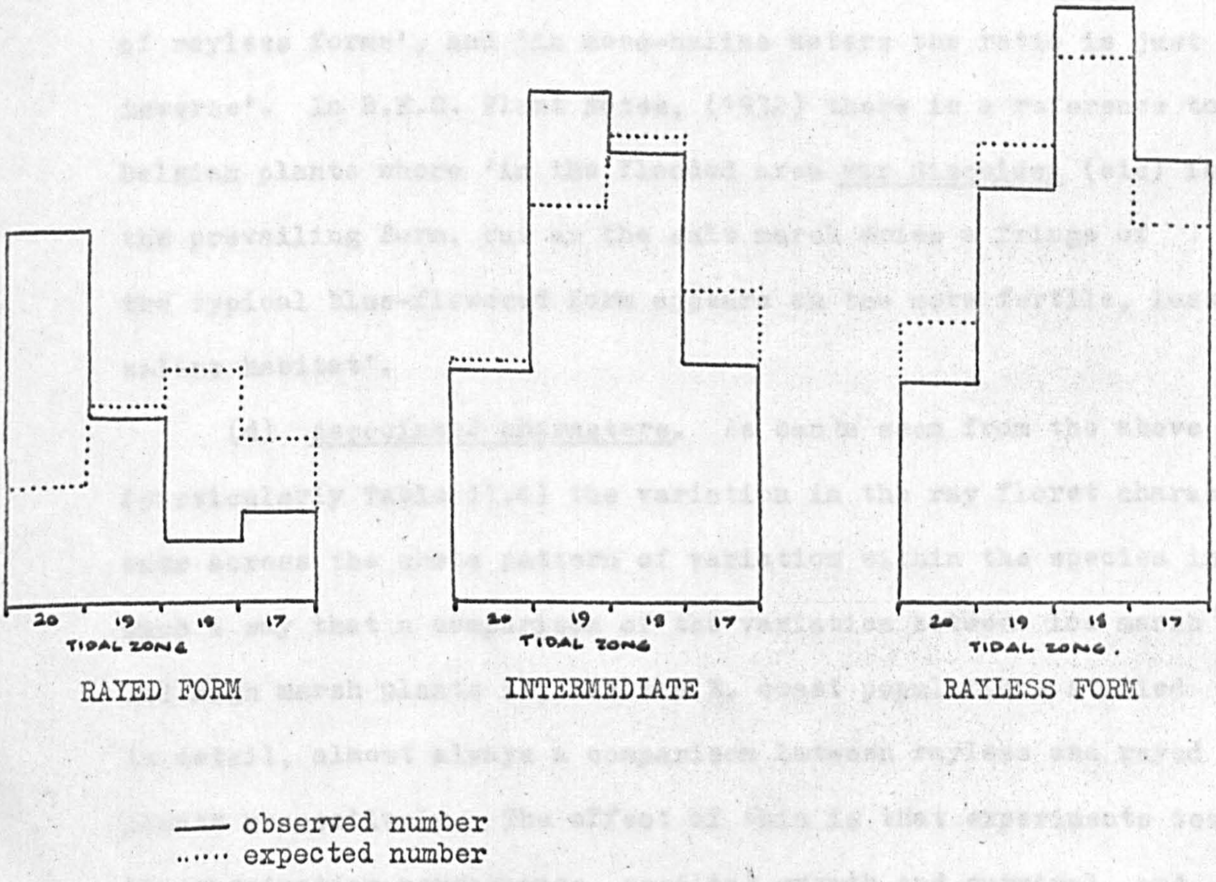
Table 11.5. Counts. Tetney Halosere.

Tidal zone	Q	Transect 1				Transect 2				Transect 3			
		a	b	c	d	a	b	c	d	a	b	c	d
20'	1	0	0	0	2	0	1	0	3	4	2	1	5
	2	0	1	1	2	1	0	0	1	0	0	0	2
	3	1	1	0	4	2	1	1	4	4	1	1	7
19'	4	1	3	2	3	0	2	1	5	2	1	0	4
	5	0	3	0	12	0	0	2	8	1	2	4	10
	6	0	2	4	3	2	2	3	3	0	2	0	5
18'	7	1	0	2	9	1	0	5	10	0	2	4	6
	8	0	0	1	10	0	1	1	3	0	0	1	7
	9	0	2	3	12	0	0	4	15	0	0	3	5
17'	10	0	1	2	10	0	0	0	16	0	1	0	15
	11	0	0	0	0	1	1	3	4	2	2	2	7
	12	0	0	2	3	0	0	0	0	0	0	1	2
Totals													
20'		1	2	1	8	3	2	1	8	8	3	2	14
19'		1	8	6	18	2	4	6	16	3	5	4	19
18'		1	2	6	31	1	1	10	28	0	2	8	18
17'		0	1	4	13	1	1	3	20	2	3	3	24

Classes

a	Fully rayed
b	High number of rays, few rayless heads
c	High numbers of rayless heads, max. no. more 4/5 per. hd.
d	Completely rayless

Fig 11.7 Differential distribution of rayed, intermediate and rayless forms. Tetney Haven saltmarshes.



(Expected number = number of each type to be expected if the three forms were distributed equally (1:1:1) within each tidal zone).

N.B. The scales of the diagrams have been altered to reveal relative observed/expected differences and are not uniform from histogram to histogram.

distribution are discussed later in section (e).

Two reports from continental Europe suggest that the pattern of differential distribution as observed in English east coast populations may be repeated elsewhere. Beeftink (personal correspondence) reports that in the S.W. Netherlands 'on the borders of eu-and poly-haline waters the ratio is 9:1 in favour of rayless forms', and 'in meso-haline waters the ratio is just inverse'. In B.E.C. Plant Notes, (1932) there is a reference to Belgian plants where 'in the flooded area var discoidea (sic) is the prevailing form, but as the salt marsh dries a fringe of the typical blue-flowered form appears on the more fertile, less saline habitat'.

(d) Associated characters. As can be seen from the above (particularly Table 11.4) the variation in the ray floret character cuts across the whole pattern of variation within the species in such a way that a comparison of the variation between low marsh and high marsh plants is, for the E. coast populations studied in detail, almost always a comparison between rayless and rayed plants respectively. The effect of this is that experiments testing the germination performance, seedling growth and survival, and so on, may be detecting the variation between rayed and rayless populations as well as that between populations from different points on the coastal sere. The data collected from work on fruit, seedling, and young plant characters has been recorded in such a way as to make the difficulty of distinguishing between the two sets of comparisons inexorable. Thus the possibility that a number of the experiments reported earlier may be interpreted from a different viewpoint cannot be ruled out. However, this does not invalidate these experiments as comparisons between high, mid and low marsh plants, (which they are whatever the genetic constitution of the plants is), and may in fact lend weight to the possibility that the spread of the rayless form has been the result of selection pressures of the type discussed later (see (e) and Chapter 12).

As the cross-pollination programme to determine the mode of inheritance of ray florets was kept separate from the other experiments, and only the variation in ray floret number scored, no direct evidence is available from this data alone of genetic linkage with mature plant characters.

It is interesting to compare, however, the data on ray/rayless variation with that on fruit size and number (Ch. 5). At the same time that fruit size and number were being measured for the data in Table 5.2 the heads were scored as being either rayed or rayless. It is possible to make a limited and tentative comparison between the sets of results from these scores. (Direct correlation is impossible as a linear relationship between fruit weight(or number) and marsh height cannot be secured, and a 2-way analysis of variance is unsafe because of the low numbers in certain cells).

It has been suggested elsewhere (Ch. 5, Ch. 9) that the variation in fruit size may be adaptive. Table 11.6 lists separately the mean weights and numbers of disc fruits taken from ray and disc plants within the same population. Certain conclusions are evident:- (1) At Gibraltar Point both the mean weights and the mean numbers of disc fruits vary little from population to population <u>in disc plants</u>. It is the variation in the weight and number of fruits in ray plants which provides the largest component of the observed variation in both fruit weight and number described in Ch. 5 (especially Fig. 5.6). As rayed plants have, overall, lower fruit weights and higher fruit numbers/head the observed cline at Gibraltar Point is partly accounted for by the variation in the ray plants and partly by the variation in the actual proportions of rayed and rayless plants in each population. (2) At Scolt Head on the other hand, where the overall numbers of rayed plants are small, there is a cline in fruit weight among disc plants. The amount of the total between-population variation which is due solely to the different proportions of the two types in the different populations is negligible or very small (the mean weights of ray and disc plants in Bch. and Srl. populations being very similar). This cline in fruit weight in disc plants is not accompanied, as in rayed plants at Gibraltar Point, by an inversely related cline in fruit number. (3) At Parkgate, (not listed in Table 11.6) where the disc genome is absent, the cline in fruit weight occurs in rayed plants only. Here there is no cline in fruit number.

It appears from this that at Gibraltar Point there is an 'association' between the ray character and fruit weight and number,

Table 11.6	Fruit weight and number in ray and disc plants at different marsh heights. (Based on mean wts. 10 disc fruits/hd.).			
(a) **Fruit weight**				
Gibraltar Point	Spa.	Ast.	Lim.	Agr.
Mean wt. disc fruits of disc plants (mgms).	13.9	12.4	14.0	-
No. Counted.	(72)	(50)	(20)	(0)
Mean wt. disc fruits of ray plants (mgms).	18.0	9.8	7.6	5.3
Nos. counted	(2)	(30)	(83)	(65)
Scolt Head	Cob.	Bch.	Srl.	
Mean wt. disc fruits of disc plants (mgms).	15.6	13.9	6.4	
Nos. counted.	(50)	(46)	(38)	
Mean wt. disc fruits of ray plants (mgms).	-	12.0	6.4	
Nos. Counted	(0)	(4)	(12)	
(b) **Fruit number**				
Gibraltar Point	Spa.	Ast.	Lim.	Agr.
No. disc fruits/hd. of disc plants,	26.1	22.2	21.3	-
Nos. counted.	(72)	(50)	(20)	(0)
No. disc fruits/hd. of ray plants.	16.5	32.7	36.7	41.5
Nos. counted.	(2)	(30)	(83)	(65)
Scolt Head.	Cob.	Bch.	Srl.	
No disc fruits/hd. of disc plants.	22.7	20.3	22.7	
Nos. counted	(50)	(46)	(38)	
No. disc fruits/hd. of ray plants	-	22.8	28.0	
Nos. counted	(0)	(4)	(12)	

rayed plants having on balance more, smaller and more variable fruits than rayless plants. The data reveal no such association among the Scolt Head populations.

What is especially interesting is that this suggests that the cline in fruit weight observed at the three areas may have arisen in different ways by the action of the environment on three very different gene pools. Although the selection may have been in all cases direct selection for fruit size (irrespective of the ray or disc character) it is clear that at Gibraltar Point, where fruit size and the ray character are associated, this will have the same effect as selection for the ray character. In fact the lack of variation in the disc fruit weights at Gibraltar Point suggests that the cline in fruit size may be a product of the differential selection of the ray and disc genotypes (this may occur alongside, and will have the same effect as, any direct selection on fruit size). At Scolt Head the response to the habitat gradient is largely in terms of the more common disc plants, and at Parkgate the same type of cline has been produced by interaction with a completely rayed population. If these tentative hypotheses were to be supported by further evidence they would underline not only the adaptive significance of fruit size but also the important point that adaptation may occur within the same species along a variety of pathways, the response of the local breeding population being a variable one, yet one producing a similar pattern of variation (the principle of the polytopic production of ecotypes).

(e) Balanced or transient polymorphism? Despite the fact that, as seems likely, the ray floret character may be a pleiotropic 'marker' for other characters of real selective value (see Ch. 12) it is still possible to ask whether its polymorphism is balanced or transient. Discounting for the moment the possibility that drift may have played a major part (an unlikely one in view of the consistency of the variation pattern) the evidence for the against a balance of the two forms may be presented as follows.

Theory 1. Balanced polymorphism.

Under this theory the rayed and rayless forms would be regarded as products of genetic response to habitat, being differentiated out of any population where differential selective factors operate (i.e.of polytopic origin).

The clear habitat preferences of the two forms in a number of E. coast populations at the present day may indicate a balance of selective agencies (tide-related factors in the low zones and competition factors in the upper zones?) to which the two forms have made a differential response. Thus the purely rayless low marsh populations and the purely rayed high marsh populations would be regarded as being at an evolutionarily later stage than the Tetney Haven population which is exhibiting the beginnings of the genetic isolation achieved by these pure populations. The clinal appearance of the Tetney Haven population could be explained in terms of its adjustment to clinally varying environmental factors. The openness and physiographical flux of the Tetney Halosere might allow the intermediate forms to gain a temporary foothold, and as Aster is a shortlived perennial one might expect a fairly gradual reduction in the amount of polymorphism as habitat factors become more stringent.

The major argument against this theory is that one has to explain the apparent recent spread of the rayless form in this country (and probably elsewhere). This can only, in theory, be accounted for if it is supposed that there has been a similar parallel increase in the type of habitat to which this form is seemingly adapted. There is some reason to suppose that this may be the case. Fig. 11.8 which indicates the position and size of Spartina anglica marshes in Great Britain, is based on Hubbard and Stebbings (1967) Fig. 1. p. 2. A comparison of the distribution of such marshes with the distribution of the rayless form of Aster tripolium (given in Fig. 11.1) clearly indicates a large number of sites in which the rayless form and Spartina are both present. A comparison of Fig. 11.1 with a more detailed distribution map of Spartina given in Goodman et al (1959 Fig. 1. p. 654) reveals further sites common to the two plants. Hubbard's map however (Fig. 11.8) provides an indication of the areas in which Spartina is present in an appreciable quantity and is thus a distribution map of a very well-defined type of salt marsh. It would clearly be of interest to know in which marshes the rayless form is the most common type as at Scolt, Gibraltar Point and the other areas visited personally.

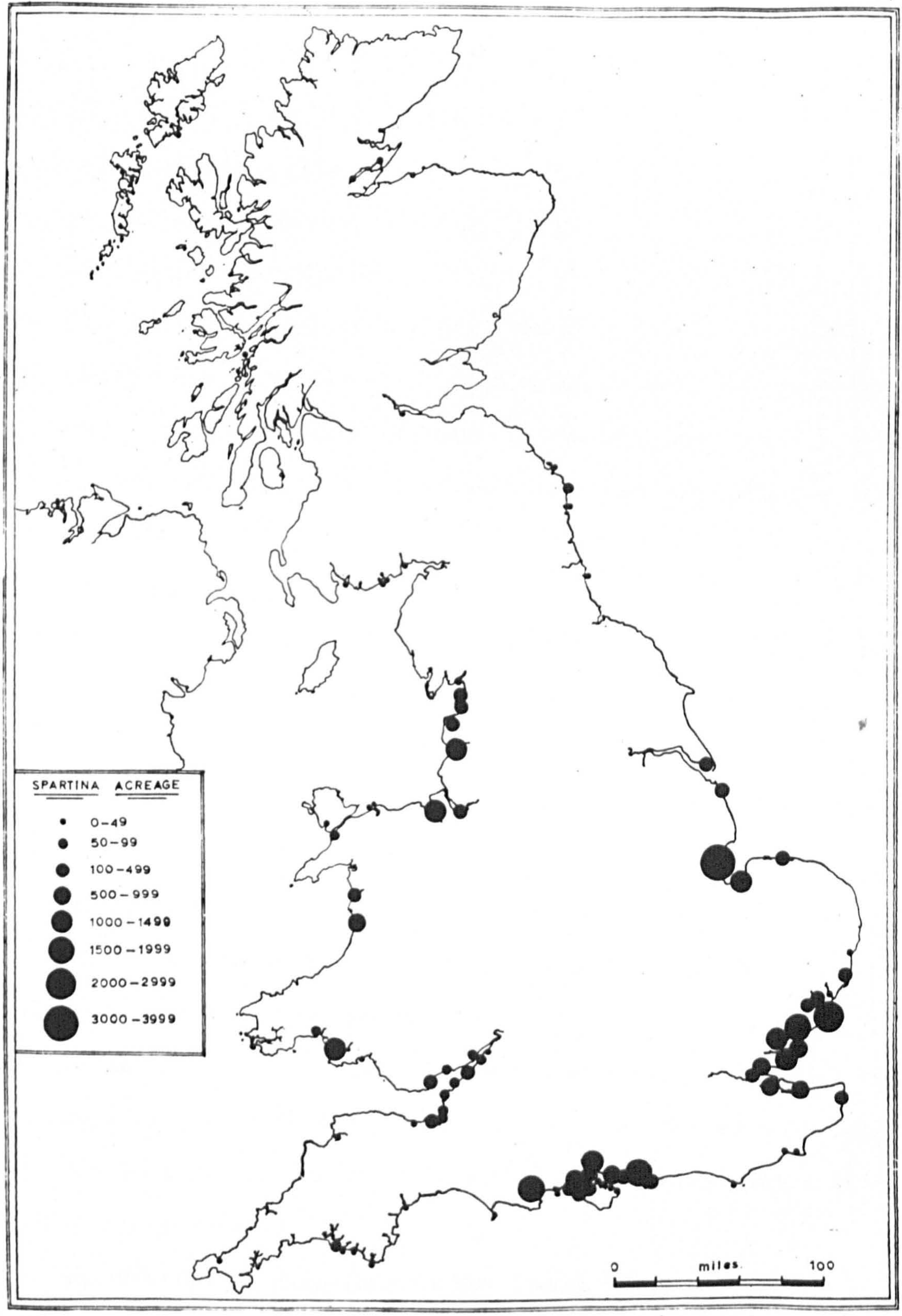


Fig 11.8 Distribution of Spartina marshes (after Hubbard and Stebbings 1967 Fig.1).

It is possible that one of the major effects of the explosive spread of <u>Spartina</u> in this country has been to add to the niches available for colonisation a further, lower, zone beyond that formerly occupied by seed plants. It may not be too outrageous to suggest that the rayless form of <u>Aster tripolium</u>, (because of its possible association with fruit size?), has been among the first plants to take advantage of the opportunity presented by this new, more stable zone which has been added to many south and east coast salt marshes. The parallel increase in the frequency of the rayless form and the two plant's coincident distribution may indicate such a possibility.

Theory 2. Transient polymorphism.

The rayless form is clearly an aggressive and invading form which has increased in relation to the type in many east coast populations within living memory. This suggests that it may be the process of replacing the rayed form and that the polymorphism is transient.

Under this theory the purely rayed populations could be regarded as ones in which isolation has thus far prevented the invasion of the non rayed genome (both the Cley and Gib. Agr. populations are at some distance from any other populations). Low marsh populations would thus be at a later stage of evolution in which the rayless gene(s) had been fixed and its allelomorph lost by selection pressure.

The pattern of variation in the Tetney Haven Halosere population would be regarded as an evanescent phenomenon in which the cline-like variation is a result of invasion from the lower zones and in which the rayed form is disappearing as a result of the greater fitness of the mutant.

Further evidence is required before either of these theories can be rejected in favour of the other. It is necessary to study the distribution of the rayless form in far more areas (for example, in the few west coast marshes in which it is said to occur in quantity (in the Spartina marsh in Bridgewater Bay for example)). It is also necessary to monitor the spread of this form in areas where it occurs at present. The task of deciding on whether a polymorphism is balanced or transient is a long term one, and in view of the spread of Spartina into mid marsh areas, it may be difficult to distinguish which criteria to apply in maintaining the distinction between the two types of polymorphism.

SUMMARY OF PART IV.

(1) A number of morphological characters were selected for comparison based on a general survey of the variation of plants in cultivation for a period of 2 years or more. These were primarily growth habit and leaf characters. A number of them varied with the environment and between plants in the same population under uniform conditions, but some general differences were evident.

(2) The retention of the initial rosette of basal leaves and the amount of both lateral and axillary branching varied within populations according to treatment. The character 'woodiness' and the tendency to develop sub-basal leaves were less variable both between plants of populations in uniform conditions and within populations in a range of conditions.

(3) Plant height varied from plant to plant within populations grown under uniform conditions and also between samples of the same population in different conditions. Of a number of dwarf forms collected, only two (from the Orkneys and from central Cheshire) retained their dwarfism in cultivation. In particular the mean plant height of the Scolt Spiral marsh population was considerably increased in plants grown from fruit as compared with those collected from the wild as plants, (and with plants _in situ_ in the wild).

(4) The pattern of variation in growth habit characters was as follows. High marsh plants were rarely, if ever, woody,

generally unbranched, and did not develop sub-basal leaves. Mid marsh plants were always woody and well branched and almost invariably developed sub-basal leaves. Low marsh plants were usually woody although sub-basal leaves rarely developed and the amount of branching, varied from population to population. The persistence of the initial rosette varied from population to population within all three types.

(5) The decumbence of the young plant was measured in five high, four mid, and four low marsh populations. The low marsh populations consisted of plants with erect rosettes when compared with the high marsh populations which were generally more decumbent. Two mid marsh populations consisted of decumbent plants and two of erect plants. This pattern of variation in habit types is the inverse of that described in Plantago maritima by Gregor (1938).

(6) Basal leaf shape was measured in populations from two east coast series, Gibraltar Point and Scolt Head Island. In both areas there was a cline in leaf shape from high to low marsh populations, the high marsh plants having significantly narrower, more lanceolate leaves than those from low marshes. The significance of this pattern of variation is unknown. Variation in basal leaf colour was investigated and it was concluded that there is possibly a quantitative difference in the plastid content of leaves from different populations.

(7) The status and distribution of the rayless form was

described. Some early records were listed and evidence was presented to suggest that there has been a recent spread of the rayless form, particularly in S. E. England. It was tentatively suggested that this phenomenon may be partly explained by the parallel spread of Spartina anglica in this country which has provided a niche to which the rayless form may be better adapted. This is supported by the differential distribution of the two forms and by some fruit weight measurements.

(8) The inheritance of the ray floret character is complex and meristic in nature and may be governed by a number of genes which vary in their penetrance. Crosses between rayed and rayless plants produce an F_1 which varies greatly in ray number from plant to plant and from head to head on the same plant. There is some evidence of segregation towards parental types in the F_2 but the general pattern of variation is confusingly wide. Ray number in some plants varied from one recording occasion to another, the least variable number being scored during the main period of flowering, a generally lower mean number mean number being scored early in the flowering season, and a highly variable number being scored as flowering finishes. In other plants there was no such breakdown of canalisation, a relatively invariable mean number of rays being produced throughout. Variation in ray floret, size, colour and shape was also described and the pattern of variation in number was compared with that in some other composites.

(9) The ray/disc polymorphism was examined from the

standpoint of Fordian theory. It was concluded that:-

(a) There was no evidence of specificity by pollen vectors but that the differences in main period of flowering may tend to isolate rayed and rayless populations.

(b) The two forms have a differential ecological distribution on the east coast marshes, a significantly higher percentage of rayless plants occuring in low marshes than in high marshes and vice versa. The proportion of the population classified as of 'intermediate' type was included in these counts and conformed to the pattern described. In one area (Tetney Haven) the proportions of rayed, intermediate and rayless forms found at different tidal levels on the marsh showed a cline of variation.

(c) There were some indications of 'association' between the rayless form and disc fruit size and number in the Gibraltar Point populations but not at Scolt Head (or Parkgate where the rayless form is absent). This suggests that in some areas selection for fruit size in the lower zones would lead to the selection of rayless plants. This may partly explain the differential distribution of the two forms although it is possible that in other areas (e.g. Scolt Head, Blakeney Point) small-fruited rayless plants could be invading the upper marshes formerly occupied by fully rayed forms.

(d) The questions of the discontinuity of the variation and the transience of the polymorphism were largely academic, the latter in view of the uncertainty with which the criteria necessary to judge the situation can be applied, the former in view of the pattern of variation in ray number.

PART V

GENERAL SUMMARY AND DISCUSSION

CHAPTER 12. GENERAL SUMMARY AND DISCUSSION.

The data relating to specific aspects of variation in Aster tripolium have been summarised and discussed in the preceeding sections of this report. The General Summary (I) below summarises the overall pattern of variation in relation to the categories of ecological similarity defined earlier (Ch. 3). The implications of this pattern are considered below in the Discussion (II).

I General Summary.

In Table 12.1 are listed twenty seven characters which have been measured during the course of this investigation in a number of high, mid and low salt marsh populations. The number of populations within each group varies from one case to another and these numbers, which give some indication of the reliability of the general statements based on them, are included in the table.

Six of the twenty seven characters listed are known to be 'plastic' (in at least one population) in the sense of this investigation i.e. there is a significant difference in the mean value of characters between samples from the same collection grown under a spectrum of cultivation conditions. These are characters related to life cycle, branching, inflorescence height and fruit production. There is some evidence that the characters' 'year of first flowering' and 'plant height' are less plastic in

Table 12.1 Summary of variation in high, mid and low marsh plants.

Character	HIGH MARSH	no.popns. tested	MID MARSH	no.popns. tested	LOW MARSH	no.popns. tested	Chapter in which variation described	Variation type (see foot of table)
Life cycle								
Year of first flowering	often first year	8	generally 2nd or subsequent year	6	2nd or subsequent yr.	5	4iv	*
(% 1st year pauciennials)	(0 - 60%)	5	(0 - 8%)	5	(0)	3	4iv	*
Overwintering ability	poor	7	good	5	fair	5	4iv, 10	U
Amount of basal development	very little	7	at maximum	5	some	6	4iv, 10	S
Time of flowering	Sept - Oct.	8	Aug. - Sept.	6	July, Aug., Sept.	5	4iv	U
Variation in popn. flowering date.	high	8	low	6	low	5	4iv	S
Morphology								
Rosette habit (brdth:ht:ratio)	decumbent (c.0.9)	5	variable (0.5 to 1.1)	4	erect (c. 1.6)	4	10	U
Loss of basal rosette	varies between popns.	8	varies between popns.	5	varies between popns	6	4, 10	*
Branching	generally unbranched	7	well branched	6	variable	6	5, 10	*
Woodiness	rarely woody	7	always woody	5	generally woody	6	4, 5, 10	S
Sub-basal leaf growth	none	7	generally extensive	5	very little	6	10	S
inflorescence height (popn. mean height)	variable (13 - 102cms)	5	medium (27 - 56cms)	3	variable (15 - 82cms)	4	10	*
Height of perennating bud	if one, several cms above ground	7	ground level	5	ground level - buried	5	10	S(*)
Basal leaf shape (length: width: ratio)	lanceolate (c. 4.4)	3	obovate - lanceolate (c.3.4)	1	obovate (c. 2.9)	3	10	U
Number of heads/plant	variable (7 - 232)	4	(64 in G. Ast)	1	varoab;e (14 - 81)	3	5	*
Relative seedling size	small	2	medium	2	large	2	8	U

continued ....

Table 12.1 continued ....

Character	HIGH MARSH	no.popns. tested	MID MARSH	no.popns. tested	LOW MARSH	no.popns tested	Chapter in which variation described	Variation type (see foot of table)
<u>Fruit</u>								
Mean number fruits/head	high (33 - 43)	4	26 in G. Ast.	7	generally low (20 - 27) except P2, P3, P4.	6	5	*
% inviable fruits/head	c. 26 - 40%	4	G. Ast. c. 30%	7	c. 12 - 19%	6	5	U
Relative fruit size ($\bar{x}$ wt./ 10 disc fruits)	small (c. 5 - 9mgms)	4	intermediate (c11 mgms)	7	large (c 14 - 24mgms)	6	5	S
Percentage of fruits germinating without prechilling	low (5 - 40%)	3	(30% and 100% - G.Ast)	7	high (68 - 100%)	2	6	U
Germination of wild-collected fruit in artificial sea water	20% germination up to 20% A.S.W.	3	20% germination up to c. 40% A.S.W.	2	20% germination up to c.60% A.S.W.	2	6 and 7iv	U
Effect of light on germination	less than in dark	3	less than in dark	2	less than in dark	3	6	U
<u>Other</u>								
Chromosome number	2n = 18	3	2n = 18	4	2n = 18	2	4	U
Response to tidal treatment	lower % survival with increased treatment	3	G. Ast. % survival lowered	1	% survival unaffected or increased (except Bch)	3	7iv	U
Growth in intense tidal treatment	poor (total biomass reduced considerably)	3	G. Ast. poor	1	fair (biomass reduced in 2 out of 3 popns.)	3	7iv	U
Survival rate in ordinary soils	high (c. 85%)	7	fair (c. 70%)	5	low (c. 40%)	5	9	U
Number of lateral roots (seedlings-1 expt.)	few (c. 4.7)	2	more than low (c. 5.6)	2	many (c. 7.7)	2	8	U

* character known to be 'plastic'.

S character known to be stable.

U stability of character not known.

mid and low than in high marsh populations. A further six characters, related to secondary thickening, sub-basal leaf development, the height of the perennating bud (the presence or absence of a perennating bud is 'plastic') and fruit size, are more stable under a range of conditions. The stability of the remaining fifteen characters is unknown.

All but four of the characters listed differe significantly in at least one group of populations. The characters which do not vary with marsh type are chromosome number, plant height, the tendency to lose the initial rosette of leaves and the relative germination rates in light v. dark conditions.

The remaining twenty three characters show less within-group (i.e. high, mid or low) than between-group variation in at least one of the three groups of populations (when compared under collateral cultivation); The nature of this variation is different for each character and ranges from discontinuous to clinal. Thus the variation within groups can be expressed as the proportion of the group to show a particular character such as branching, basal development or first year flowering (e.g. when grown in pots in the greenhouse one out of seven high marsh populations was branched, five out of five mid marsh populations were branched and two out of six low marsh populations were branched); or it can be expressed by reference to a particular point on a cline of variation in characters such as fruit size, basal leaf shape or rosette habit.

In addition to the characters listed in Table 12.1 there is limited evidence of population differentiation in leaf colour (Ch. 8) and germination pattern in transplanted fruits (Ch. 9), but the numbers of populations tested are too small on which to base any general conclusions. The variation in the ray floret character is a special case known to occur in the east coast populations studied and to which variation in some other characters may be related.

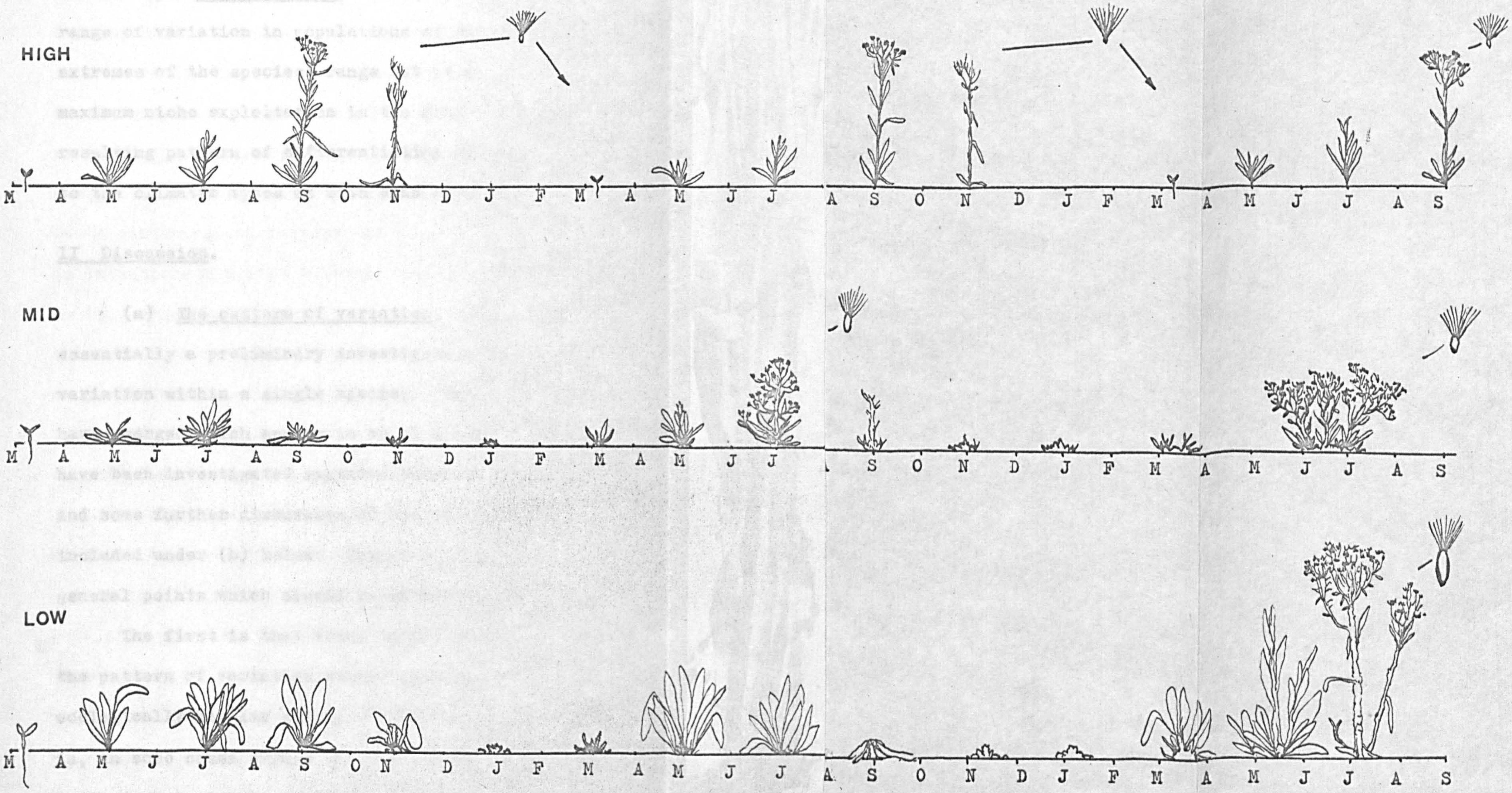
The general pattern of differentiation which emerges from this study is as follows. Populations of <u>Aster</u> from high marshes contain a high percentage of plants which can flower and produce fruit in one season from fruit, have no or limited means of vegetative propagation, produce single unbranched flowering stems from decumbent young plants, have lanceolate basal leaves, are late flowering, produce in each capitulum high numbers of small disc fruits which require pretreatment to break their dormancy and show (when wild collected) poor germination in saline solutions above 20% sea water, show extreme plasticity of certain related characters such as branching and fruit production, and greatly reduced survival and yield under sea water treatment. It is of particular interest that a number of these characteristics are commonly associated with 'weedy' species (see later).

By contrast populations from mid marshes generally contain plants which take at least two seasons to flower from fruit, have extensive means of vegetative propagation, produce numbers of extensively branched flowering stems, have more obovate leaves (1 popn.), are earlier flowering, produce fewer, larger fruits a greater proportion of which require little or no pretreatment before germination, and give good germination in saline solutions up to 40% sea water. In addition yield is less depressed in sea water treatment (1 popn.).

Although less extensively branched and with fewer characters associated with vegetative propagation than mid marsh plants, low marsh plants generally represent the opposite extreme of the variation pattern from high marsh plants. This applies to the characters 'time to first flowering, rosette shape, flowering date, basal leaf shape, capitulum fruit number and size of disc fruits, germination requirements and response to sea water treatment'. Some of this variation is summarised in Fig. 12.1. The general variation pattern is further discussed under II below.

There are a number of parallels between the types from high marsh populations and those from the southern, and eastern salt-desert areas of Europe, and between mid and low marsh types and those from the northern part of the species' range. High marsh populations share with the southern <u>var longicaulis</u> and <u>var pannonicus</u> characters such as the panciennial life cycle, the high per capitulum fruit number, narrow basal leaf shape, high ray floret number, and have a similar general appearance. (It is of interest that the characters 'loss of basal rosette' which varies from population to population in British material also varies in the two former

Fig 12.1 Variation in life cycle in High, Mid, and Low marsh populations.



varieties - see Figs. 2.1 and 2.2). Similarly mid and low marsh populations share the perennating and general vegetative properties of the populations sampled from Scandanavia and Finland and from the Orkneys (<u>var. arcticus</u>). There is a need to sample the range of variation in populations at the northern and southern extremes of the species' range but it may be that there is maximum niche exploitation in the British Isles and that the resulting pattern of differentiation has produced types similar to the climatic types at both ends of this range.

II Discussion.

(a) The pattern of variation. This study is regarded as essentially a preliminary investigation over a broad front of variation within a single species. Where specific differentiiae have emerged which appear to be of ecological importance these have been investigated experimentally (especially Chs. 8, 9, and 11) and some further discussion of specific trends of variation is included under (b) below. There are, however, a number of general points which should be made at this stage.

The first is that there is an inexact correspondence between the pattern of variation within the species and the groupings of ecologically similar sites. Variation of individual characters is, in some cases cruder and, in others, more subtle than the defined variation in the environment. Discontinuities in variation of characters do not always coincide with discontinuities in the ecological groups. For example a character may be common to one group and not to the other two, or it may be possible to rank populations within groups in a clinal series. In certain cases of characters showing clinal variation there is a close correspondence between the dispersion about the population mean for that character and the (assumed) ecological heterogeneity of the marsh from which it was collected (e.g. fruit size). There is no a priori reason why variation in any one character should correspond closely with a predetermined grouping of populations based on ecological factors the importance of which are not known. In fact there are good reasons, listed below, to suppose that, in this case, such a correspondence would be unlikely. Nevertheless this contrast in the patterns of genotype/environment interaction serves to emphasise the value, as well as the danger, of attempting to construct and compare groups of populations believed to share similar environments.

A second and related point is that, despite the overall patterns of variation described in I above, the variation for any particular character is rarely clear cut. Thus one does not find, for example, a clear contrast between an annual and a perennial life cycle but a comparison in terms of the 'paucienniality' of a population. Or, similarly, the character 'branching' must be defined in terms of the proportion of each population which become branched in a specific environment and the proportion of those populations within a particular group which have a high percentage of branching in that environment. The cases of clinal variation are further examples of this tendency to non-discrete patterns of variation.

There are a number of possible theoretical reasons why the pattern of variation revealed in this investigation is of the sort described. The most important of these, which may be related to the methodology or to the 'real' variation, are outlined below.

(i) Mechanisms of inheritance. A primary point is that the pattern of variation in an interbreeding population will depend to a large extent on the genetic structure of that population. At the level of the individual character the variation pattern will depend on the numbers of genes responsible for its expression and their respective modes of inheritance. Hiesey (1963) points out that, in ecotype studies in Achillea, Potentilla and Mimulus groups, the inheritance of characters used to distinguish ecological races was mostly governed by multiple genes, and that simple Mendelian segregation was rare. Many of the characters measured in this study are of the sort which have been shown to be under polygenic control in other species (e.g. leaf shape, growth habit), although no evidence is available for Aster from the present work,

Although polygenic inheritance does not preclude the formation of sharp discontinuities between closely adapted types*

---

* Hiesey 1963, has suggested that strong linkage relationships play an important part in racial divergence, a phenomenon which he refers to as 'coherence'.

it is to be expected that, in panmictic populations, segregation of polygenes will tend towards the production of continuous patterns of variation between extreme types, with many intermediates. This may be especially true when selection pressures are low.

(ii) Environmental gradients. As was emphasised at the outset (Ch. 2) the variation in ecological factors across the coastal belt, as represented here by the series high to low salt marsh, is imperfectly known. The grouping together of marshes of ecological similarity involves the grouping together of ecological factors which may vary considerably between populations of the same group. This is because a number of environmental gradients may be involved (e.g. in submergence, salinity, soil type, exposure, edaphic factors such as nutrient level and aeration properties, competitive factors) which may vary independently in the same locality and also vary from locality to locality. Other factors, unrelated to the maritime gradient, such as intensity of grazing or disturbance may be important. In addition there will be, in maritime gradients, marked temporal variation occuring within the environment. In the absence of direct experimental evidence the relation between a plant variable and an environmental variable must be extrapolatory (see Ch. 2) and it is only when this relation has been demonstrated that the pattern of variation can be understood.

This situation is in direct contrast to that found, for example, in the study of heavy-metal tolerance in certain grasses

(Bradshaw et al 1965) where both the relationship between the character (root growth in solutions containing higher than normal concentrations of the metal compared to root growth in solutions without the metal) and the environmental variable (contaminated v. non-contaminated soils) is apparently direct, and where the changes in the environmental variable, occuring over relatively short distances, are known to be sharply marked.

Thus in Aster tripolium it is possible that characters which show a clinal pattern of variation may be varying in direct response to a clinally-varying environmental factor whilst others may be the products of sharper discontinuities in the environment.

(iii) Exchange of genetic material. It has been shown that Aster tripolium is both self and cross fertile and that, in artificial conditions, plants normally separated by considerable distances are capable of exchanging genetic material. It has not been possible however to estimate effectively the amount of natural crossing, and therefore the size and limits of populations sharing the same gene pool, and the amount of gene flow between adjacent populations, are unknown. As was outlined earlier these are important factors which have a fundamental effect on the total variability of a species at the population level.

Limited evidence suggesting that gene flow could be fairly extensive is provided by the entomophilous mode of pollination and high frequency of suitable widely foraging pollen vectors. If this were the case one would expect a low rate of population divergence and a dilution of the characters produced by adaptation to the different habitats within the species' range. One manifestation of this would be the blurring of discontinuities between adjacent populations which may nevertheless be in the process of actively diverging.

A recent series of papers based on theoretical analysis, computer simulation studies and studies of natural populations of grasses (Jain and Bradshaw 1966, Aston and Bradshaw 1966, McNeilly 1967, McNeilly and Antonovics 1968, Antonovics 1968a, 1968b), have demonstrated that, in closely adjacent plant populations, gene flow and adaptive divergence are, to a large extent, opposed forces and that, where the latter is at a premium, as for example in heterogeneous environments, one might expect the evolution of isolating mechanisms specifically selected to reduce the former (gene flow) and counteract its effects. Two such mechanisms are self-fertility (Antonovics 1968a) and flowering time (McNeilly and Antonovics 1968).

Any mechanism which effectively circumvents outbreeding (including geitonogamy) will reduce gene flow and reduce the dilution of adaptive characters. It would be of considerable interest to discover the amounts of natural self-fertilisation which occur at the respective marsh levels at which _Aster_ occurs. For, as well as enabling divergence to occur more rapidly, the retention of self-fertility in this species may have important ecological consequences, particular at the extremes of the plant's range where establishment may depend on the reproductive success of a few well scattered individuals (Baker 1955, Antonovics 1968a).

The differences in flowering time on marshes at Scolt Head Island, (reported in Ch. 4) and the observed variation elsewhere, suggest that there is a high probability that plants on high and low marshes are effectively prevented from exchanging genetic material. Rayless plants were found to flower earlier than rayed plants on a mid marsh at Morston (Ch. 11). As McNeilly and Antonovics (1968) point out, such differences in flowering time may be a result of either adaptation to local ecological conditions or they may be a direct response to gene flow, evolving as an isolating mechanism. There is insufficient evidence to suggest whether, in Aster, the isolating barrier produced by differential flowering time could have arisen as a direct result of the selection for a mechanism to restrict gene flow or as an 'accidental' by-product of selection for some other attribute. The similar pattern of variation in different areas i.e. earlier flowering on all low marshes, possibly argues against the direct selection of an isolating barrier. Also it is clear that, in the annual high marsh populations, late flowering may be simply a by-product of selection for the annual life habit, there being a developmental restriction on the time required to first flowering. It is of considerable interest to compare the flowering time of perennial rayed and perennial rayless plants as the evidence from Morston suggests that early flowering may effectively isolate the two forms, and that the early stages of sympatric speciation may be in progress. Further work is needed on this aspect of variation but, were this process in force, it would further help to explain the rapid recent spread of the rayless allebmorph, which is not dominant over its corresponding allelomorph.

A final aspect of genetic exchange at the population level is the spread of fruits into neighbouring populations; for if complete selection against these does not occur they will have the effect of diluting the adaptive characteristics of a diverging population (cf Antonovic's (1968b) model for 'seed flow' in which selection was exercised on the pre-existing population prior to the influx of new genes and on the incoming genotypes before they were mated). Again evidence from the wild is limited but fruits from low marsh plants are probably carried to high marshes by tides, and fruits from high marsh plants are capable of being wind dispersed to low marshes. Selection against high marsh genotypes in low marshes may occur at the fruit (poor germination in saline media) and seedling (small size and mechanical elimination) stages and they may be prevented from flowering by the extreme factors of the tidal environment (tidal treatment experiment). Similarly low marsh fruits on high marshes, having no delayed germination, may germinate in the autumn (but see below) and fail to overwinter, and be unable to compete with glycophytes. Their size may prevent them from being dispersed to areas infrequently inundated by tides.

To summarise: in areas where non-discrete patterns of variation occur the continuity of variation may be maintained in the face of disruptive selection and adaptive divergence by high rates of genetic exchange between adjacent populations involving two methods, cross-pollination and fruit dispersal. Selfing and the differences in flowering time may counteract the first method and disruptive selection ~~and~~ the second.

(iv) *Phenotypic plasticity*. Significant shifts in the sample mean value of a character (in plants grown from fruit collected from the same population at the same time) under different conditions of cultivation have led to this character being described in this report as 'plastic'. This plasticity was assumed at the outset to be directly adaptive. However this aspect of the variation pattern needs to be examined more closely.

The subject of phenotypic plasticity has been fully discussed by Bradshaw (1965) who reviews the evidence which indicates that it is '(a) specific for a particular character (b) specific in relation to particular environmental influences, (c) specific in direction, (d) under genetic control not necessarily related to heterozygosity, and (e) able to be radically altered by selection'. He concludes that, although not all plasticity is directly adaptive, in plants, since they are static organisms, it is a widespread method of adaptation in a number of situations where selection is operating.

The type of plasticity detected in *Aster* is, strictly speaking, 'between-population'. This estimate of plastic response is necessarily cruder than one using clones or pure lines and some criticism of the method has already been included (Ch. 5). Those characters which show between-plant plasticity, together with those which do not, are listed below (Table 12.2).

Table 12.2	Plasticity
Plastic	Not Plastic
Year of first flowering	Presence sub-basal leaves
Branching	Woodiness
Inflorescence height	Variation in population flowering time.
Presence of perennating bud	Height of perennating bud
Number of heads/plant	Size of disc fruits
Number of fruits/head (very low)	
Persistence of basal leaves.	

Although a somewhat curious mixture, the characters which show plasticity generally are 'formed by long periods of meristematic activity' and are of the same order as those listed by Bradshaw (1965). There are, however, some apparently anomalous cases, and an explanation based on the original data is required.

Plasticity of the characters 'year of first flowering' and 'presence of perennating bud' apply only to some high marsh populations (except induced 1st year flowering in one low marsh population). Although these populations overwinter in the protected conditions of the greenhouse, and thus show a plastic response, they always carry the perennating bud in a rosette of leaves raised some distance from the ground (as opposed to ground level or buried). In this sense the presence of a perennating bud is a plastic character whilst its height above ground is not. Similarly, whilst flowering may occur in the second year it is invariably more erratic than in mid and low marsh populations. Thus year (and number of times) of flowering is plastic, whilst variation in sample flowering time is not. These phenomena may be explained in terms of contrast between 'all-or-nothing' irreversible types of plastic response (e.g. floating leaf development in certain submerged aquatics) and those in which there is a continuous, and sometimes reversible, adjustment to the environment (e.g. seed output in relation to density). Bradshaw discusses this point in some detail, quoting the work of Schmalhausen (1949). Thus the 'decision' to flower for the first time in the second year and carry a perennating bud can be invoked by a specific stimulus (the continuation of temperatures conducive to growth?) and once the 'switch' is made the alternative developmental pathway is taken, and faithfully followed. The degree of branching(and thus head production) is subject to continuous adjustment and independent of whether the switch is made or not; so that, in plants which are flowering for the first time in the second year, branching and head production may be determined by the environmental conditions which they experience during the second year. Some indications that this is so are given in Chs. 4 and 5.

The development of sub-basal leaves does not vary between treatments within single populations although the persistence of the basal leaves does. Woodiness is stable but is a more difficult character to define and is not absolute. Also relative is the distinction between the 'stability' of fruit size on the one hand and 'plasticity' of fruit number on the other. It has been argued earlier that, in the light of the limited evidence available, it really depends where one decides to draw the line. On the basis that the mean fruit weights of individual populations of two clinal series of populations did not overlap, whereas the mean fruit numbers/head did overlap, fruit size was assessed as being less plastic than fruit number (Ch. 5). This does not take account of the general variability of the population, is not supported by statistical analysis, and leaves the point open to argument. Further work is required. It is clear however, that the distinction between a plastic and a non-plastic character is not absolute, and that some characters are more plastic than others.

Thus variation within the species can be seen to be a mixture of genetic and plastic components. The effects of these components may be additive or they may act to neutralise one another. On the one hand, for example, the tendency of high marsh populations to flower after only a short period of vegetative growth appears to be genetically determined, whilst the plasticity of this character enables some populations (e.g. Gib. Agr., Cley, P1) to be truly annual in the wild, whilst others (Scolt Srl., Gib. Lim.) are not. By contrast the phenotype of the 'dwarf' character is determined genetically in the Orkney Island and Winsford A populations but is the product of a plastic response in the Spiral marsh and Parkgate wall populations. A number of similar examples in other species has been listed by Bradshaw (1965). He points out that increased plasticity may, in cases of severe directional selection allow the population further adaptation in addition to normal, possibly limited, directly adaptive genetic variation. Further, in cases of stabilising selection it may enable adaptation to a uniform environment to proceed in a population without interference with what may be a considerable amount of genetic variation. Perhaps, in this context, the most pertinent example quoted by Bradshaw is that of Gregor's work on Plantago maritima. This provides a demonstration that within the same species in different areas plasticity may enable genotypically similar plants to appear phenotypically very different (Gregor 1956b) (or, more strictly, to enable genotypically dissimilar plants to appear phenotypically even more different) and also to enable genotypically dissimilar plants to appear phenotypically alike (Gregor 1956a) (or, again more strictly, to enable genotypically very different plants to appear phenotypically less different).

It is relevant to ask why, if they are inherited independently of the character which they affect, genes giving higher phenotypic plasticity should be selected for in some cases and selected against in others. This is related to the question why in some cases adaptation to the environment occurs largely as a plastic response whereas in others it occurs as a genetic response. In discussing the low plasticity of fruit size (Ch. 5) it was suggested that fruit size was of adaptive importance and subsequent experimental evidence on seedling vigour and establishment in tidal environments lend some support to this suggestion. The validity of this suggestion does not, however, cast much light on the apparent selection for low plasticity of fruit size. Indeed, if large fruits are at a selective advantage why not also genes for high plasticity, which could, as suggested above enable even larger fruits to be produced by augmenting the genetic adaptation? (This situation has been suggested in actual cases of selection in <u>Drosophila</u> (Thoday 1958) and mice (Falconer and Robertson 1956)). The answer can only be that indicated earlier, namely that just as fruit size is of adaptive importance, so also is stability of fruit size. It is possible that, if fruit size was plastic, any small fruits produced by genetically large-fruited plants would not survive in low marsh environments, (given the hypothesis advanced here), but could only survive and grow in high marsh environments, and <u>vice versa</u>. This would lead to gene flow. If selection is acting against gene flow, then this would have a disadvantageous effect. Related to this is the point that it is better for selection to act early in the life cycle, rather than late, since it reduces competition with well-adapted genotypes. Thus one might expect selection against gene flow to produce low plasticity of fruit size.

Hypothetical reasons for the adaptive importance of fruit size stability in wild populations of sunflower have been advanced by Khan (1967) who points out that stabilising selection for seed size at the germination and establishment phase will act to retain canalisation. This hypothesis may apply equally to Aster, as may Khan's alternative hypothesis that seed stability genes are linked with other genes (e.g. branching) for which selection is occuring. No evidence is available in the present study to support either of these hypotheses as they relate to Aster. They are part of the general thesis that the stability of certain characters, especially floral and reproductive ones, may be important for the fitness of the individual (Berg 1959). However it is not difficult to envisage that linkage or pleiotropy could be involved in the selection of stable fruit size in Aster. The clinal pattern of variation indicates that disruptive selection is occuring and that the selection for large fruits on low marshes is reversed on high marshes. Selection for stable fruit size could occur if these are linked to, say, genes controlling germination characteristics.

Certainly further work incorporating a more rigid control of the environment is required. It would be of particular interest to examine, for example, the behaviour of the character 'ray floret number' under a range of environments. Although not mentioned immediately above this character is known to be unstable in certain genotypes (Ch. 11) and in view of the smaller size of ray fruits, the fruit size cline, and the ray floret number cline, may provide a further example of phenotypic plasticity masking the pattern of genetic variation.

(v) Sampling and culture conditions. Finally it is necessary to consider three aspects of the method used in this investigation which may have prejudiced the variation pattern disclosed. First, in a number of the experiments, wild-collected fruit from the same population has been used and the variation of this fruit sample has been used as a measure of population variation. This is unsatisfactory, in that the fruit (and young seedling) populations, not having borne the brunt of selection in the environment of their maternal parent, may differ widely from the mature plant populations with respect to characters of selective importance. This will be particularly relevant where there are high rates of gene flow between adjacent populations and has been demonstrated in a number of studies (e.g. in an Agrostis stolonifera population, studied by Aston and Bradshaw (1966), in which, among other examples, the seed population contained a number of A. stolonifera X A. tenuis hybrids, none of which were present as mature plants in the population). In particular one would expect a seed population to show a wider range of variation than a selected mature plant population.

A second aspect of the method which may have tended to emphasise the variability of single populations is their culture in a range of environmental conditions. Normally in studies based on the uniform garden trial between-site (i.e. in the garden plot) variation is deliberately absorbed into the background residual variation by randomisation, and regarded as error or 'noise'. Such studies may tend to play down the within-population variation by minimising the plastic response. However, when, as in this case, an attempt is made to measure this 'noise' the overall impression of very wide variation may be given by the superimposition of phenotypic plasticity on to a background of genotypic variation. This emphasises the value of comparative studies of plasticity in related species, where between-species variation in plasticity may be relatable to differences in ecology.

A third, and related, point was made in Chapter 2. This is the fact that, in techniques based on collateral cultivation, one is comparing variation at one point on what may be a wide spectrum of reponse and that, in situations such as the growth of maritime plants in ordinary soils, there is a possibility that 'distortion' will tend to obscure differences which are important in the field. It is not difficult to envisage a situation in which, say, a species has either red, white or blue flowers, genetically determined, but with an ability to respond to artificial light by producing pink flowers. In this situation the growth of plants in artificial light would fail to detect inherent differences in flower colour. Thus, particularly where the 'standard' environment is extreme or in some basic way different from any of the natural range of environments, this type of 'stretched' response may tend to obscure certain variation of adaptive importance. The use of single pots in the cold house as the standard conditions, necessitated by heavy predation of Aster in the botanic garden, may have produced such a stretched response. Plants in the greenhouse were generally taller and more 'lush' than their counterparts in the wild (with minor exceptions see Ch. 10). A stretched response of this sort is, in effect, an extreme example of plasticity tending to blur or obscure variation between individuals.

(A summary of these points is contained in the Abstract).

(b) Adaptation to maritime environments.

(i) General

It was suggested in Chapter 1 that there are theoretical reasons for supposing that plants occupying the coastal zone will be under the influence of selective forces which will tend to favour adaptive divergence, particularly in species with an apparently wide ecological amplitude. The wide variation in Aster tripolium lends support to this thesis. Indirect evidence is available from a number of studies on other coastal species to suggest that divergent patterns of variation may be commonly produced in maritime environments. Although the adaptiveness of such variation remains to be proved, it is frequently in characters of fundamental importance such as life cycle, breeding system and fruit production.

A number of salt marsh species belong to taxonomically confusing groups or show well differentiated patterns of infraspecific variation, Some have been the subject of studies aimed at circumscribing such patterns of variation, e.g. *Salicornia* species (Dalby 1962, Ball 1964, Ferguson 1964) and *Limonium* species (Boorman 1966). In others the use of varietal names, as in the case of *Suaeda maritima* vars. *prostrata*, *macrocarpa*, *procumbens*, *flexilis*, *linifolia* and *scabra* (Chapman 1960), is a substitute for lack of knowledge of adaptive patterns. In a detailed study of *Halimione portulacoides*, Sharrock (1967) has shown that, whereas the varieties *parvifolia* and *angustifolia* remain, on the basis of leaf measurements, morphologically distinct from one another in cultivation, *latifolia* is very plastic and, in different environments, embraces the whole range of variation so as to resemble *parvifolia* when grown on sand and *angustifolia* when grown on pebbles. Other species have been the subject of important studies on the dimensions of variation within and between populations, as in the heterostyly studies of Baker on *Armeria* and *Limonium* species (Baker 1953), and the classic work of Gregor on *Plantago maritima*. Indeed the impressive array of variation in coastal species must have contributed much to Turesson's original formulation of the ecotype concept, a number of examples being described in his early papers. (Turesson 1920, 1922, 1925).

The general thesis that variation may be at a premium among species with at least a partly inter-tidal range might be supported by further studies, especially within the notoriously 'weedy' families such as the Chenopodiaceae to which many salt marsh species belong. It may apply also to maritime animals with limited mobility as suggested by Battaglia (1958a) who describes a striking balanced polymorphism in the estuarine copepod Tisbe reticulata (Battaglia 1958b). Moyse (1969 unpublished) has recently discussed the presence of a morph ratio cline of variation in winkles related to exposure gradients on rocky shores, and the maritime gastropod Hydrobia ulvae shows extreme between-population variation (personal observation). The case of viviparity in salt marsh mites, cited below, may be a further example of differentiation in response to coastal conditions.

In many cases where variation in coastal species has been studied there has been either no attempt to relate variation to ecology or, where this has been attempted, the implications of this relationship have not been worked out. Thus one is faced, for example, with the array of variation in Suaeda maritima without a study of the ecology of the species in respect of this, and the observation that diploid and tetraploid species of Salicornia herbacea agg. have a differential distribution on salt marshes without a sufficient knowledge of the differential biology of the two types.* (Both Dalby, 1962 and personal communication, and

---

* but see later reference to Ball and Brown (1970).

Bakker et al (1966), have observed that the long-spiked, little branched tetraploids ($2n = 36$) are generally pioneers on soft mud whereas the short-spiked, strongly branched diploids ($2n = 18$) are found in higher, drier habitats). In some cases where more details are known differences between taxa are fundamental and require further investigations, as for example with the two most common salt marsh Spergularia species. S. marina is short-lived, inbreeding, small-flowered, and has a reduced number of stamens and wingless seeds, whereas S. media is generally perennial, outbreeding, has large flowers, a higher number of stamens and winged seeds (Ratter 1959). The two species commonly occur together (there are no intermediates due to cross sterility) and are said to have a differential ecological distribution in the areas of Holland where they have been studied by Sterk (1968), the characteristically weedy S. marina occupying disturbed transient habitats, S. media being a member of mature swards.

There are, however, one or two well documented studies on coastal plants which relate genotype to environment (e.g. Boorman 1966, Sharrock 1967). In the cases of Halimione portulacoides (Sharrock 1967) and Plantago maritima (Gregor 1938, 1939, 1956) adaptation to the coastal zone appears to have consisted of a mixture of genetic divergence and plastic response. The most pertinent example is provided by a study on Rumex crispus and its maritime form Rumex crispus var littoreus, (Cavers and Harper 1964, 1966, 1967a, 1967b), and a discussion of the results is of particular interest in the light of the variation pattern in Aster tripolium.

Table 12.2 contains a comparison of variation between high and low marsh populations of Aster with that between inland and maritime Rumex crispus. The details for the latter species have been extracted from the series of papers by Cavers and Harper especially 1967b. It can be seen from this table that there are a striking number of parallel trends in differentiation involving characters of fundamental importance such as life cycle, fruit size, root growth and seed dormancy. In discussion of the variation in R. crispus var littoreus Cavers and Harper (1967b) say "The following characteristics seem likely to hinder the establishment of plants of the maritime form inland: (a) the large, bulky nature of the propagule; (b) the relative lack of dormancy of the seeds; (c) the more aggressive character of the inland form whem growing in fertile soil in mixture with the maritime form; and (d) the inability to flower in the seedling year". This phrase can be applied, unaltered, to the putative reasons for the lack of success of the low marsh form of Aster tripolium in high marsh areas. Conversely the lack of success of high marsh forms in low marshes can be ascribed to a number of characteristics, none of which are sufficient in themselves to be solely responsible for the failure of these types.

Many of the characters shared by the high marsh Aster and the inland R. crispus are the sort commonly associated with weedy

Table 12.2 A comparison of the variation between high and low marsh populations of <u>Aster tripolium</u> with that between inland and maritime forms of <u>Rumex crispus</u>

CHARACTER	LOW MARSH ASTER COMPARED WITH HIGH MARSH	REF.	MARITIME R. CRISPUS COMPARED WITH INLAND FORM	REF.
Flowering and life cycle	Perennial, only first flowering in 2nd or 3rd year (high marsh popns. commonly flower in 1st yr)	Ch.4	Perennial, flowering in 2nd year. (Inland form commonly flowers and sets seed in first year).	*p.79 ⌿ p.680
Longevity	Long lived perennial (High marsh pauciennial).	Ch.4	Longer lived (maritime 5 years, inland 3 years (evidence limited))	Ø p.760
Fruit size	Larger (up to 3 x wt. of high marsh).	Ch.5	Larger (c. 1.5 x wt. of inland form).	* p.77
Dormancy of fruits	Precocious germination, lack of dormancy.	Ch.6	Lack of dormancy (inland form has dormant fruits).	X p.69
Response to sea water treatment	Not so severely affected by increased tidal treatment (grown in soil).	Ch.7	Not so severely affected by application of sea water to young plants in nutrient culture.	* p.77
Root growth	Larger roots produced by larger fruits at germination.	Ch.8	Faster rate of radicle growth at germination.	* p.80
Growth in ordinary soils etc.	Survival rate in ordinary soils lower than that of high marsh plants.	Ch.9	Depressed by inland form in mixtures grown on garden soil (and <u>vice versa</u> on shingle).	* p.80

* Cavers and Harper 1967b
⌿ Harper and Chancellor 1959

X Cavers and Harper 1967a
Ø Cavers and Harper 1964

species e.g. flowering in the seedling year, the delayed germination of the fruit. The adaptive significance of such characters have been discussed by a number of authors, referred to earlier, and some brief discussion of specific aspects is included below. It is of particular interest that in an impressively parallel situation Baker (1954) states as follows; "In Picris echoides (Compositae) a race from the sea-cliffs east of Brighton is perennial, self-incompatible, late flowering and decumbent, while a race in culture from the margin of an arable field near Clayton, Sussex, is annual or biennial, self-compatible, relatively early flowering, and possesses an upright habit. The characters of the latter were interpreted as adaptations to life as a weed of arable land".

(ii) Life cycle and reproductive capacity.

The annual habit is commonly interpreted as an adaptation enabling plants to occupy temporary habitats or to avoid severe seasonal fluctuations in climate. It is often found in pioneer, colonising, and (by definition) ephemeral, species, and in weeds of arable land. The overall north/south cline in year to first flowering in Aster, which gives some indication of the perenniality of the populations, is understandable in terms of an overall climatic and day-length variation with latitude, Such clines are possibly common in species with a sub-arctic to sub-tropical range. Bocher (1949, 1963) describes a north/south cline in year of first flowering in European populations of Prunella vulgaris; a cline which is superimposed on local variation in flowering year between plants from high and low altitudes.

In view of the variation in life cycle from high to low marshes in Aster it is tempting to draw a picture of adaptation in terms of analogy with weed invasion of 'disturbed' or 'open' habitats at the upper edges of salt marshes, and perennial growth, with the accent on vegetative spread, in 'closed' mid marsh communities. However such analogies are unsafe, partly because of the immeasurability and vagueness of terms such as 'open' and 'closed'. Extreme environments such as the mobile mud of low salt marshes, despite the apparently large areas of available space between pioneer plants, may be as 'closed' as the dense swards of mid marshes, in so far as the number of available microsites for plant growth may be severely limited by the stringency of the habitat factors. Generalisations with respect to the adaptive properties of life-cycle phenomena are equally unsafe. Whilst the annual habit may be a means of avoiding certain extremes of environment which occur on a cyclic or seasonal basis, extremes which the perennial must endure in a vegetative state, it is not necessarily the favoured means of adapting to such environments. In the lower zones of salt marshes the annual habit may allow pioneer species to survive by enabling them to grow and set seed between the equinoctial spring tides, but the perennial with highly developed plastic and genetic adaptation to cyclic change is equally suitable as a pioneer. In fact, perennials may have a distinct advantage in the early stages of colonisation as they suffer a lower reduction of frequency of the genes which may be enabling them to adapt to the extreme environment in the face of deleteriously high gene flow. In addition the members of each generation are added to the next and do not have to be established *de novo* (Antonovics 1968a). The two pioneer species, *par excellence*, of British salt marshes, annual *Salicornia* species and *Spartina anglica*, may bear witness to the fact that both avoidance and complex physiological adaptation are equally successful strategies.

It is of some interest, however, to consider the relationship between life cycle and reproductive output. This is done in Appendix VIII by a simple mathematical model. The model is idealised and has a number of important limitations, but illustrates the effect of variation in seed output, year of first flowering, and numbers of times of flowering, on the potential growth rate of a population in a colonising situation. It illustrates the following points of interest. First-year flowering annuals, under equal conditions of fruit production and selection pressure, are able to exploit a newly-available niche more rapidly than perennials which flower for the first-time in their second or third year of growth; this difference between first-and second-year flowering types is relatively more pronounced at higher reproductive rates; at these higher reproductive rates the relative advantage of flowering more than once is less than at low reproductive rates. Further, perennials which do not flower until the second or third year of growth suffer relatively less from the effects of selection than do first-year flowering types, as do perennials which flower more than once.

In a disturbed environment such as the Gibraltar Point Agropyron marsh where conditions vary from year to year and the population size fluctuates from year to year (App. IV) the survival of the population may depend on the ability to produce fruits within a single season and to avoid adverse conditions, such as the development of tall grasses, as dormant fruit (see below). Although as the figures in Ch. 5 suggest, fruit production is lower (probably because of a plastic response to intensive competition) than on mid and low marshes, the advantages of first year flowering will enable a viable fruit reserve to be maintained which is not necessarily very different in number from that of mid and low marsh populations. Alternatively on mid and low marshes where conditions vary less from year to year (but probably more within the lifetime of the individual) the slow intrinsic rate of natural increase may be compensated for by an increased resistance to selection (App. VIII). The increased number of flowering occasions in low marsh perennials also means that single individuals will produce many more fruits than individual high marsh plants and, in conditions of intense directional selection the likeness to their parents of the individuals which develop from these fruits may be of paramount importance. The complex physiological adaptation required to survive in inter-tidal conditions will be unnecessary to opportunist high marsh plants, whose main reserves of energy are devoted to the rapid production of a genetically variable seed reserve.

The variation in flowering time (i.e. earliness or lateness in a given year) between high and low marsh populations has been discussed above (aiii). Such variation is commonly found within plant species and has been the basis of the delimiting of a number of ecotypes (McNeilly and Antonovics 1968 p. 213). As Suggested above such variation may have arisen, (1) as part of the annual/perennial variation (parallel situations of early flowering perennial and late flowering annuals have been described in Onobrychis populations from the Caucasus mountains by Sinskaya (1958) and in a number of other species), (2) as an isolating mechanism or (3) as a specific adaptation to ecological conditions. Considering this last possibility from the aspect of adaptation to a maritime environment, it should be noted that tidal submergence, when it occurs during daylight, will seriously alter the natural photoperiod and may affect the flowering rhythmn. Hubbard (1969) has discussed this point in relation to the earlier flowering of the more seaward clones of Spartina anglica and suggests that flowering may be determined by the daylength regimes experienced during the preceding autumn. This of course does not explain the differences in flowering time of rayed and rayless Aster observed at Morston.

(iii) Germination.

The variation in dormancy-breaking requirements from high to low marshes is of particular interest in view of the association between innate dormancy, fruit polymorphism, and annual weeds (Harper 1959). The ecological consequence of such a dormancy mechanism is that "it maintains a reserve of seeds free from exposure to the hazards met by a growing plant in a particular season" (Harper 1964 p. 466). The polymorphism in germination requirements of the fruits from high marsh plants can be interpreted as an aggressive feature adapting the plant to a life-habit similar to that of an annual weed. (The work on Rumex crispus, quoted above, is particularly apposite here). The precocious germination of the low marsh fruits is less easy to interpret. Its advantage under conditions of tidal action can be seen (Ch. 9) but it is difficult to see how the fruit is able to overwinter, unless by the enforced dormancy of extreme saline conditions. Occasionally autumn germinants may survive to the following spring but, apart from at Winsford, no quantities of seedlings have been found during the autumn and there is a large flush of newly germinated seedlings on many low marshes each spring. Tsopa (1939) describes var pannonicus as commonly germinating in the autumn in saline desert areas. Cochlearia species are able to avoid the extreme salinities of midsummer by autumn germination and growth and flowering in early spring (Binet 1965).

The precociousness of low marsh fruits is paralleled by at least two interesting examples. The first is the observation on a number of occasions of viviparous fruits in the heads of Spartina anglica in the Gibraltar Point Spartina marsh. The second is the trend within the Acarina of salt marshes which contain an exceptionally high proportion of viviparous species. Luxton (1964) has suggested that viviparity in mites is an adaptation to intertidal conditions, particularly since one species (Sefus necorniger) lays eggs in laboratory culture but exhibits facultative viviparity in salt marshes. This trend to precocious reproductive systems, although by no means universal, may be worthy of further investigation.

The cline in ability to germinate in sea water dilutions is in the expected direction and, as wild collected fruits were used could be genetically or developmentally determined. This requires further study.

(iv) Fruit size, seedling growth and elimination.

The increase in fruit size and associated seedling vigour on low marshes has been interpreted above as a possible adaptation to survival under conditions of mechanical elimination on mobile substrates. That the cline should be in the direction it was found to be however, it is not obvious. It is in fact the reverse of the variation pattern in Plantago maritima, where larger seeds are found in plants from the fertile coastal meadows above the tide mark (Gregor 1946): Gregor suggests that the higher nutritional demands of large plants may act to their disadvantage at the lower edaphic (and presumably tidal) levels (Gregor 1946). The trend in Aster is also at variance with Salisbury's general dictum that large seeds are generally 'associated with' the more advanced phases of succession (Salisbury 1942). The generalisation, often made, that small-fruited species tend to be characteristic of open habitats and large-fruited species tend to be characteristic of closed habitats involves the danger, referred to above, of finding an adequate definition of the terms 'open' and 'closed', but in so far as they are applicable, Aster also appears to be exceptional in this respect.

The importance of high embryonic capital, and the concomitant seedling vigour, for establishment in the lower zones of salt marshes is suggested by the pattern of seedling elimination described in Chapter 9. It is possible to envisage that large fruits may have an advantage in mobile substrates, particularly if the statement made by Shirley (1943) that large seed reserves are associated with the initial development of the root rather than the shoot is correct. The contrast in rooting pattern (the extent of branching) between fruits from low and high marshes (Ch. 8) lends support to the hypothesis that anchorage may be an important function of the seedling root system. Ball and Brown (1970) have recently discussed the possible advantage which the tetraploid Salicornia dolichostachya may have over the diploid S. europaea in open areas of the Dee estuary, and have suggested that the more rapid radicle growth of S. dolichostachya seedlings may be important in the early stages of establishment. This provides very recent support of Wiebe's earlier (1935) work and may be related to Dalby's observation of fruit size variation in diploid and tetraploid species of Salicornia (the tetraploids having larger fruits - Dalby 1962). It is equally possible to envisage that, in Aster, large fruits may have an advantage in pure Spartina swards where rapid short elongation (often associated with large fruits - Black 1960) in conditions of reduced daylight could be important.

In addition to the mechanical difficulties of establishment small fruits may be restricted to areas of higher mineral nutrients than large fruits. This point, which throws doubt on Gregor's explanation of fruit size variation in Plantago maritima (above) is made by Myerscough and Whitehead (1967) in relation to differences in the nutrient requirements of four different species immediately following germination. They suggest that low seed weights and the high growth commitments of their seedlings restrict Tussilago farfara, Chamaenerion angustifolium, Epilobium montanum and Epilobium adenocaulon to sites in which adequate nutrients (and light) are present. In Aster large fruits may have a further advantage in low marshes where the nutrient supply is often a limiting factor (Pigott 1969).

It is less easy to postulate the possible selective value of small fruits in high marsh environments. Two interrelated possibilities may be considered. The first is that small fruit size is a byproduct of selection for large fruit number, important in fluctuating populations of annuals. A similar balance between fruit size and number to the one observed in Aster is reported within the British Papaver species by Harper (1966) who suggests that 'Papaver lecoqii which has the largest seed output may have had to compensate for this in its reduced individual seed weight' (Harper 1966 p. 29). It was suggested earlier that there may be, in high marsh environments, a positive advantage in increasing the number, rather than the size, of the disseminating units. Secondly small fruit size may be necessary for effective dispersal in areas where tidal dispersal does not operate. It would be interesting to compare the relationship between fruit size and efficiency of dispersal in populations of Aster.

The contrast in vigour between seedlings which develop from small fruits and those which develop from large fruits, seen in experimental situations, may not be so marked, or even measurable, in the wild. The relative growth rates of the two extreme types will be affected by their respective environments. The response of seedlings to tidal treatment (Ch. 7) suggests that, despite their high initial seed weight, the low marsh plants have drastically lowered growth rates during periods of tidal coverage, and their growth rate in these conditions is much lower than that of the small-fruited seedlings in tide-free environments. This illustrates how the stringency of maritime environments demands that extreme caution is used in interpreting the results of experiments based on ordinary-soil culture.

The discovery, reported in the preceeding chapters, of a 'weedy' element within the total variability of British Aster tripolium populations is particularly encouraging in the light of studies during the past two decades on the reclaimed polderlands of Holland. Aster tripolium has consistently turned up among a number of somewhat unexpected species which have become important colonisers of the newly-reclaimed land, exhibiting remarkable properties of explosive population growth. Although, unlike the similarly dispersed Tussilago farfara and Cirsium arvense, it rarely persists as a troublesome weed once the polders are drained for agriculture (Bakker 1960a), it shares a phase of dominance, generally during the second year of exposure, with Senecio palustris (S. congestus), often forming dense stands covering tens of hectares. (Bakker 1960b, Bakker et al 1960). It was recorded from 23% of the releves counted by Van de Toorn in southern Flevoland (the southern most Ijsselmeer Polder in the former Zuyder Zee) only three months after the completion of pumping operations in May 1968, (Van de Toorn, personal communication), and during September 1969 dominated large areas of open mud between (sown) Phragmites reedswamp (personal observation).

Aster plants up to 10ft in height are commonly found on the fertile soils of the Dutch polderlands (Fig. 12.2) where it is commonly associated with characteristically nitrophilous species (Urtica and Atriplex species). That British populations may retain this nitrophilous weedy element is suggested by the fact

Fig.12.2 Aster tripolium in newly reclaimed S.E. Flevoland Polder (Ijsselmeer) in September 1969 following reclamation in May 1968.

that Aster is occasionally found in areas where algal decay has occurred, in open areas created by the death of other plants in the upper reaches of salt marshes, and even as a plant of the drift line of tidal debris, a niche which it shares with Atriplex species.

(c) Conclusion.

Returning, in conclusion, to the questions posed in Chapter 1, the results of this study suggest that (1) Aster tripolium is limited from spreading into ordinary non-saline habitats by factors related to its inability to compete successfully on a long-term basis with the plants which are found in these habitats, and that it is prevented from further seaward spread by the severity of physiological factors and extreme instability of the lower most intertidal zones, and that (2) the variation within the species, especially at the upper and lower limits of its distribution along the coastal belt, has been produced by adaptive divergence in direct response to selection pressures imposed by the partial onset of these (eventually) limiting factors. The limiting role of competitive factors may be indicated in the occurence of A. tripolium in inland areas such as Winsford, where competition is reduced by extreme soil environments. (Goldsmith's study of sea cliff vegetation (Goldsmith 1967) similarly suggests that there is a sense in which adaptation to maritime conditions can be regarded as adaptation away from conditions of severe competition).

This divergence has resulted in a complex pattern of differentiation affecting a number of characters of fundamental biological significance such as life cycle, fruit size, and germination requirements. A number of these characters have been used in the past to delimit infraspecific taxa, generally prefixed by the term 'variety', and it is suggested, in view of the variation pattern disclosed, that these taxa are of doubtful status and, with the possible exception of extreme climatic types such as salt desert <u>var pannonicus</u> and the northern <u>var arcticus</u>, their use is inadvisable.

Divergence has arisen within the species by both the genetic and plastic response of characters to the disruptive effect of the variation in habitat factors across the coastal zone. Both clinal and discontinuous patterns of variation have resulted, although a number of factors may contribute to the commoner occurence of continuous patterns. In addition to the examples of morphological differentiation which have been described, it is suggested that extensive complex physiological adaptation must occur of which only one aspect (the preferential absorption by adapted types of potassium ions in the face of high concentrations of sodium ions) has been investigated.

The results of this study further suggest that selection in maritime environments is complex and, as is often supposed, may operate effectively at all stages of the plants' life cycle. Thus adaptation to ensure successful germination (e.g. in saline media) must be accompanied by adaptations enabling successful seedling establishment, growth, flowering, seed set and dispersal. Failure to survive in a given zone can occur through non adaptedness of plants at any one of these stages.

Divergence has occured within the species alongside the apparent retention of chromosomal and genetic compatibility over a wide (geographical) area. This is in contrast to the development of cytologically isolated units observed by a number of authors in other species (e.g. *Plantago media*, Rhan 1954). Gene flow between neighbouring populations may be prevented by variation in flowering times and this may have been an important factor enabling the recent spread of the rayless form, especially into the *Spartina anglica* zone on British salt marshes. It is suggested that the ray/rayless polymorphism in *Aster tripolium* may be a striking illustration of evolutionary divergence, and that certain critical aspects of this polymorphism are among the most important questions generated by this project which could be the subject of further investigation.

APPENDICES

APPENDIX I.

LIST OF MATERIAL IN CULTURE

All plants (or fruit) collected or received was given a code number according to the year and accession order. Populations are listed below with a two figure code (e.g. 65/44) - individuals were further coded (e.g. 65/44/9). Plants which were involved in the breeding programme were given an additional code and are not listed here individually (see Appendix VII). S indicates the original source was fruit, P that plants were collected.

65/1 to 65/40. Plants from Humberstone, Tetney and North Cotes - breeding programme.

65/41A	(S)	Agropyron marsh, Gibraltar Point, Lincs.
65/42A	(S)	Spartina marsh, Gibraltar Point, Lincs.
65/43A	(S)	Limonium marsh, Gibraltar Point, Lincs.
65/44	(P)	Morston Norfolk.
65/45	(P)	Beach Point, Scolt Head Island, Norfolk.
65/45A	(S)	" " " "
65/46A	(S)	Cley, Norfolk.
65/47	(P)	Naze, R. Ribble, Lancs.
65/47A	(S)	" " "
65/48A	(S)	R. Wyre, Lancs.
65/49	(P)	Knott End, Lancs.
65/49A	(S)	" "
65/50A	(S)	R. Lune near Glasson, Lancs.
65/51	(P)	Hest Bank, Morecambe Bay, Lancs.
65/51A	(S)	" " "
65/52	(P)	Oyce, Firth, Orkney Islands.
65/53	(S)	Bad Durrenberg. E. Germany.
65/54	(S)	Zierow bei Wismar. E. Germany.
65/55	(S)	Cluj Rumania
65/56	(S)	Swansea, S. Wales.
65/57	(S)	Helsinki, Finland.
65/58	(S)	Oslo, Norway.
65/59	(S)	Uppsala, Sweden.
65/59A	(S)	Askim (Vastergotland) Sweden.
65/59B	(S)	Oland Island, Sweden..
65/60	(S)	Mecklenburg. E. Germany.
65/61	(S)	Eiselben, E. Germany.
65/62	(S)	Halle Salle, E. Germany.
66/1A	(S)	Fal Estuary, Cornwall.
66/2 to 66/13		Plants in breeding programme.
66/14A	(S)	Sites at Winsford, Cheshire.
66/15	(P)	Tetney Haven, Lincs.
66/16	(S)	Cluj, Rumania.
66/16A	(S)	Lasi Oras, Rumania.

66/17	(S)	Porto, Portugal.
66/17A	(S)	Ciombra Portugal.
66/18	(P)	Agropyron marsh, Gibraltar Point, Lincs.
66/19	(P)	Limonium marsh, Gibraltar Point, Lincs.
66/20	(P)	Aster marsh, Gibraltar Point, Lincs.
66/21	(P)	Spartina marsh, Gibraltar Point, Lincs.
66/22	(P)	Anglesey. N. Wales (coll. K. M. Goodway).
66/22A	(P)	" " "
66/23	(P)	Winsford A. Cheshire.
66/24	(P)	Winsford B. Cheshire.
66/25	(P)	Winsford C. Cheshire.
66/26	(P)	Winsford D. Cheshire.
66/27	(P)	Beach Point, Scolt Head Island, Norfolk.
66/28	(P)	Spiral marsh, Scolt Head Island, Norfolk.
66/29	(P)	Upper Cockle Bight, Scolt Head Island, Norfolk.
66/30	(P)	Plover marsh, Scolt Head Island, Norfolk.
66/31	(P)	Morston, Norfolk.
66/32	(P)	Parkgate, Cheshire.
66/32A	(S)	" "
66/33	(P)	" "
66/33A	(S)	" "
66/39 to 66/41		Plants in breeding programme.
67/1	(S)	Vienna, Austria.
67/2	(S)	Porto, Portugal
67/3 to 67/9		Plants in breeding programme.
67/10	(P)	Upper Cockle Bight, Scolt Head Island, Norfolk.
67/11	(P)	Beach Point, Scolt Head Island, Norfolk.
67/12	(P)	Spiral marsh, Scolt Head Island, Norfolk.
67/13	(P)	Agropyron marsh, Gibraltar Point, Lincs.
67/14	(P)	Limonium marsh, Gibraltar Point, Lincs.
67/15	(P)	Aster marsh, Gibraltar Point, Lincs.
67/16	(P)	Spartina marsh, Gibraltar Point, Lincs.
67/19 to 67/32		Plants in breeding programme.

APPENDIX II

BRIEF NOTES ON THE MARITIME SITES VISITED PERSONALLY AND SAMPLED AS PART OF EXTENSIVE SAMPLING PROGRAMME

HEST BANK, MORECAMBE BAY. LANCS. (Grid ref. SD 467670). Typical N,W, coast sandy marsh, dominated by Puccinellia maritima and ½ mile to seaward edge from sea wall. Seaward edge marked by cliff of P. maritima. Built up on extensive sand flats (about 18" mud). Aster commonly scattered throughout. Other species: Salicornia sp.(C) Suaeda maritima (O) Spergularia media (C) Armena maritima (a), Triglochin maritima (l.d.) in belt near sea wall. Spartina anglica in isolated clumps at seaward edge of marsh. Plants and fruit collected.

R. LUNE nr. GLASSON, LANCS. (Grid ref. SD 455561). Fruit of Aster collected from a rayed community near to the river bank on the extensive salt marshes fringing the coast road from Knott End to Lancaster. Typical W. coast marsh species similar to Hest Bank. Spartina present only on river bank.

KNOTT END. LANCS. (Grid ref. SD 351487). A small salt marsh built up on sand close to the promenade wall. Many pools, Puccinellia maritima dominating flat turf between these. Spartina townsendii in pools and at edges. Also on turf with Aster,- Glaux maritima (O), Armenia maritima (a), Plantago maritima (C), Halimione portulacoides (O), Plants and fruit collected.

R. WYRE. LANCS. (Grid ref. SD 368413 and SD 363414). Two sites close to the toll bridge where the A580 crosses the river. Spartina anglica dominating the river bank. Aster on small marsh above the Spartina which contained Atriplex hastata (C) Limonium vulgare (C), Plantago maritima (a) Triglochin maritima (a). Plants and fruit collected.

NAZE, LANCS. (Grid ref. SD 434272). A small strip of very wet pasture on the north bank of the river Ribble about 5 miles from Lytham St. Annes. Strip about 50 yards wide, occasionally grazed (cattle). Eroded at edge. Aster common in Puccinellia sward with Triglochin maritima (O), Festuca rubra (C), Agrostis stolonifera (C) Plantago maritima (C), Glaux maritima (I), Spergularia media (C) and Atriplex litoralis (C). Meadow fringed by tall Crataegus, Fagus and Sambucus hedge. Plants and fruit collected.

BURTON POINT, CHESHIRE. (Grid ref. SJ 289755). On mature marsh close to coastal road. Heavily grazed (sheep). Festuca rubra dominant with Puccinellia maritima and several common non-coastal grasses. Halimione portulacoides fringing deeply bisecting creeks. Other species: Plantago maritima (a) on path, Triglochin maritima (C), Artemisia maritima, Spergularia media, Cochlearia officinalis (C). Fruit only collected.

ANGLESEY A. (Grid ref. SH 479885). (Coll K. M. Goodway 20.7.66 area visited A. J. G. Aug. 1967). From Llys Dulas Bay, a long flat wide estuary with shingle bar across mouth. Very sandy substrate. Old narrow marsh fringing bay (eroding at edges) Puccinellia maritima common fringing of Juncus maritima and J. gerardii. Other species: Plantago maritima (C), Cochlearia officinalis (C), Agrostis stolonifera (C), Agropyron pungens (C), Agrostis gigantea (C), Sonchus arvensis (O), Aster largely in middle strip many young plants. Fruit and plants collected.

ANGLESEY B. From a site about 400 yards further down the estuary. The marsh here is wider 1 - 2' of mud above sand. Puccinellia sward with Armeria maritima, Limonium vulgare, (L. humile?). Open pans water fulled between areas of Juncus maritima. Salicornia scattered throughout. Area probably grazed. Aster plants and fruits collected.

CALSTOCK, CORNWALL. (Grid ref. SX 428688). On the banks of the R. Tamar some distance inland. Tall Aster plants growing on river edge fringing bare mud and in cracks in old jetty. With common inland grasses. Fruits only collected.

WELLS, NORFOLK. (Grid ref. TG 916445). Plants on edge of shingle bar (dominated by Festuca rubra, Agropyron pungens) close to the Harbour. Plantago maritima (C), Armeria maritima (C), Limonium sp. (O), Silene sp. (C). Fruits only collected.

R. OUSE, KINGS LYNN NORFOLK. (Grid ref. TF 612184). On bank of the R. Ouse close to bridge (A47) with other halophytes including Triglochin maritima, Spergularia media, Plantago maritima, Puccinellia maritima, Agropyron repens, and Atriplex littoralis.

GIBRALTAR POINT, LINCOLNSHIRE. (Grid ref. TF 559583). From close to path across the mature saltings (between the Spartina marsh and the Limonium marsh). In area dominated by Limonium vulgare. Halimione portulacoides, Puccinellia maritima, and Agropyron repens locally common.

SALTFLEETBY - THEDDLETHORPE, LINCOLNSHIRE. (Grid ref. TA 469935). On open mud below sand dunes south of the coastquard lookout. Marsh dominated at landward edge by Puccinellia maritima sward containing Agropyron juncieforme, (common on western fringe)

Halimione portulacoides (I.C), Suaeda maritima (A), Atriplex littoralis (C), Limonium vulgare (C), Artemeria maritima (O) Spergularia media (O). Aster plants collected from here and from a dense, broad community of Salicornia on open sand and mud to seaward.

GRAINTHORPE HAVEN. LINCS. (Grid ref. TA 386013). On mature deeply bisected marsh with Puccinellia maritima dominant in the sward and the creeks fringed by either Agropyron repens or Halimione portulacoides. Artemesia maritima locally common in large patches. Fruits of Aster collected from sward where Limonium vulgare (O), Triglochin maritima (O), Armeria maritima (O), Spergularia salina (r), and Plantago maritima also occurred.

NORTH COTES POINT, LINCS. (Grid ref. TA 370040). A small marsh on sand near sea wall (not unlike the Saltfleetby marsh in type). A number of rayless plants collected and used for controlled crosses. Marsh dominated by Puccinellia sward with Agropyron repens Plantago maritima and Spergularia media also common. Spartina in lower areas and pans on higher marsh.

HUMBERSTONE, LINCS. (Grid ref. TA 340050). This marsh is continuous with the series of marshes at Tetney Haven but differs from it in having developed in the lea of a dune ridge. Very mixed salt marsh community with Agropyron repens and Puccinellia maritima locally dominant. Spartina present near by. Rayed plants collected. Other species Plantago maritima (C), P. coronopus (O), Glaux maritima (C), Armeria maritima (C), Limonium vulgare (C).

Other areas from which samples were received are listed in Appendix I. The vegetation of the intensively sampled areas are listed in Appendix III. Ecological Notes on some other sample areas are given in the text and in Appendix IV.

APPENDIX III

(a) SPECIES RECORDED AT THE MARITIME SITES SAMPLED AS PART OF THE INTENSIVE SAMPLING PROGRAMME

The following lists of species were transcribed directly from field notebooks and are not in any particular order within each site. Aster tripolium was recorded from all sites and is not listed. Species noted from the immediate sampling area are listed under S; additional species from nearby areas on the same marsh are listed under N.

Gibraltar Point

Spartina marsh

S:
Spartina anglica
Salicornia herb. agg.
Suaeda maritima
Puccinellia maritima
Enteromorpha prolifera

N:
Enteromorpha intestinalis
Halimione portulacoides
Cochlearia (?) officinalis
Atriplex littoralis
Limonium vulgare

Aster marsh

S:
Puccinellia maritima
Suaeda maritima
Salicornia herb. agg.
Halimione portulacoides
Limonium vulgare
Cochlearia officinalis
Armeria maritima
Spergularia media
Glaux maritima
Plantago maritima
Triglochin maritima

N:
Spartina anglica
Plantago coronopus
Agropyron pungens
Agropyron junceiforme
Ammophila arenaria
Salsola kali
Cakile maritima
Artimesia maritima
Sedum acre
Senecio jacobaea
Ononis repens
Honkenya peploides
Atriplex hastata
Calystegia soldanella
Centaurium minus
Chamaenerion angustifolium
Carex arenaria

Limonium marsh

S: Limonium vulgare
Limonium humile
Puccinellia maritima
Artimesia maritima
Festuca rubra
Halimione portulacoides
Atriplex hastata
Spergularia marina
N: Plantago maritima
Armeria maritima
Triglochin maritima

Agropyron marsh

S: Agropyron pungens
Agropyron juncieforme
A. junceiforme x pungens
Festuca rubra
Agrostis stolonifera
Agrostis gigantea
Plantago coronopus
Scirpus maritimus
Poa pratensis
Agropyron repens
Juncus gerardii
Juncus maritimus
Carex distans
Carex extensa
Holcus lanatus
Dactylis glomerata
N: Cirsium arvense
Cirsium palustre
Festuca arundinaceae
Anacamptis pyrimidalis
Carex nigra
Dipsacus fullonum
Cerastium holosteoides
Atriplex hastata
Polygonum aviculare
Oenanthe lachenalii
Glyceria fluitans
Leontodon taraxacoides
Epilobium hirsutum
Epilobium montanum
Torilis japonica
Hippophae rhamnoides
Sambucus nigra
Rosa canina
Crataegus monogyna
Carduus nutans
Galium aparine
Sonchus asper
Ranunculus repens
Potentilla anserina
Rubus fruticosa agg.
Rumex acetosa
Rumex crispus
Carex otrubae
Plantago lanceolata
Plantago media
Deschampsia caespitosa
Poa annua
Myosotis arvensis
Urtica dioica
Claux maritima
Foeniculum vulgare
Althaea officinalis

Scolt Head Island

Cockle Bight

S: Spartina anglica
Suaeda maritima
Salicornia herb. agg.
Enteromorpha prolifera
Ulva lactuca
N: Enteromorpha nana
Monostroma grevillei
Zostera hornemanniana
Cladophora sp.

Beach Point

S:
Salicornia herb. agg.
Puccinellia maritima
Halimione portulacoides
Suaeda maritima
Spartina anglica
Salicornia perennis
Pelvetia caniculata
Bostrychia scorpiodes

N:
Triglochin maritima
Enteromorpha nana
Uloturix speciosa
Lola tortuosa

Plover marsh

S:
Suaeda maritima
Puccinellia maritima
Halimione portulacoides
Cochlearia officinalis
Salicornia herb. agg.
Limonium vulgare
Spergularia media
Armeria maritima
Plantago maritima
Triglochin maritima
Limonium humile
Artemisia maritima
Juncus maritimus
Juncus gerardii

N:
Parapholis incurva
Atriplex littoralis
Atriplex hastata
Plantago coronopus
Limonium bellidifolium
Suaeda fruticosa
Agropyron pungens
Glaux maritima
Phormidium autumnale
Pelvetia caniculata
Vaucheria thurettii

Spiral marsh

S:
Limonium vulgare
Puccinellia maritima
Triglochin maritima
Festuca rubra
Spergularia marina
Plantago maritima
Plantago coronopus
Suaeda maritima
Salicornia herb. agg.
Limonium bellidifolium
Limonium binervolsum
Suaeda fruticosa

N:
Armeria maritima
Frankenia laevis
Glaux maritima
Silene maritima
Halimione portulacoides
Sedum acre
Agrostis stolonifera
Ammophila arenaria
Carex arenaria
Artemisia maritima
Senecio jacobaea

Tetney Haven

The Halosere

S:
Spartina anglica
Salicornia herb. agg.
Puccinellia maritima
Limonium vulgare
Suaeda maritima
Halimione portulacoides
Cochlearia officinalis
Spergularia media

Enteromorpha prolifera
Ulva lactuca
Plantago maritima
Triglochin maritima
N: Armeria maritima
Agropyron pungens
Spergularia marina
Festuca rubra

Old marsh

S: Limonium vulgare
Agropyron pungens
Plantago maritima
Artemisia maritima
Festuca rubra
Puccinellia maritima
Triglochin maritima
Spergularia marina
N: Plantago coronopus
Juncus gerardii
Halimione portulacoides
Suaeda maritima

Morston

S: Puccinellia maritima
Limonium vulgare
Halimione portulacoides
Cochlearia officinalis
Armeria maritima
Agropyron pungens
Plantago coronopus
Plantago maritima
Triglochin maritima
Artemisia maritima
Suaeda maritima
Salicornia herb. agg.
Atriplex hastata
Limonium humile
Festuca rubra
Suaeda fruticosa
N: Lolium perenne
Juncus gerardii

Cley

S: Phragmites communis
Juncus maritimus
Agropyron pungens
Scirpus maritimus
Agrostis stolonifera
Holcus lanatus
Carex extensa
Juncus gerardii
Dactylis glomerata
Typha angustifolia
Agropyron repens
N: Cirsium palustre
Cirsium arvense
Juncus conglomeratus
Carex otrubae
Malva sylvestris
Potentilla anserina
Butomus umbellatus
Heracleum sphondylium
Iris pseudacorus
Vicia hirsuta
Ranunculus repens
Cynosorus cristatus

Parkgate

P1

S: Phragmites communis
Scirpus maritimus
Festuca rubra
Juncus gerardii
Agrostis stolonifera
Cochlearia officinalis
Ranunculus sceleratus
Puccinellia maritima
N: Glaux maritima
Cochlearia danica

Atriplex hastata
Plantago maritima
Plantago coronopus
Triglochin maritima
Spergularia media
Ranunculus baudotii
Rumex crispus
Halimione portulacoides
Stellaria media

P2

S: Puccinellia maritima
Halimione portulacoides
Cochlearia officinalis
N: Atriplex sp.

P3

S: Puccinellia maritima
Suaeda maritima
Salicornia herb. agg.
Spartina anglica
Halimione portulacoides
Spergularia media
N: Cochlearia officinalis

P4

S: Suaeda maritima
Salicornia herb. agg.
Spartina anglica
Enteromorpha? prolifera

A P P E N D I X

I I I (b)

Site	1 G. Spa	2 G. Ast.	3 G. Lim.	4 G. Agr.	5 S. Cob.	6 S. Bea.	7 S. Srl.	8 S. Plover	9 Tetney Haven	10 " Old marsh	11 Morston	12 Cley	13 Parkgate 1	14 " 2	15 " 3	16 " 4	17 Anglesey A	18 Anglesey B	19 S. Bch. '65	20 R. Lune	21 Hest Bank	22 Knott End	23 Naze	24 R. Wyre
Aster tripolium	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Spartina anglica	+				+				+						+	+			+			+		
Salicornia herb.agg.	+	+			+	+	+	+	+		+				+	+		+	+		+			
Suaeda maritima	+	+			+	+	+	+	+		+				+	+			+					
Puccinellia maritima	+	+	+			+	+	+	+	+	+		+	+	+		+	+		+	+	+	+	
Halimione portulacoides		+	+			+		+	+		+			+	+						+			
Limonium vulgare		+	+				+	+	+	+	+							+						+
Cochlearia officinalis		+						+	+		+		+	+			+			+	+	+		
Enteromorpha prolifera	+				+				+							+								
Armeria maritima		+						+			+							+		+	+	+		
Spergularia media		+						+	+				+		+					+	+			
Agropyron pungens				+						+	+	+					+							
Glaux maritima		+																				+	+	
Plantago maritima		+					+	+	+	+	+		+				+			+	+	+		+
Plantago coronopus				+			+				+		+				+				+			
Triglochin maritima		+					+	+	+	+	+		+							+	+		+	+
Atriplex hastata			+								+		+							+			+	+
Limonium humile			+					+			+													
Artemisia maritima			+					+		+	+													
Festuca rubra			+	+			+			+	+		+										+	
Spergularia marina			+				+			+														
Agropyron juncieforme				+																				
Agrostis gigantea				+													+							
Agrostis stolonifera				+								+	+				+						+	
Scirpus maritimus				+								+	+											
Poa pratensis				+																				
Holcus lanatus				+								+												
Carex extensa				+								+					+							
Carex distans				+																				
Dactylis glomerata				+								+												
Juncus maritimus				+				+				+					+							
Juncus gerardii				+				+				+	+				+							
Salicornia perennis						+																		
Pelvetia caniculata						+																		
Bostrychia scorpiodes						+																		
Limonium bellidifolium							+																	
Suaeda fruticosa							+				+													
Limonium binervosium							+																	
Ulva lactuca					+				+															
Phragmites communis												+	+											
Typha angustifolia												+												
Ranunculus sceleratus													+											
Agropyron repens				+								+					+							

APPENDIX IV.

DETAILED DESCRIPTION OF THE AREAS STUDIED AS PART OF AN INTENSIVE SAMPLING PROGRAMME

An account is given of those areas, the ecology of which was studied in detail. In addition to being the areas in which intensive sampling was carried out, these areas were also used as sites for particular experiments (e.g. seedling elimination expts., transplant expt.) and the material collected from these areas was used in laboratory experiments (e.g. germination, seedling culture, ray floret breeding programme). Therefore they are described below in some detail. (An attempt to shorten the descriptive accounts has been made by the liberal use of interleaved figures).

The general location of the four major east coast sites is given in Fig. IV.I.

(a) Gibraltar Point, Lincolnshire.

Gibraltar Point Nature Reserve is an extensive area of sand dune, shingle beach, and salt marsh lying between the resort town of Skegness to the north and the outflow of the River Steeping at the head of the Wash to the south. Within the total area of about 1,200 acres at least three major types of salt marsh can be distinguished. These are the new marsh being formed below the storm beach to the south of the reserve, the mature

Fig.IV.1 Location of east coast sites.

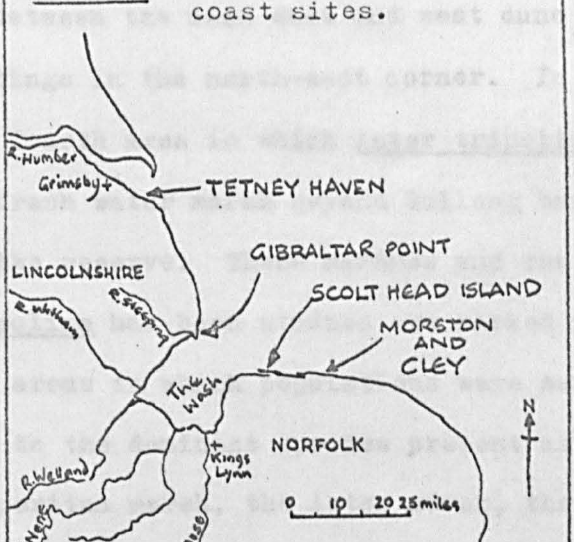
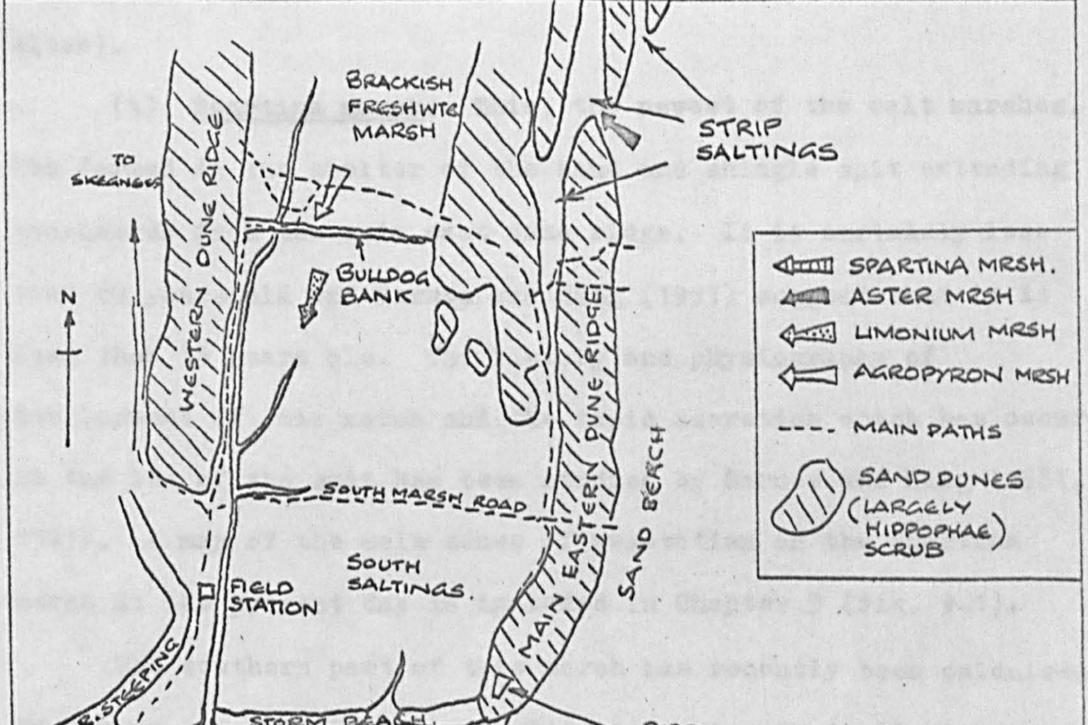


Fig.IV.2 Gibraltar Point, showing sampling areas.



saltings between the main east and west dune ridges, and the strip saltings in the north-east corner. In addition to these marshes a fourth area in which Aster tripolium is found is the brackish/fresh water marsh beyond Bulldog bank towards the north limit of the reserve. These marshes and the sites in which Aster tripolium has been studied are marked in Fig. IV.2.

The areas in which populations were sampled have been named according to the dominant species present at each site. These are the Spartina marsh, the Aster marsh, the Limonium marsh and the Agropyron marsh. (The use of the most common species to label the areas is not meant to carry any phytosociological implication- the names are used throughout simply to refer to sites).

(i) Spartina marsh. This, the newest of the salt marshes, has formed in the shelter of the sand and shingle spit extending southwards from the main east dune ridge. It is certainly less than 60 years old and Barnes and King (1957) suggest that it is less than 35 years old. The history and physiography of development of this marsh and the rapid accretion which has occured in the lee of the spit has been studied by Barnes and King (1951, 1961). A map of the main zones of vegetation on the Spartina marsh at the present day is included in Chapter 9 (Fig. 9.1).

The southern part of this marsh has recently been colonised by a pure sward of Spartina anglica (see Fig. IV.3(a)). The lower edge of the sward is fringed by scattered clumps and single

Fig.IV.3(a) Spartina marsh Gibraltar Point looking north east through *Spartina* sward to east dune ridge.

b) Aster among dense *Spartina* on Spartina marsh. Note dense clump of *Aster* seedlings (bottom right).

plants of the same species growing in very hummocky soft silt with many pools and shallow incipient creeks.

Towards the north-east corner of the marsh the Spartina gives way to an area of less fluid, more sandy mud which supports a flora dominated by annual Salicornia species. Most of the sand in this area is derived from the spit from which it has been blown or washed by exceptionally high tides. The storm surge of 1953 carried a great deal of sand through the spit and on to the eastern edge of the marsh (Barnes and King 1955). Borings in the area of the marsh reveal that it is composed of alternate layers of sand and mud. The sand layers may accumulate on the marsh during periods of neap tides as the mud dries and hardens whilst during high spring tides the main sediment deposited is mud. (Barnes and King 1951).

The north-west area of the marsh between the main creek and the storm beach supports a more general salt marsh flora. Halimione portulacoides is locally dominant, forming pure swards on the edges of creeks and on the well-drained firm silt immediately below the storm beach. Puccinellia maritima dominates the remainder of this area with Aster tripolium and Suaeda maritima locally common. Spartina also appears to be colonising this marsh.

At the lower (seaward) edge of the Spartina marsh the tide rises and falls as a continuous sheet of water, having overflowed deep unvegetated creeks running into the main creek. These creeks are rescoured by each tide as it drains off the marsh. Both high spring and neap tides overspill the main creek onto this very fluid 'slobland' (King 1959) and, according to their height, advance towards the highest area, the north-west corner, (see Fig. 9.1).

Barnes and King report that they could not find Aster tripolium anywhere on the new marsh in 1951. At the present day it is particularly common on the general salt marsh in the north-west corner and extends down into the dense Spartina sward (see Fig. IV.3(b)), a few plants being found seawards of this on the open mud among scattered Spartina as well as eastwards into the area dominated by Salicornia. The scattered distribution of Aster plants on this marsh suggests that they are commonly spread by seed. Plants and fruit were sampled from the Spartina area and beyond.

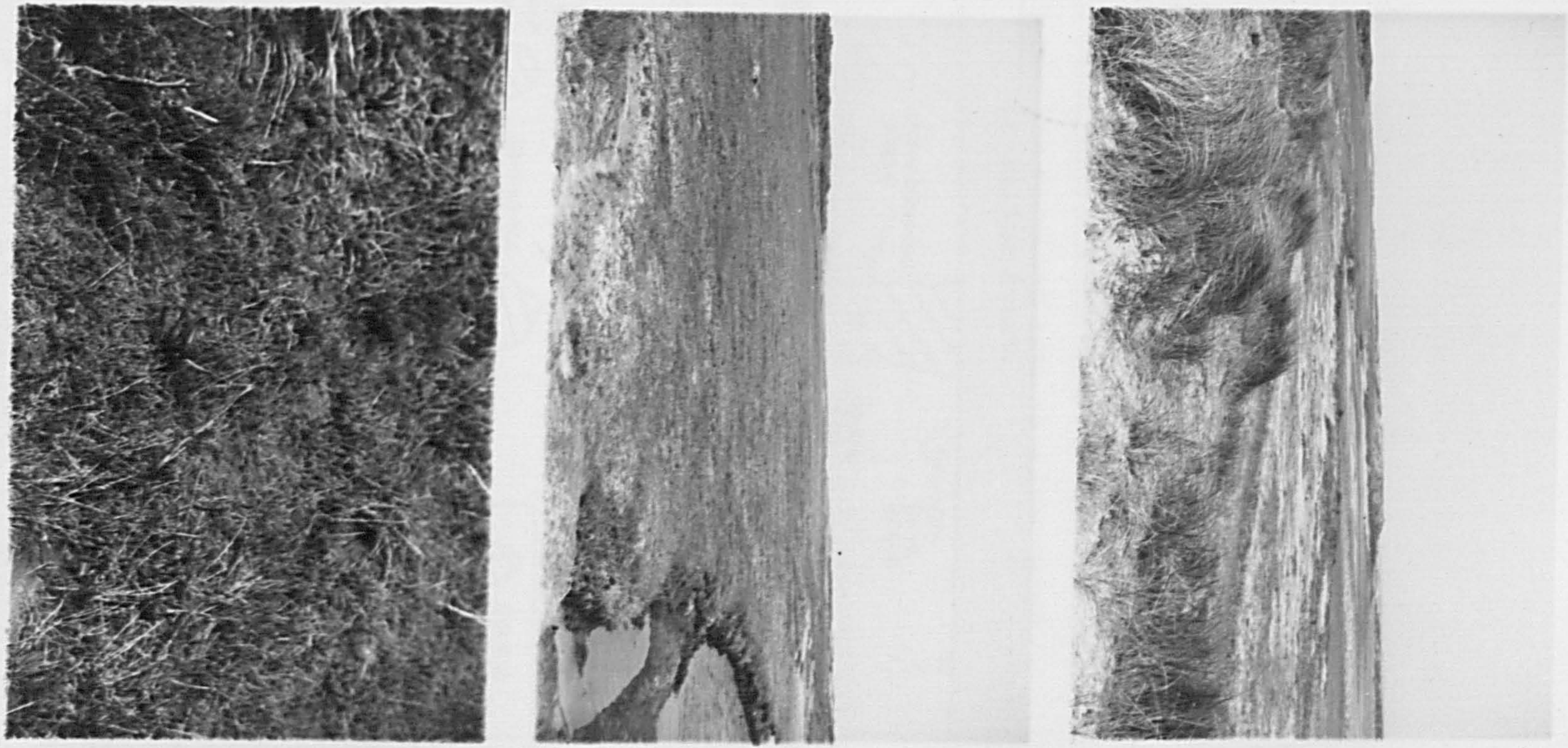
(ii) Aster marsh. This is one of a series of inter-dune marshes in the north-east corner of the reserve. These marshes, referred to as 'strip saltings' by Barnes and King (1961), form between parallel beach ridges running in the general direction north-south. The north eastward growth of the most seaward ridges protect those to landward which, deprived of material, become stabilised at a relatively low height. The unprotected southern part of the ridge tends to swing landwards enclosing a runnel between it and the nearest landward ridge. Served by the tide through a system of channels penetrating the ridges, these runnels develop a salt marsh flora on a very laminated substrate of alternating water and wind-borne sediments. The occasional isolation of such marshes by wind blown sand at their southern end has led to a complex of different marsh types (Chesters 1951), and the occasional curious juxtapositioning of sand dune and salt marsh plants is not uncommon. (I have observed, for example, Salsola kali intermixed with Halimione portulacoides and Eryngium maritimum close by Cochlearia officinalis).

The Aster marsh is served by a main channel which runs close to a seaward dune ridge (see Fig. IV.4. a and b). Some blown sand across its southern end carries Ammophila arenaria, Agropyron juncieforme, Salsola kali, Glaux maritima, Honkenya peploides, Cakile maritima and, perhaps unusually, Artemesia maritima, The main marsh area is principally a sward of Puccinellia maritima co-dominant with Aster tripolium (see Fig. IV.4c), although a variety of other species are found (see Appendix III). Plants and fruit were collected from the area marked in Fig. IV.5.

Two high spring tides observed in September 1966 and one in March 1967, covered this marsh well before they reached the main salting, removing as they did so a good deal of the enclosing sand ridge at the southern end. The marsh remains exposed however for much of the summer.

(iii) Limonium marsh. This area is situated in the northern part of the mature salting north of the hard core road from the car park to the eastern dune ridge (see Fig. IV.2). The area sampled was about 50 yards south of Bulldog bank where the marsh is dominated by a close sward of Limonium vulgare (L. humile is

Fig.IV.4 Aster marsh Gibraltar Point.

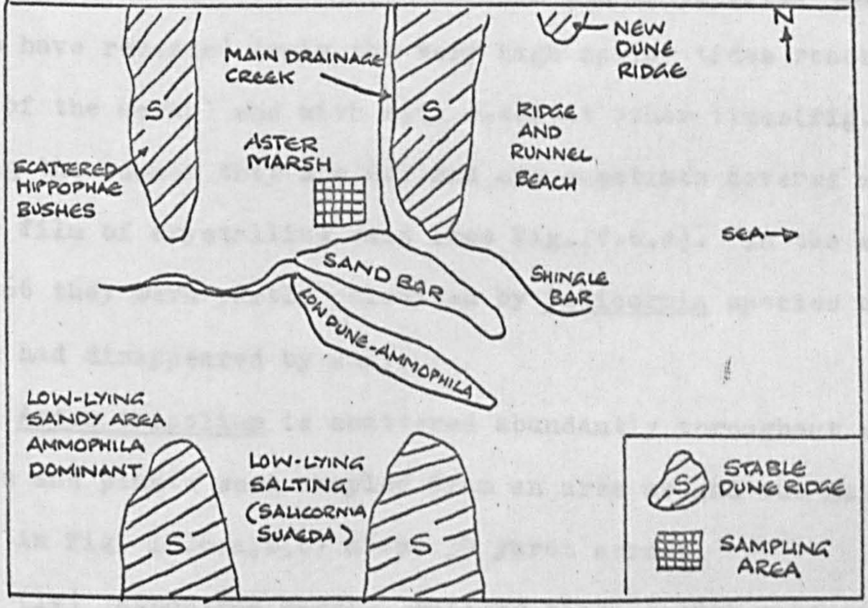


(a) General position between dune ridges to east and west looking north.

(b) Aster marsh looking north. Main drainage creek on right.

(c) Aster plant in Aster marsh with Puccinellia maritima.

Fig. IV.5 The sampling area on Aster marsh, Gibraltar Point.



also present near by).

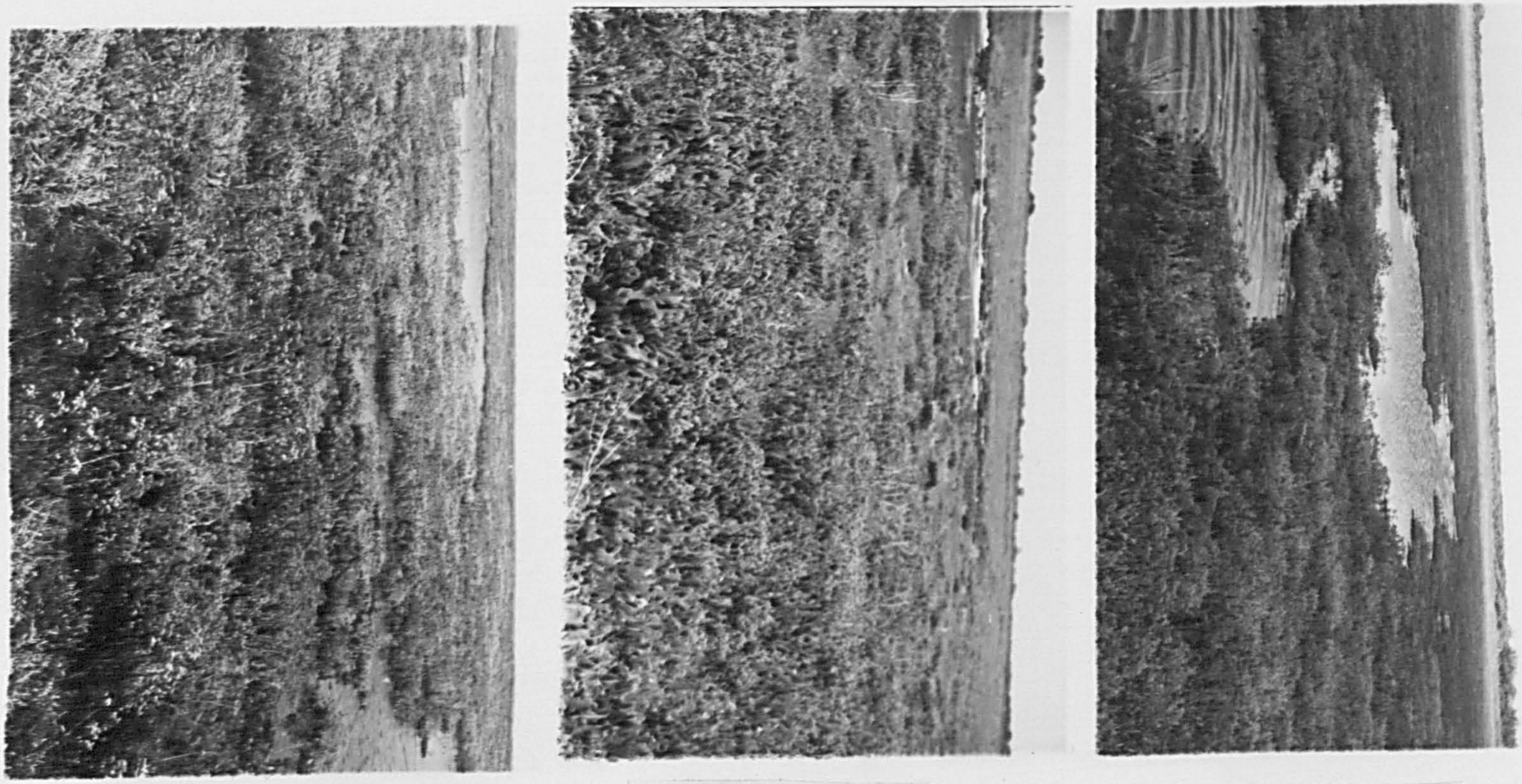
To the west of the Limonium sward a dense stand of Halimione borders the drainage creeks of this marsh which all run south westwards into the main creek close to the west dune ridge. To the east it gives way to sand dune and Hippophaea rhamnoides scrub, to the south to a general salt marsh community and to the north to an area dominated by Agropyron pungens (see Fig. IV.6.a).

Between the close stands of Limonium, Puccinellia maritima is locally dominant and there are a number of areas of bare mud (pans). These pans become filled with sea water after the high tides have receeded (only the very high spring tides reach this part of the marsh) and with rain water at other times(Fig. IV.6.c). During the summer they are dry and are sometimes covered with a white film of crystalline salt (see Fig.IV.6.d). In the spring of 1966 they were partly colonised by Salicornia species but these had disappeared by July.

Aster tripolium is scattered abundantly throughout this area. Fruits and plants were sampled from an area around the main pan (seen in Fig. IV.6.a,b,c) about 30 yards across.

(iv) Agropyron marsh. Bulldog bank, a 19th century reclamation bank, crosses the northern part of the mature salting from east to west enclosing a fresh water marsh to the north (see Fig. IV.7a). This area is almost entirely removed from tidal influence although exceptionally high tides combined with north westerly gales may occasionally reach it. (At Gibraltar

Fig.IV.6 Limonium marsh Gibraltar Point.



(a) Looking north to Bulldog Bank.

(b) Looking south east.

(c) *Aster* in flower in sampling area.

Fig.IV.7(a) Bulldog Bank Gibraltar Point. Looking east along top. Lim. and Agr. marshes arrowed.

Fig.IV.7(b) Agropyron marsh looking north from Bulldog Bank.

Point direct onshore winds have the unexpected effect of lowering tide heights in the mature saltings, whereas north westerlies 'pile up' water behind the spit from whence it overflows the Spartina marsh on to the mature salting). All of the high spring tides whose course has been mapped during this investigation failed to reach even the lower part of Bulldog bank. The main ditch beyond the bank carries *Ranunculus aquatilis*, suggesting that it contains almost fresh water. The area behind the bank is dominated by grasses, particularly *Agropyron pungens* (Fig. IV.7.b). *Agropyron junceiforme* is common on the eastern fringe and many of the very variable couch grasses on this marsh were identified as the male sterile *A. junceiforme X pungens*. (*A. repens*, itself common nearby may also be involved in hybridisation with the other two species). Other common grasses in this marsh include *Festuca rubra*, *Poa pratensis*, *Agrostis stolonifera*, *Agrostis gigantea*, *Holcus lanatus* and *Datylis glomerata*.

Cutting across the Agropyron marsh are shallow ditches which carry a number of sedges. These include *Carex otrubae*, *C. distans* and *C. extensa*. Patches of *Scirpus maritimus*, *Juncus maritimus* and *J. gerardii* also occur along these ditches and fringing the occasional pools.

Aster tripolium was sampled from the central grassy area of the Agropyron marsh where it is found with most unlikely associates including *Potentilla anserina*, *Ranunculus repens, Rubus* species, *Rumex acetosa*, *Cirsium arvense*, and occasionally small bushes of

Fig.IV.8(a) Aster plants in Agropyron marsh, Gibraltar Point.

Hippophae rhamnoides and Sambucus niger (a dense scrub comprised of these two species appears to be the local 'climax' vegetation). The Aster plants were tall and generally unbranched, (Fig. IV.8a), and the population varied in number from year to year. In 1966 a large number of plants were scattered throughout the area as they were in 1967 (when Fig. IV.8a was taken). In 1965 only a few plants were found in among the grasses although a large linear colony fringed the main ditch (Fig. IV.8b). Despite the apparently large numbers of fruit set in autumn 1967, a search for seedlings in the central area during the spring of 1968 was entirely unrewarded, the plant being confined to the ditch edge as in 1965 (Fig. IV.8b). Only plants from the central area were sampled.

(b) Scolt Head Island, Norfolk.

The physiography and development of the marsh systems on Scolt Head Island, off the North Norfolk coast, have been extremely well documented. They formed the study area for Chapman's pioneer work on the ecology of salt marshes and were the subject of a number of his early papers (Chapman 1938, 1939, 1940, 1941). This work has recently been included in a general review of the plant ecology of the island (Chapman 1960a).

The physiography and development of the island has been fully treated by Steers (1960) and it is not proposed to review this here. A map of Scolt Head is given as Fig. IV.9.

For the purposes of the present study it was necessary to

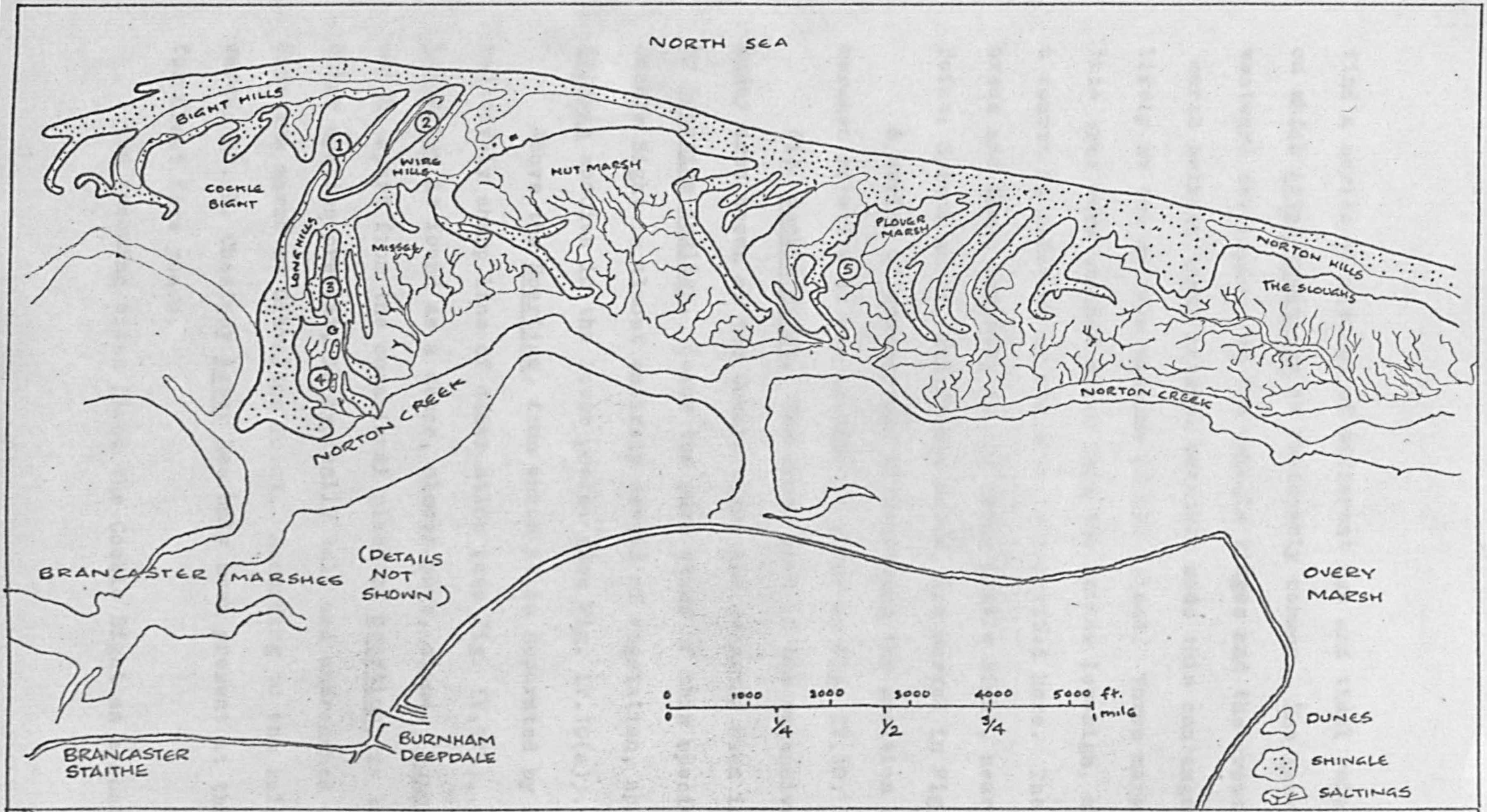


Fig. 1V.9 Scolt Head Island, Norfolk

populations sampled:

① Cockle Bight
② Spiral marsh
③ Beach Point '65
④ . Beach Point
⑤ Plover marsh

find a series of marshes of different age and tidal relations on which Aster tripolium is reasonably common. The general westward development of the shingle ridges and the growth of salt marsh between their lateral branches made this contingency most likely at the western extreme of the island. Three marshes in this area were studied which form the series low-high, although a fourth is referred to and will be described here. The sampling areas and these marshes, in the upper Cockle Bight, near Beach Point, Spiral marsh, and Plover marsh, are marked in Fig. IV.9.

A series of photographs illustrating the position of these marshes relative to one another is given as Fig. IV.10.

(i) Cockle Bight. The upper part of the extensive flat muddy area known as the Cockle Bight has recently been invaded by Spartina anglica. Below the pure stand of this species the Cockle Bight is almost entirely devoid of vegetation, apart from Zostera species in the lower pools. (See Fig. IV.10(a)).

Above the Spartina, from which it is separated by a relatively sharp line of demarcation (see Fig. IV.11b), Aster tripolium is found as a dense, almost pure, stand. Suaeda maritima which, apart from the occasional plant of Spartina, is the only other species present, is typically tall and unbranched as in the Spartina marsh at Gibraltar Point. According to the island's warden Mr. R. Chestney Aster has only been present at this site for about five years.

The incoming tides flood the Cockle Bight as a continuous

Fig IV.10(a) Scolt Head Island. Upper Cockle Bight and Spiral marsh looking north from Long Hills.
C = Cockle Bight, pools containing Zostera sp.
A = Aster population in Upper Cockle Bight.
F = Suaeda fruticosa on shingle ridge.
S = Spiral marsh.

Fig IV.10(b) Scolt Head Island. Looking west from Long Hills.
S = Spiral marsh.
W = Wired Hills (low ridge running west).
P = Plover marsh in distance behind Privet Hills.
M = Missel marsh in middle distance.
B = Upper part of Beach Point.

Fig.IV.11(a) The upper Cockle Bight, Scolt Head Island.

Fig.IV.11(c) Looking through dense *Aster* to *Spartina* and the unvegetated lower Cockle Bight.

Fig.IV.11(d) *Aster* in the upper Cockle Bight with *Suaeda maritima*.

sheet of water reaching the upper marsh via the Spartina sward. Later on, the overflowing of the single drainage creek takes place on to the region of the marsh where Aster tripolium occurs. Although the tides arrive here almost simultaneously with their arrival at the lowest part of Beach Point their upward seepage on to the Cockle Bight is far more rapid and the upper Cockle Bight marsh remains covered for a longer period. High neaptides partially cover the zone occupied by Aster.

Plants and fruits were sampled from the area of the most dense Aster tripolium.

(ii) Beach Point. The marsh near Beach Point is again dominated by Aster tripolium, but here the plant is rather more scattered. (Fig. IV.12a, c and d). Towards the distal end of Beach Point the marsh, which has developed between the shingle bar on which Long Hills stand and that on which the dunes known as Felter's Hill stand, is still very 'open' (sensu Chapman 1960a p. 112) although accretion is probably very rapid due to the presence of Spartina in Norton Creek (see Fig. IV.9). The area studied, close to the unstable sand bank on a shingle base known as Beach Point, is, like the Aster marsh at Gibraltar Point, subject to invasion by sand. This is carried by westerly winds off Beach Point. When the marsh was visited in the spring of 1968 a large area of the marsh had been covered by sand (Fig. IV.12b).

As well as Aster tripolium, Puccinellia maritima, Suaeda maritima Halimione portulacoides and Spartina anglica are also common

Fig.IV.12(a) Beach Point marsh, Scolt Head Island looking east from Beach Point.

Fig.IV.12(b) Part of Beach Point marsh covered by sand blow out (April 1968).

Fig.IV.12(c) The Aster population at Beach Point, Scolt Head Island.

Fig.IV.12(d) Aster on Beach Point with Spartina, Salicornia, Halimione and Puccinellia.

on this part of the marsh. Lower down the marsh *Salicornia* species become co-dominant with *Aster*. A number of algal species, including fucoids, are present throughout this marsh and become particularly common at the lower end near Norton Creek. These include *Enteromorpha prolifera*, *E. nana*, *Vaucheria thuretii*, *Oscillatoria sancta*, *Ulothrix speciosa*, *Fucus vesiculosus*, and dense mats of *Pelvetia caniculata* and *Bostrychia scorpioides*. (see also Appendix III).

The changes in the marsh vegetation of the island from 1932 to 1957 have been discussed by Chapman (1959) who pays some attention to the Long Hills marsh, part of which fringes the northern end of the marsh studied here.

Aster tripolium plants and fruits were sampled in the lower part of Beach Point marsh in 1965 and more extensively from the middle part close to the southern limit of the dunes on Long Hills in 1966 and 1967. Unless otherwise stated reference to the Beach Point population will be to these later samples.

(iii) *Spiral marsh*. The area known as Spiral marsh is separated from the *Aster* population in the upper Cockle Bight by a low shingle ridge covered with *Suaeda fruticosa* and is at a straight line distance from it of less than 50 yards (see Fig. IV.10a). Despite this the vegetation and substrate are very different. In contrast to the deep fluid mud of the Cockle Bight the substrate on Spiral marsh is composed of a shallow silt above coarse shingle. (Some of which can be seen in the drainage creek Fig. IV.13a).

The general height of the vegetation too is very different, Spiral marsh being covered by a very low sward dominated by Limonium vulgare and Aster tripolium. The general composition of the vegetation mat is not unlike that of the Limonium marsh at Gibraltar Point, although at its fringes shingle plants such as Suaeda fruticosa and Limonium binervosum occur. The density and low height of the vegetation can be seen in Figs. IV.13b and c).

Spiral marsh is one of the highest marshes on Scolt Head, being completely covered by only the high spring tides (of 27' or over). Coverage occurs through overflowing of the main drainage creek which sloped steeply (in salt marsh terms) down to its exit in the upper Cockle Bight.

Plants and fruit of Aster tripolium were sampled from the centre of the sward along a line running parallel to the creek and the shingle ridge to the east, and about midway between them.

(iv) Plover marsh. Some plants and fruits of Aster tripolium were collected from a fourth marsh on Scolt Head. This marsh, to the east of the others, supports a general salt marsh flora. In places it is bisected by deep creeks (Fig. IV.14a) between which plateaux of vegetation are dominated by Puccinellia maritima and Aster tripolium (Fig. IV.14b). Halimoine portulacoides is here largely confined to edges of the creeks.

The tidal relations of this marsh are less easy to establish by either direct observation or by inference from the vegetation. The incoming tide enters the marsh through the network of creeks

(a) Spiral marsh Scolt Head Island from south west.

(b) Spiral marsh. Close sward of Limonium and Aster

(c) Aster on Spiral marsh. Note plant size.

and local lower areas of vegetation may be covered on many more occasions than others (for example on the plateaux). Differences in the rates of lateral seepage through the soil will also complicate the pattern of tidal flooding.

Aster tripolium plants and fruit were sampled from the plateaux in areas surrounding the many 'pans' on this marsh.

(c) Tetney Haven, Lincolnshire.

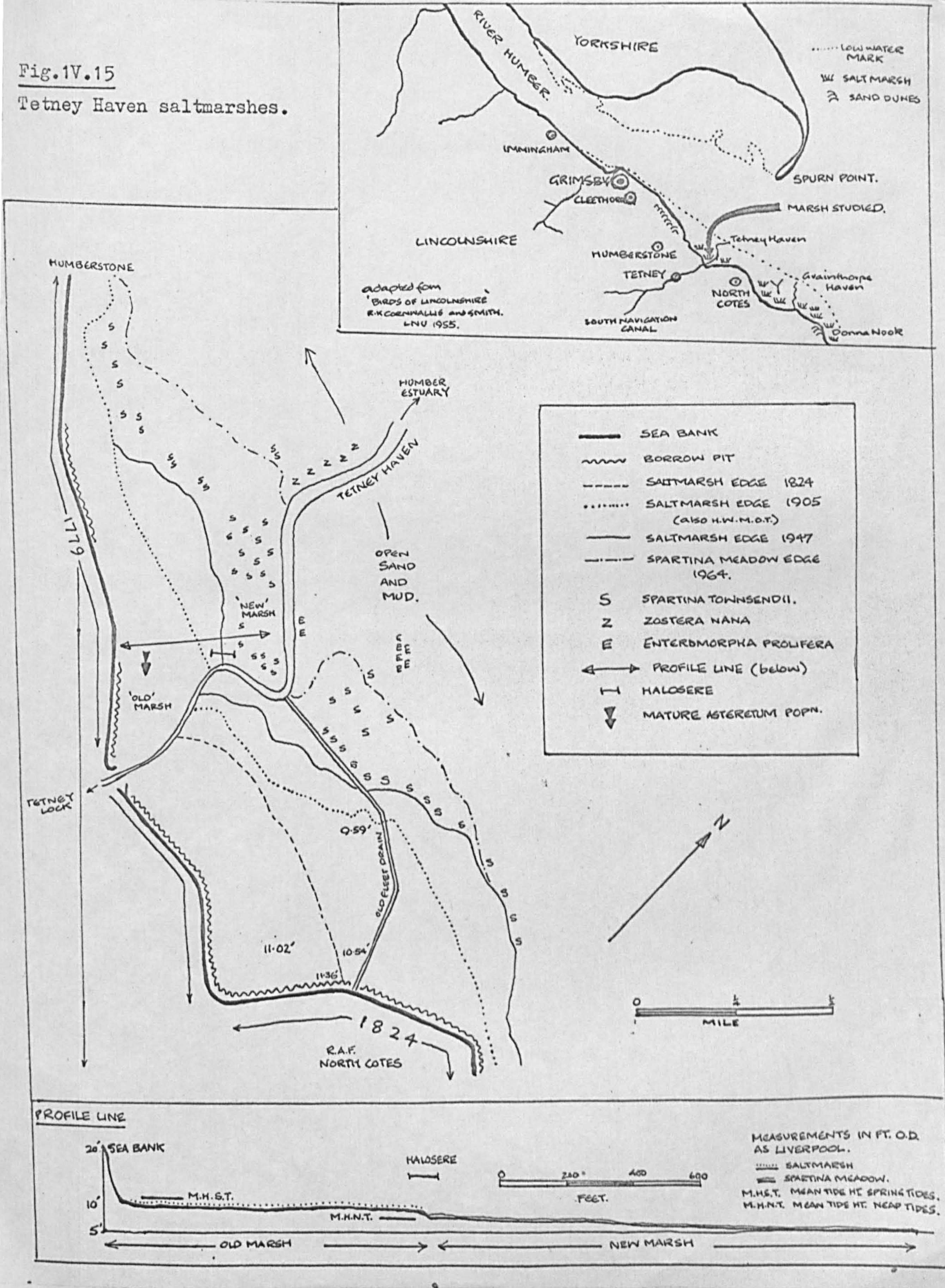
Tetney Haven salt marshes are situated on the North Lincolnshire coast at the mouth of the River Humber, their long axis running approximately N.W. - S.E.

They were the subject of an earlier investigation by the present author, at first in relation to the role of Spartina townsendii s.l.in their stabilisation (Gray 1959), but later in a study of the influence of tides on the vertical distribution of the main species (see App. VI and Ch. 7). Four populations of Aster tripolium in this area are referred to in the present study; those at Humberstone and North Cotes (particularly in Ch. 11), the area known as 'the Halosere' (in Chs. 7, 11 and throughout) and the 'old marsh' (throughout). The location of these areas is shown in Fig. IV.15. The 'Halosere' and the 'old' marsh are described below.

(i) The Halosere. Since 1774 when a special act was passed for 'enclosing the open Fields, Meadows and common Stinted Pastures... in the Parish of Tetney' (Wild 1900), and a bank

Fig.1V.15

Tetney Haven saltmarshes.



adapted fom 'Birds of Lincolnshire' R.K Cornwallis and Smith. LNU 1955.

built enclosing the pre-existing saltings, the marsh has progressed seawards at a steady rate of accretion.

By 1947 the seaward edge of the marsh in the region of the Haven estuary was showing signs of regression by erosion. This was largely due to the growth of Sand Haile Flats pushing the mouth of the Haven estuary further towards Humberstone, and thus altering the direction and force of local currents (see Fig. IV.15). In 1947 the area to seaward of the eroded edge of the Old marsh was bare mud with isolated clumps of Spartina townsendii with occasional pioneer plants of Salicornia dolichostachya Ulva lactuca, or Entermorpha prolifera (aerial photographs and Robinson 1956).

At the present day, despite the considerable raising of its level due to the explosive growth of Spartina, there is a drop of 3' from 9 to 6 feet ordnance datum from the 'old' marsh on to this area. This drop occurs over a distance of no more than 100 yards and provides a conveniently compacted transition zone from mature marsh to new marsh. This zone, referred to as the 'Halosere', has been the subject of investigations into tidal relations (App. VI) and the distribution of the rayless form of Aster (Ch. 11). The species present are listed in Appendix III.

(ii) The Old marsh. Fruits and plants were also sampled from the mature saltings at Tetney Haven known as the 'Old marsh'. The sample area was close to the sea wall in a general salt marsh community at about 13'O.D. and is marked on Fig. IV.15. The

Fig.IV.16(a) The Halosere, Tetney Haven salt marsh.

Fig.IV.16(b) Part of Old marsh community, Tetney Haven saltmarshes.

vegetation, dominated by Puccinellia maritima, is listed in Appendix III.

(d) Morston and Cley, Norfolk.

It was hoped that a series of marshes representing well-defined stages in the succession from salt to fresh water marsh could be located in the area of Blakeney Point Nature Reserve, and used for the current purpose. However the search in this area was only partly successful. Fruits sampled from the generally very low marshes on Blakeney Point itself, were collected on a very wet day and on arrival at Keele it was discovered that many of these had already germinated and the remainder failed to dry out. However fruits from two other populations, did dry out and were successfully cultivated. The two areas were later revisited. They were at Morston, near the departure point of the boat for Blakeney Point, and at a point near to the village of Cley at the eastern end of the Blakeney shingle ridge.

(i) Morston. The marsh at Morston is one of the series of mature saltings which fringe the mainland opposite Blakeney Point and Scolt Head Island. The particular area sampled was close to a path across the marsh leading to Blakeney Point. Fringed to landward by Agropyron pungens and Artemesia maritima, the community in which Aster tripolium was found was of the general salt marsh type, dominated by Limonium vulgare and Puccinellia maritima (Fig. IV.17 a and b).

Fig.IV.17(a) (Above)
The mature marsh at Morston. Artemisia maritima in foreground.

Fig.IV.17(b) (Left)
Aster on Morston marsh with Limonium, Halimione, Triglochin etc.

Aster tripolium on this marsh shows a wide range of variation in the colour of the ray florets, from deep blue through pink to white (see Ch. 11). A number of these different colour forms were collected and have been deposited in the Herbarium at Keele.

(ii) *Cley.* Samples were obtained from the edges of fresh water pools on the landward side of the sea bank which runs from Cley village to the base of the Blakeney shingle bar (see Fig. IV.18). These pools, alongside the road from Cley to the coastguard observation post, are separated from the mature saltings which lie between the village and the shingle bar by a high sea bank. They are fringed by *Phragmites communis*, *Phalaris arundinacea*, *Scirpus maritimus* and *Juncus maritimus*. The bank itself is dominated by grasses including *Dactylis glomerata* and *Agropyron repens*.

Fruits were sampled from the tall-growing *Aster tripolium* at the edges of these (probably fresh water) pools.

(e) *Parkgate, Cheshire.*

The salt marsh at Parkgate is situated on the eastern shore of the Dee Estuary, a funnel shaped embayment running S.S.E. - N.N.W. and emptying into Liverpool Bay a few miles west of the River Mersey. Although heavily grazed in the S.E. corner near Burton the Dee marshes in the region of Parkgate remain relatively undisturbed.

The progressive silting of the Dee and the history of the

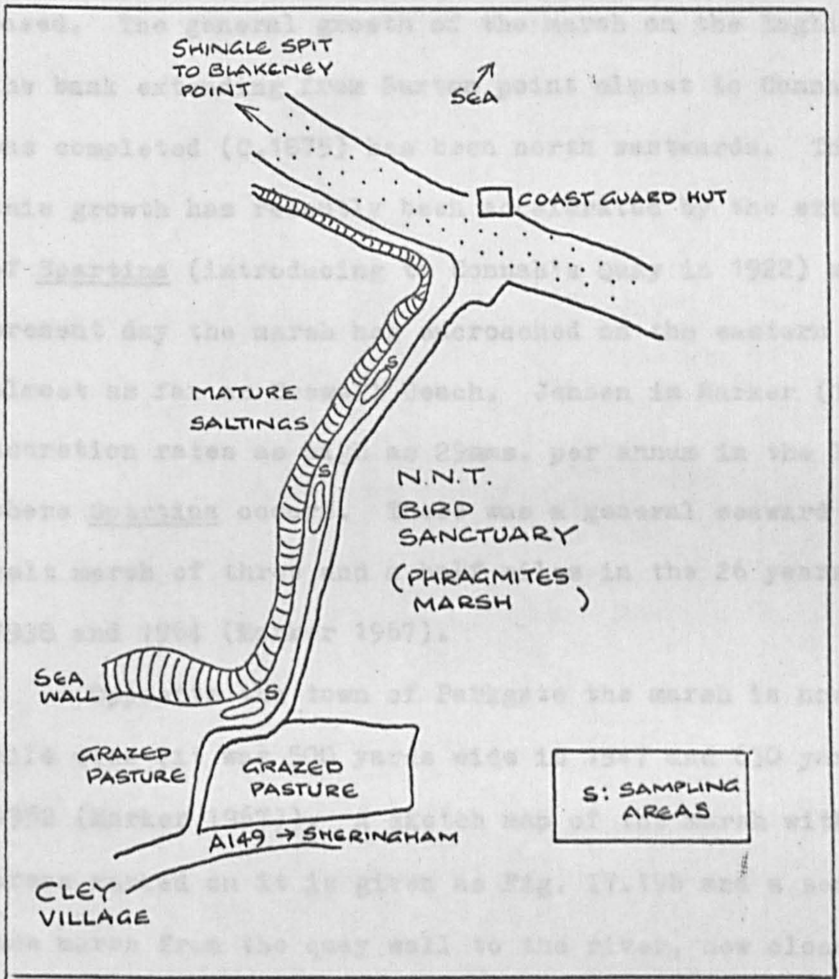


Fig. 1V.18 Sketch map showing sampling sites near Cley, Norfolk.

development of the salt marshes here have been outlined by Stopford (1951) and Marker (1967) on whose work Fig. IV.19a is based. The general growth of the marsh on the English shore since the bank extending from Burton point almost to Connah's Quay was completed (C.1875) has been north westwards. The rate of this growth has recently been accelerated by the extensive spread of <u>Spartina</u> (introducing to Connah's Quay in 1922) and at the present day the marsh has encroached on the eastern fore shore almost as far as Heswall Beach. Jensen in Marker (1967) recorded accretion rates as high as 29mms. per annum in the lower zones where <u>Spartina</u> occurs. There was a general seaward growth of salt marsh of three and a half miles in the 26 years between 1938 and 1964 (Marker 1967).

Opposite the town of Parkgate the marsh is now almost a mile wide (it was 500 yards wide in 1947 and 630 yards wide in 1952 (Marker 1967)). A sketch map of the marsh with the sample areas marked on it is given as Fig. IV.19b and a section across the marsh from the quay wall to the river, now close to the Welsh side, is given as Fig. IV.19c. The samples populations are referred to as Parkgate 1, (P1), Parkgate 2, (P2), Parkgate 3 (P3), and Parkgate 4 (P4), in order of maturity, Parkgate 1 being the oldest. They will be described in reverse order, starting with the young area of marsh at P4.

(i) <u>Parkgate 4</u>. Although nearer to the quay wall than P3 (see Fig. IV.19b) the site at P4 is at a lower elevation and is

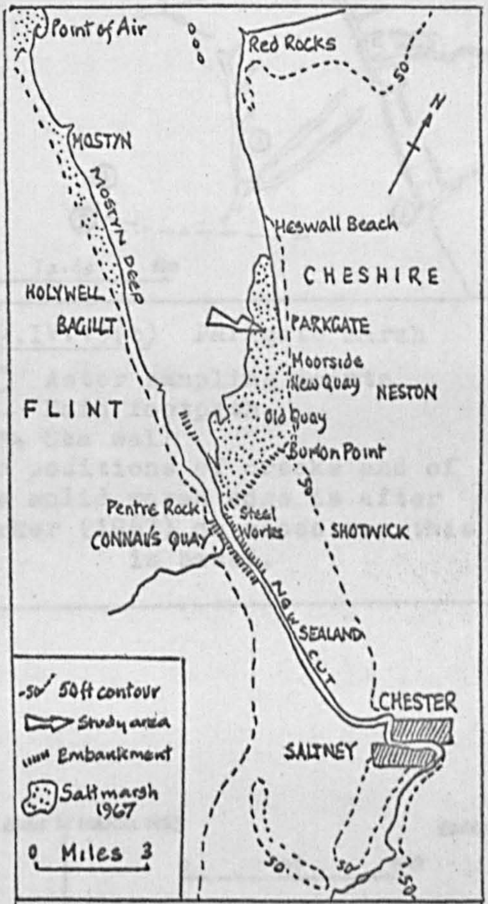


Fig. IV.19(a) The Dee Estuary showing study area. (After Marker 1967).

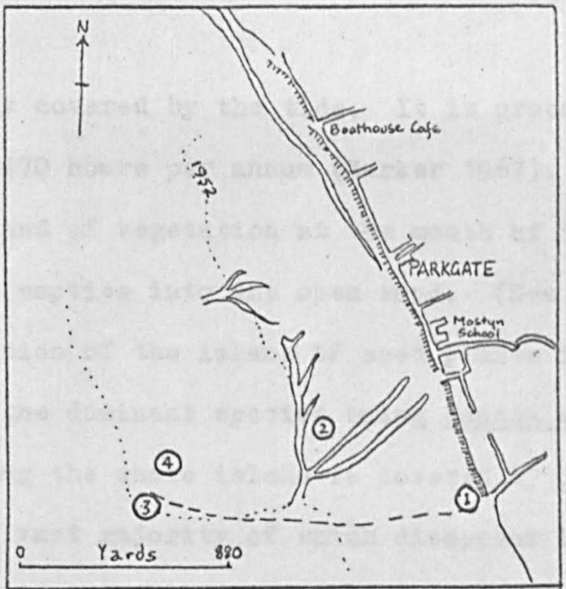


Fig.IV.19(b) Parkgate marsh

○ Aster sampling points
---- Main footpath
Sea wall
The positions of creeks and of the solid marsh edge is after Marker (1967) on whose map this is based.

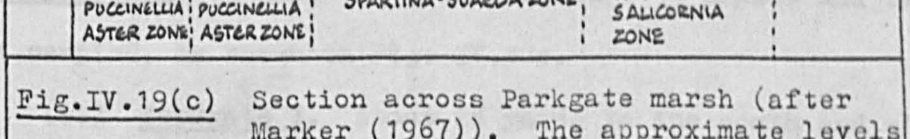


Fig.IV.19(c) Section across Parkgate marsh (after Marker (1967)). The approximate levels of the sampled populations of *Aster* are shown. Vegetation zones according to Marker.

more frequently covered by the tide. It is probably submerged for more than 470 hours per annum (Marker 1967). The site itself is a small island of vegetation at the mouth of the main drainage creek where it empties into the open sand. (See Fig. IV.20a).

The invasion of the island by seed plants is in its very early stages, the dominant species being Suaeda maritima. During the early spring the whole island is covered by Salicornia seedlings, the vast majority of which disappear before the summer. A species of Enteromorpha encircles the island, marking the lowest limit of vegetation. This is followed by Suaeda maritima and Salicornia maritima and the highest part of the island supports a very thin carpet of Puccinellia maritima (see Fig. IV.20b). Despite its presence in a pure sward to the north and as large clumps to the south (as P3) only two isolated seedlings of Spartina anglica were found on the island in 1967. (A much larger number of seedlings were found here in July 1968). A number of seedlings of Halimione portulacoides (but no mature plants) were also found in 1967 and 1968. Twenty seven mature Aster tripolium plants were found on the island in 1967 and a number of seedlings were also present. This number had increased by only two in 1968. Aster tripolium at this site, from which both plants and fruits were sampled, is shown in Fig. IV.20c.

(ii) Parkgate 3. About 25 yards to the south and slightly to seaward of P4 an area which is being actively invaded by Spartina was chosen for sampling. The vegetation at this site

Fig IV.20(a) Parkgate site P4 partially under tide (looking N.E. from P3). White Object in middle distance marks position).

Fig.IV.20(b) Parkgate site P4 showing Salicornia, Suaeda and Puccinellia under tide.

Fig.IV.20(c) Aster on P4 with Suaeda and Puccinellia.

which is close to the path leading across the marsh to the open sandflats, is more mixed than at P4 and at a later stage of succession, Marker (1967) has calculated that the type of vegetation of which P3 is typical is submerged for between 282-369 hours per annum. Large clumps of Spartina are mixed with similar clumps of *Puccinellia maritima* and between these rather more open areas are dominated by *Suaeda*, *Halimione* and *Salicornia* (see Fig. IV.21a) In addition *Cochlearia officinalis* and rather unexpectedly *Spergularia media* occur. In general the substrate is rather more muddy than at P4 although both these areas are predominately sandy.

Aster tripolium is well scattered throughout this area particularly on the low hummocks formed by the *Puccinellia* turf. Plants and fruit were sampled from both these hummocks and the lower more open areas (and may thus represent a mixture of types). A plant growing in an open area is shown in Fig. IV.21b.

(iii) *Parkgate 2*. The marsh at Parkgate is somewhat uncharacteristic of west coast salt marshes in that there are one or two relatively sharp breaks in the zonation. Towards the southern end of the marsh the limit of an upper grassy zone dominated by *Festuca rubra* can be clearly seen at certain times of the year. (See Fig. IV.22a). To seaward of this sharply marked 'cliff' the marsh is dominated by a well-drained turf of *Puccinellia maritima*. *Aster* is the only other plant commonly found in this sward, throughout which it is abundantly scattered (see Fig. IV.22b). This area is deeply dissected by drainage creeks, the distinctly

Fig.IV.21(a) Parkgate P3 looking S. from path.

Fig.IV.21(b) Aster at P3 (with Suaeda, Halimione and Puccinellia).

Fig.IV.22(a) Parkgate P2 (in foreground) (note the sharp lower limit of Festuca in distance).

Fig.IV.22(b) Aster at P2.

raised edge of which are covered by *Halimione*. *Cochlearia officinalis* is occasionally found in the turf. Both plants and fruit of *Aster* were sampled from this area.

(iv) *Parkgate 1*.

The area of marsh close to the quay wall is at a lower elevation than the marsh referred to as P2 (see Fig. IV.19c). It is poorly drained and the pans are more frequent. Close to the path on the southern edge of the marsh a fresh water spring feeds into the marsh. This area is dominated by *Scirpus maritimus*, *Phragmites communis* and in the local drier parts, *Festuca rubra*. Other common species include *Triglochin maritima*, *Plantago maritima*, *Glaux maritima*, *Spergularia marina*, *Cochlearia officinalis*, *Atriplex hastata* and *Ranunculus sceleratus*, the presence of which suggests that the salinity may be considerably lowered by the fresh water spring. The whole marsh is submerged less than 8 times a year when there is a tide of 29' or higher (Marker 1967).

Aster tripolium is very common on this part of the marsh even extending at times into the beds of *Phragmites* and *Scirpus* (see Fig. IV.23). The plants in this area are tall growing and generally unbranched. Plants and fruits were sampled from an area about 30 yards in diameter on the north side of the path close to the quay wall (see Fig. IV.19b).

The areas P1, P2, and P3 were used in transplant experiments and further photographs are given in Fig. 9.4.

In addition to the four sample areas described above plants

Fig.IV.23(a) (Above) Aster at Parkgate P1 among Scirpus maritimus.

Fig.IV.23(b) (Below) Parkgate site P1, general view.

were also collected from crevices in the sandstone quay wall at Parkgate. Here Aster shared the crevices with a number of other species, including Tripleurospermum maritimum, Lolium perenne, Plantago coronopus, P. maritima and Epilobium sp.

APPENDIX V.

INLAND SITES

(a) Winsford.

Close to the Imperial Chemical Industries rock salt mine near Winsford in central Cheshire the approximate grid reference being SJ 653687 are a number of pits into which waste material from the purification process has been dumped. This material, largely Calcium carbonate and Magnesium hydroxide, forms a dense white sticky 'slurry' which is largely unvegetated (see Fig. V.1). The pits, which are separated from the main works by a canalised stretch of the River Weaver, are enclosed by a number of high grassy banks. The bottom of these banks supports a flora which, despite the nearest coast being at least 15 miles away, includes *Glaux maritima*, *Spergularia salina*, *Triglochin maritima* and *Aster tripolium*. Four sites were sampled at Winsford, as follows:

Winsford A. Plants and fruits of *A. tripolium* were collected from the eastern margin of the largest, most southern pit. This area is depicted in Figs. V.2a and b. The plants here showed considerable vegetative development, flowering stems occuring only occasionally.

Winsford B. A small number of plants were collected from the surface of the pit close to site A.

Winsford C. The most northerly of the pits contains no waste material from the mine and is in fact a large open pool fringed by *Phragmites Communis*, *Typha latifolia*

Fig V.1 The inland site at Winsford showing the waste pits.
A, B, C, and D = *Aster* sampling sites.

Fig.V.2(a) Winsford A site (above).

Fig.V.2(b) *Aster* at Winsford A (below).

and *Schoenoplectus tabernaemontani*. The north-west facing bank carries a fringe of *Aster tripolium* at the base which gives way to a grassy slope locally dominated by *Chaemanerion angustifolium* (see Fig V.3a). Plants and fruits of *A. tripolium* were collected from this population on the margins of the pool and from among the reed beds where it was locally scattered (see Fig. V.3b). The plants were generally tall and unbranched.

Winsford D. A number of plants and fruit were collected from the actual slope of the west facing bank sites A and B. Here *Aster tripolium* is intermixed with a bizarre list of associates including *Calluna vulgaris* and *Ulex europaeus*. Fig. V.3c shows one of these plants among the mixed grass and *Juncus* species with *Valeriana officinalis* and *Matricaria recutita* evident.

(b) *Sandbach flash*.

Although no samples were collected from this area it is of interest as an example of an unusual site for the species. The flash is a large pool near Sandbach which has been created by salt mining subsidence (grid reference SJ 728607). It is fringed on its eastern side by an extensive area of waterlogged mud dominated by a species of *Polygonum* (most probably *P. bistorta*) with local patches of *Schoenoplectus tabernaemontani*, and *Ranunculus sceleratus*. *Aster tripolium* occurs with these

Fig.V.3(a) (Above)
General view of
Winsford C population.

Fig.V.3(b) (Left)
Aster at Winsford
with *Schoenoplectus*
tabernaemontani.

Fig.V.3(c) Winsford D site.

Fig.V.4(a) Sandbach flash (Watch lane in background).

Fig. V.4(b) <u>Aster</u> fringing Sandbach flash.

species among a grove of Alnus glutinosa, many of which are dead (Fig. V.4b).

There is also a small quantity of Aster on the north margin of the flash near the point where the former Watch Lane disappears under the flash east of Watch Lane Farm (see Fig. V.4a). Here it is heavily grazed, but flowers when mixed with Bidens cernuus which may be unpalatable to cattle.

APPENDIX VI.

ZONATION AND THE CALCULATION OF CRITICAL LEVELS.

A major feature of interest concerning maritime salt marsh vegetation is that it is subject to periodic immersion by sea water. In general plants on the lower marshes are flooded more frequently than those on the higher ones, and a number of early authors (Yapp et al (1917), and Richards (1934)) have suggested that the vertical distribution of salt marsh species is controlled solely by the amount of tidal coverage.

The tides are certainly the most important factor contributing to the zonation of vegetation although the species composition of a particular area may be modified by local conditions of surface topography, drainage, water table, aeration, and substrate. Chapman's pioneer work on salt marsh ecology (1938, 1939, 1940, 1941b) has done much to evaluate the relative importance of the various factors controlling the distribution of vegetation on British salt marshes, and his recent monograph (Chapman 1960) out-lines the most important aspects of our present knowledge of these.

The general subject of the zonation of the intertidal environment has an extensive literature, most of which is concerned with specific sites. That relating to rocky shores has been authoritatively reviewed by Lewis (1964). From the point of relating zonation to tidal behaviour the distribution of higher plants on salt marshes has been less studied than that of algae or animals on rocky shores. Nevertheless there are features common to both types of area which affect the zonation of all types of organism. One of these, the concept of 'critical' levels, was used as a basis for the subdivision of marshes in this investigation, and has been briefly described in Chapter 3. The theoretical background is discussed below and the way in which these levels were calculated is described.

The position of standard tidal levels (as obtained from Admiralty chart data) are shown in Fig. VI.1, the 'shape' of the curves corresponding the height of a single tide as it rises and falls. The 'critical level' theory, probably attributable to Coleman (1933), relates to the periods of emersion (over a long period e.g. 1 year) at these different levels. The shape of the tidal curve at a particular station is calculated from data in the Admiralty Tide Tables, and this is used in conjunction with graphs of the times and heights of low and high water of a sample of tides to estimate the yearly percentage emersion at different levels. The shape of the emersion curve thus obtained (see Fig. VI.2), discloses a number of 'zones' in which the generally gradual change in the overall rate of change of emersion is sharply accelerated over a correspondingly small increase in height. (Evans, 1957, has suggested that the critical nature of such levels is not due to sudden increases in the amount

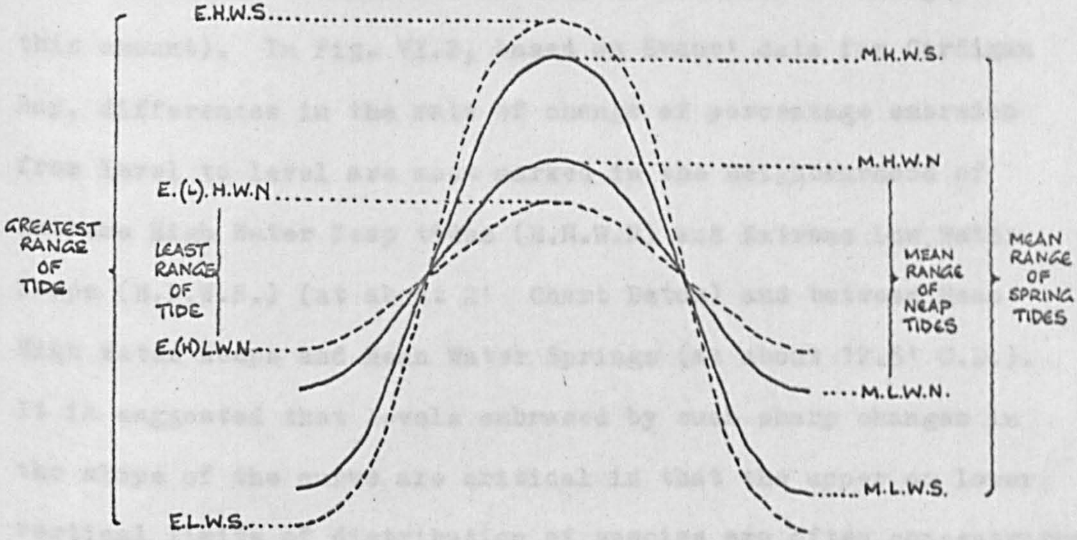


Fig.VI.1 Diagrammatic representation of tidal range and standard tidal levels (after Lewis 1964).

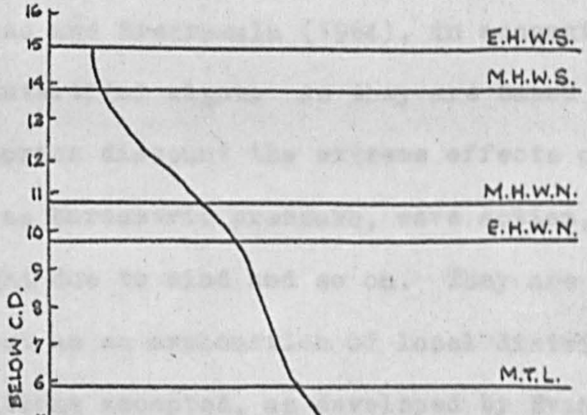


Fig.VI.2 An emersion curve - see text (after Evans 1947).

of emersion but to sudden increases in the rate of change of this amount). In Fig. VI.2, based on Evans' data for Cardigan Bay, differences in the rate of change of percentage emersion from level to level are most marked in the neighbourhood of Extreme High Water Neap tides (E.H.W.N) and Extreme Low Water Neaps (E.L.W.N.) (at about 2' Chart Datum) and between Mean High Water Neaps and Mean Water Springs (at about 12.5' C.D.). It is suggested that levels embraced by such sharp changes in the slope of the curve are critical in that the upper or lower vertical limits of distribution of species are often concentrated within them.

This type of theory has been applied by Rees (1940), ~~Moore and Sproston (1940)~~, Chapman (1941), and more recently by Umamaheswararao and Srecramulu (1964), in accounting for the zonation of intertidal algae. As they are based on predicted data such theories discount the extreme effects of modifying factors such as barometric pressure, wave action, spray, increase of tidal height due to wind and so on. They are therefore at their safest as an explanation of local distributions with these reservations accepted, as developed by Evans (1947a, 1947b, 1957) in comparative studies of tidal phenomena and zonation at a number of sites, and at their most susceptible when extended as a general theory relating to the intertidal distribution of organisms, as suggested by the 'tide factor hypothesis' version of Doty (Doty 1946, Doty and Archer 1950).

A somewhat cruder form of the 'emersion curve' theory can be used to demonstrate the existence of critical levels in salt marsh systems. This differs from that of Evans and others described above in (1) considering only the heights of high water, and (2) calculating the numbers of days on which tidal submergence occurs, rather than the period in hours of tidal submergence. A description of data relating to the Tetney Haven area will serve as an example of the application of this theory.

Figure VI.3 shows the predicted heights of all tides at Immingham (Lincolnshire) for the period February to October 1967 (based on data obtained from the Admiralty Tide Tables vol. 1 1967). The heights of low water are not shown but provide a mirror-image of high tides so that large spring tides have a large diurnal range, small neaps a small diurnal range, and so on. This pattern is repeated, with minor variations, from year to year. It can be seen that the equation of predicted tide heights with actual levels in the field would enable calculations to be made estimating the amount of tidal flooding at a particular point in the field. This was done at Tetney Haven in 1960 as part of a previous investigation and repeated again in 1965. A conveniently compacted transition zone over which the tide ebbed and flowed as a continuous sheet of water overspilling a main drainage creek was chosen, and the edges of flooding tides of predicted heights were marked with pegs along


HT ft.
23
22
21
20
19
18
17
16
15
1
7
14
MARCH
21
28
1
7
14
APRIL

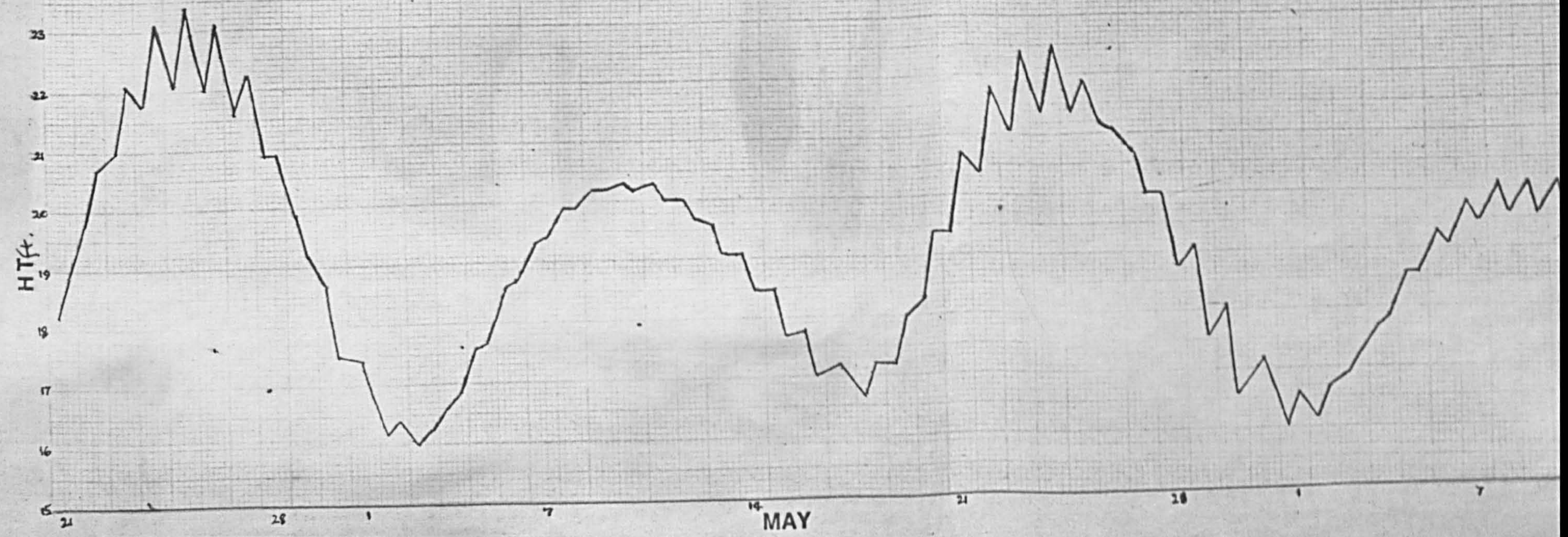
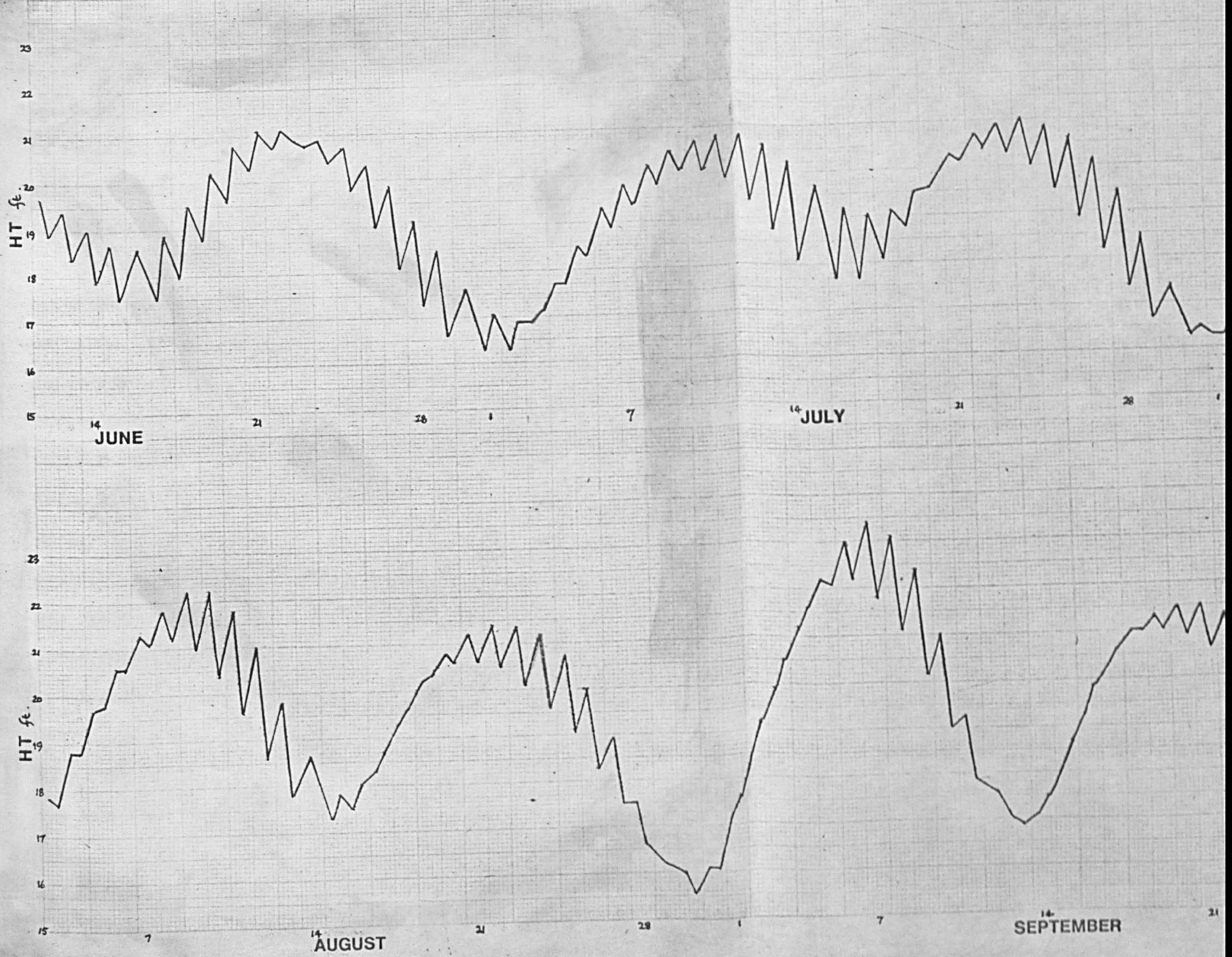

HT ft.
23
22
21
20
19
18
17
16
15
21
28
1
7
14
MAY
21
28
1
7

Fig.VI.5 (continued)



three line transects of tarred string. This was done by visiting the area at the times of a number of high tides during the March and April spring cycles. This type of exercise can be repeated for any marsh without reference to Ordnance Data, all that needs to be known being the relation between tide level (chart datum) and actual shore level.

In fact it is not necessary to know this relation in order to calculate the predicted amounts of submergence and emersion. This purely theoretical exercise can be done by reference to Fig. VI.3 from which the periods of non-tidal emersion can be calculated. For example, plants at the 23' tide level enjoy a period of twenty five tide-free days in March (March 1st - 25th), twenty five tide-free days in April (March 30th - April 23rd), and a long period free of tides until the autumn equinoctial springs of early September; plants at the 21' level are emersed for two periods of ten days in March, for twenty three days from March 31st to April 23rd, twenty three days from April 29th to May 22nd, twenty five days from May 27th to June 20th, thirty one days from June 23rd to July 23rd, thirteen days from July 25th to August 6th, eight days from August 13th to August 20th, ten days from August 25th to September 3rd, and so on.

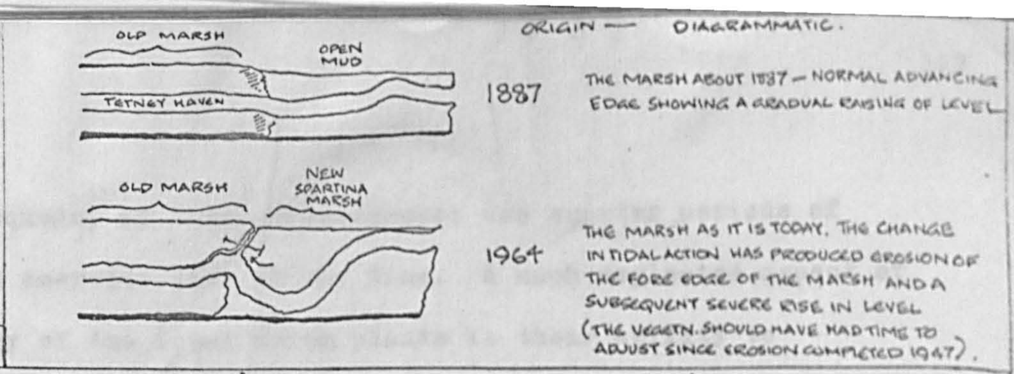
The plot of the total number of tide-free days against the tide level was given in Chapter 3 (Fig. 3.2). At Tetney Haven the tide levels have been related to actual shore levels and the vegetation within each zone mapped - see Fig. VI.4. (In fact the prior work of Robinson (1965) enabled in this case corrections to be made from Chart datum to Ordnance datum Liverpool, but as already stated this is not a necessary step). The vertical range of some of the common species on the Tetney Halosere was given as Fig. 3.3. The fact that a 'critical' level can be recognised from these data was also discussed in Chapter 3, III(a).

In addition to the total amounts of emersion experienced by plant communities at different levels there are interesting differences in the patterns of emersion at these levels.

Although the total number of emersion hours (and days) may be particularly important in, say, the case of rocky shore animals in directing their amounts of locomotory and feeding activity, it is felt that it is the pattern of alternating neap and spring tides which is of particular relevance to the establishment and growth of higher plant species in the lower zones of salt marshes. This pattern must therefore be examined more closely.

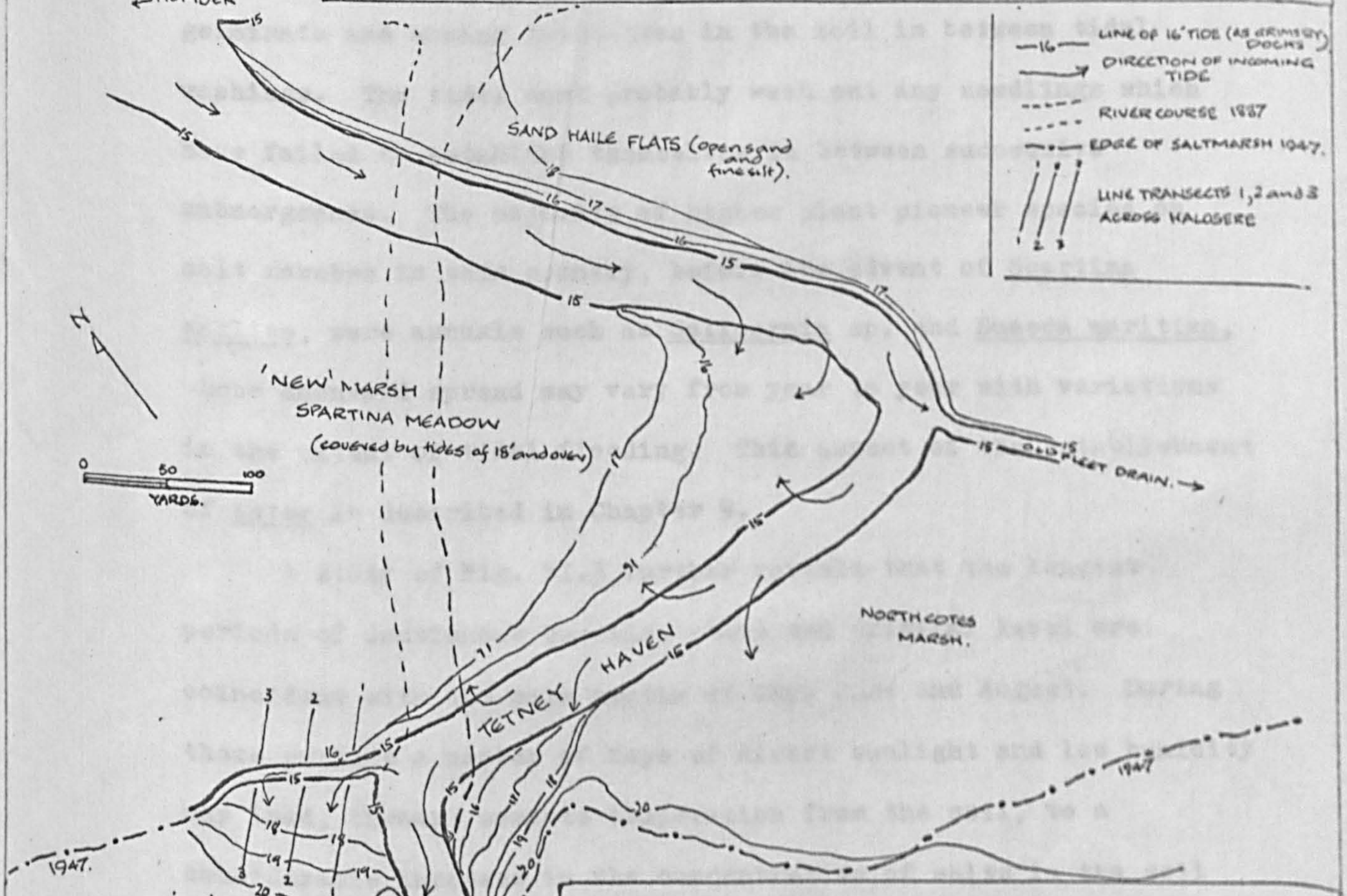
Returning to Fig. VI.3 it can be seen that there is a coincidence of peaks in the tidal curve with critical phases of the plant's life cycle. Intertidal regions are flooded to the highest levels by the equinoctial spring tides of March and September. These high spring tides coincide with the periods of seed germination and seed dispersal respectively. Seeds germinating in the lower zones experience during the Spring a

Fig.VI.4
The mapping of tidal levels on the Halosere at Tetney Haven. The origin of the Halosere is shown (adapted from earlier work).

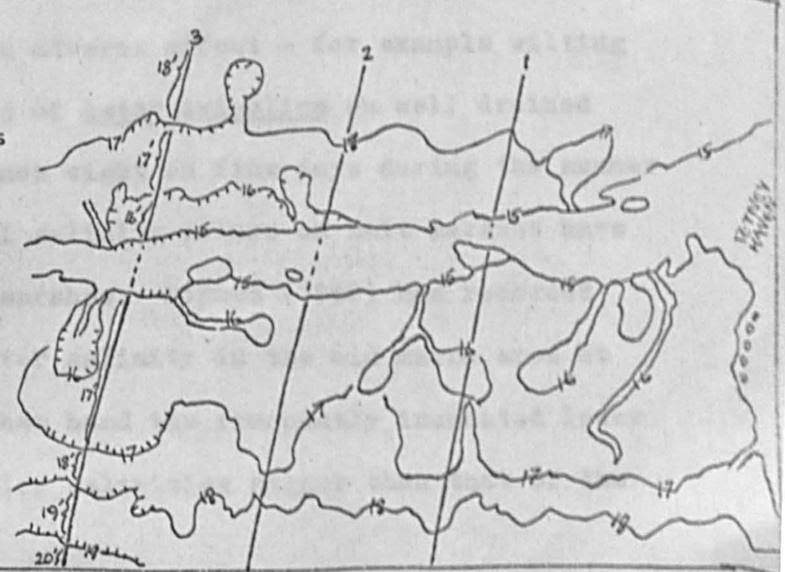


1887 THE MARSH ABOUT 1887 — NORMAL ADVANCING EDGE SHOWING A GRADUAL RAISING OF LEVEL

1964 THE MARSH AS IT IS TODAY. THE CHANGE IN TIDAL ACTION HAS PRODUCED EROSION OF THE FORE EDGE OF THE MARSH AND A SUBSEQUENT SEVERE RISE IN LEVEL (THE VEGETN. SHOULD HAVE HAD TIME TO ADJUST SINCE EROSION COMPLETED 1947).



—16— LINE OF 16' TIDE (AS GRIMSBY DOCKS)
DIRECTION OF INCOMING TIDE
RIVER COURSE 1887
EDGE OF SALTMARSH 1947.
LINE TRANSECTS 1, 2 and 3 ACROSS HALOSERE



A MAP OF THE HALOSERE SHOWING THE LINE TRANSECTS IN POSITION AND THE COMPLEX SYSTEM OF PANS AND CREEKS DRAINING SURFACE WATER INTO THE LATERAL CREEK. (adapted from previous work)

THE WAY IN WHICH THE TRANSECTS WERE ZONED IS SHOWN ON QUADRAT 3 AND IN THIS REGION THE TIDE LINES ARE SHOWN AS FOLLOWS:-

not submerged
16
water

FOR THE ASTER COUNTS THE TRANSECT LINES WERE USED AS POSITIONS FROM WHICH TO DISTRIBUTE METRE QUADRATS WITHIN EACH TIDAL ZONE.

higher frequency of tidal submergences and shorter periods of continuous emersion than at any time. A much neglected aspect of the biology of the lower marsh plants is their ability to germinate and anchor themselves in the soil in between tidal washings. The tides most probably wash out any seedlings which have failed to establish themselves in between successive submergences. The majority of higher plant pioneer species on salt marshes in this country, before the advent of Spartina anglica, were annuals such as Salicornia sp. and Suaeda maritima, whose downward spread may vary from year to year with variations in the extent of tidal flooding. This aspect of the establishment of Aster is described in Chapter 9.

A study of Fig. VI.3 further reveals that the longest periods of continuous emersion above the critical level are coincident with the warm months of May, June and August. During these periods a number of days of direct sunlight and low humidity may lead, through surface evaporation from the soil, to a considerable increase in the concentration of salts in the soil water. This must have an adverse effect - for example wilting and death of large plants of Aster tripolium on well drained 'upper' marshes is a common sight on fine days during the summer months. The highest soil salinity values on salt marshes have been recorded from such marshes. Holmes (1960) has recorded values up to twice seawater salinity in the mid marsh area at Tetney Haven. On the other hand the frequently inundated lower marsh levels rarely develop salinities higher than that of the tidal water flushing them (Chapman 1964, Ranwell, personal communication 1964).

Thus further differences in the tidal regimes of the marshes above and below the 'critical level' may be recognised. These are listed in Table 3.2 under the headings 'Type A' and 'Type B' marsh. The division of salt marshes into upper and lower categories on the basis of a critical level dividing areas experiencing markedly different degrees of non-tidal emersion may well be reinforced by the coincidence of decreased periods of continuous emersion with seedling establishment, and of increased periods of such emersion and dry conditions with the major period of vegetative growth prior to flowering.

It would be of great interest to discover whether the categorisation applied to the marshes examined in this study is a satisfactory basis for the universal division of all British salt marshes. Chapman's work on Norfolk salt marshes (particularly Chapman (1938) and Chapman in Steers (1960)) led him to recognise two types of marsh, which he called 'upper' and 'lower', which exist under rather different conditions. He found that twelve higher plant species occured almost exclusively on upper marshes and another twelve almost exclusively on lower marshes whereas only six were found on both (these included Aster tripolium). A similar ratio was observed for algal species. He suggested that the downward spread of species normally found on the upper marshes was limited by the increasing number of tidal submergences, while the upward spread of lower marsh species was limited by the increasing degree of exposure (= emersion). More recently Hinde (1954), in relating the distribution of plants to tide levels, has grouped a series of Californian salt marshes into upper and lower categories. Adams' scheme of zonation in Nth. Carolina salt marshes, a division into upper and lower zones, is also based on tide-elevation influences (Adams 1963).

As Chapman has suggested (Chapman 1960) such divisions may well be universal features of maritime salt marshes where tidal patterns of the type described above are operative. In such a case it is suggested in the present work that the demarcation line between the two will be at or about a 'critical level' as recognised above. The position of such a level will vary in relation to mean sea level depending on the mean tidal range and on local tidal phenomena and will be modified by subsidiary factors of drainage, water table, substrate, and so on, which may tend to blur or sharpen the line of demarcation.

Local conditions may tend to obscure such divisions, for example the presence of microseres on the edges of drainage creeks will nodoubt confuse the general pattern. In estuarine marshes the position of the marsh in relation to the estuarine gradient will be important. Despite this it has been possible to recognise, in specific areas, a division of the main salt marsh communities into at least two types. This recognition of a critical level in some areas separating marshes existing under markedly different tidal regimes has been the basis of a categorisation (into type 'A' and type 'B') of the populations studied during this investigation.

It should be pointed out that the marsh types I have finally distinguished (i.e. high, mid and low - see Chapter 3) relate in the following way to the universally accepted scheme of intertidal zone terminology devised by the Stephensons (Stephenson and Stephenson (1949), especially Fig. 3. p. 299); the low and mid marshes are contained by the upper part of the midlittoral zone and the supralittoral fringe, and the high marshes are high in the supralittoral zone. The lower midlittoral and infralittoral zones are rarely colonised by higher plants on salt marshes and, apart from marine algae, and in some areas <u>Zostera</u> species, are often devoid of vegetation.

APPENDIX VII

BREEDING PROGRAMME TO DETERMINE THE MODE OF INHERITANCE OF THE RAY FLORET CHARACTER

TABLE 1. List of plants (in order of culture number) showing crosses made.

Plants for the original crosses were taken from three populations in N. Lincolnshire, the old marsh at Tetney Haven (T) a pure stand of rayless plants at North Cotes (N) and a pure stand of rayed plants near Humberstone (H). They were allocated a code number as follows:- Area: date (of Sept. 1963): no. of head in order of operation on day: code letter of plant (e.g. H.15 3.L).

Key. R = Rayed plant D = rayless plant.

Table 2, which follows, is in 4 sections A - C. The final column of this Table lists the section and experiment no.

VII: Table 1.

Plant	description	operation	date	fruit collected	to produce	no. plants grown to maturity	no. plants scored	continued as	for Table 2 Sect.	Expt.
N.14.1.H	D	XD(T)	Sep.1963	+	not continued.					
N.14.2.H.	D	XD(T)	"	+	F1	9	9	65/1	C	8
N.14.5.H	D	XD(T)	"	+	not continued					
N.14.10.K	D	XR(H)	"	+	F1	7	7	66/41	A	1
N.14.11.K	D	XR(H)	"	+	F1	1	1	66/39	A	2
N.14.12.K	D	XR(H)	"	+	F1	37	26	65/4	A	3
T.15.1.L	R	XD(T)	"	+	F1	10	10	Fruits mixed at sowing - not continued	B	4
T.15.2.L	R	XD(T)	"	+						
T.15.4.M	R	XD(T)	"	+						
T.15.5.M	R	XD(T)	"	+						
H.15.9.N	R	XR(T)	"	+						
H.16.1.P	R	XR(T)	"	+	F1	8	8	Fruits mixed at sowing- not continued.	D	13
H.16.4.P	R	XR(T)	"	+						

continued......

VII. Table 1 (cont)

Plant	description	operation	date	fruit collected.	to produce.	no. plants grown to maturity	no. plants scored	continued as.	for Table 2. sect.	expt.
65/1/1	F_1(DXD)	selfed	Aug1965	+	F_2 fruits sown 25/4/66 no germination.					
65/1/2	F_1(DXD)	selfed	Sep1965	+	F_2 " " " " "					
65/1/5	F_1(DXD	selfed	"	+	F_2 lost. (bag washed off in rain)					
65/4/1	F_1(DXR)	selfed	"	+	F_2	1	1		A	3
65/4/2	F_1(DXR)	selfed	"	+	F_2	10	7	66/40 67/19	A	3
65/4/3	F_1(DXR)	selfed	"	+	F_2	1	1	!	A	3
65/4/4	F_1(DXR)	XD(N.14. 12.K)	"	+	test cross	2	2	—	A	3
65/4/6	F_1(DXR)	XD(65/1/1)	"	+	test cross.fruits sown 14/12/65 no germination					
65/4/11	F_1(DXR)	XD(N.14. 12.K)	"	+	test cross	2	1	—	A	3
65/4/12	F_1(DXR)	XR(H.15.T.L)	"	+	test cross	7	plants died.			
"	"	emasculated		-	not apomictic					
65/4/13	F_1(DXR)	selfed	"	+	F_2	1	1	—	A	3
65/4/17	F_1(DXR)	selfed	"	+	F_2	2	1	—	A	3
65/4/18	F_1(DXR)	selfed	"	+	F_2	1	plant died			
65/4/19	F_1(DXR)	selfed	"	+	F_2	1	1	66/9	A	3
65/4/20	F_1(DXR)	selfed	"	+	F_2	3	plants lost			
65/4/21	F_1(DXR)	selfed	"	+	F_2	3	3	66/5	A	3

Continued......

VII Table 1 (cont.)

Plant	description	operation	date	fruit collected.	to produce.	no. plants grown to maturity	no. plants scored	continued as.	for Table 2.	
									sect.	expt.
65/4/24	F_1(DXR)	selfed	Sep1965.	+	F_2	3	1	66/8	A	3
65/4/25	F_1(DXR)	selfed	"	-	F_2	poor fruit formed				
65/4/26	F_1(DXR)	selfed	"	-	F_2	poor fruit formed				
65/4/27	F_1(DXR)	selfed	"	+	F_2	1	1	66/12	A	3
65/4/28	F_1(DXR)	selfed	"	+	F_2	1	plant died			
65/4/29	F_1(DXR)	emasc.	"	-	not apomictic					
65/4/32	F_1(DXR)	selfed	"	+	F_2	9	4	66/4	A	3
65/4/36	F_1(DXR)	selfed	"	+	F_2	3	0			
65/4/37	F_1(DXR)	selfed	"	+	F_2	1	0	66/13	A	3
65/9/1	R	XD(65/14/1)	"	+	F_1	2	2	66/1	B	5
"	R	emasc.	"	-	rays not apomictic					
65/10/1	D	selfed	"	+	Dself	2	1	____	C	9
65/14/1	D	selfed	"	+	D self	1	1	66/2	C	10
65/15/1	D	selfed	"	+	D self	1	1	66/3	C	11
65/16/1	FimbriateR.	XD(65/23/1)	"	+	F_1	1	1	66/11	B	6
"	"	selfed	"	+	fimb. R self	3	1	66/10	D	14
65/22/3	R	selfed	"	+	R self	15	8	66/6	D	15
65/23/1	D	selfed	"	+	D self	3	2	66/7	C	12
65/40/2	R	emasc.	"	-	not apomictic					

Continued.........

VII. Table I (cont.)

Plant	description	operation	date	fruit collected.	to produce.	no. plants grown to maturity	no. plants scored	continued as.	for Table 2.	
									sect.	expt.
65/46A/2	R	XR(65/48A)	Sep1966		F_1 R self	1	0	not continued		
65/46A/3	R	"	"			3	0	not continued		
65/46A/5	R	"	"	-	poor fruit formed.					
66/1/2	F_1(RXD)	selfed	Aug1966	+	F_2	5	4	—	B	5
66/2/1	F_1(DXD)	selfed	Sep1967	+	F_2	1	0	—	C	10
66/3/1	F_1(DXD)	selfed	Sep1967	+	F_2	2	0		C	11
66/4/1	F_2(DXR)	selfed	Oct1967	+	F_3	2	0	—	A	3
66/4/3	F_2(DXR)	selfed	"	+	F_3	3	0	—	A	3
66/5/2	F_2(DXR)	selfed	"	+	F_3	1	0	—	A	3
66/6/1	F_1(R self) XD(65/45/8)		"	+	F_1(RXD)	1	1	—	B	7
66/6/6	"	selfed	"	+	F_2	5	0	—	D	15
66/7/1	from self D	selfed	Sep1967	+	pure line	1	0	—	C	12
66/8/1	F_2(DXR)	selfed	Oct1967	+	F_3	2	1	—	A	3
66/9/1	F_2(DXR)	selfed	"	+	F_3	13	0	—	A	3
66/10/1	from fimd. self	selfed	"	+	poor fruit none germinated to date.					
66/11/1	F_1(FRXD)	selfed	"	-						
66/12/1	F_2(DXR)	selfed	"	+	F_3	5	0	—	A	3

Continued.

VII. Table 1. (cont.).

Plant	description	operation	date	fruit collected.	to produce.	no. plants grown to maturity	no plants scored	continued as.	for Table 2. sect.	expt.
66/13/1	F_2(DXR)	selfed	"	+	F_3	1	0	—	A	3
66/22A/7	R	XR(66/22/2)	Oct1967	+	F_1	10	0	—		
66/22A/9	R	XD(66(19(9)	"	+	F_1	10	0	—		
66/39/1	F_1(DXR)	selfed	Nov1967	+	F_2	2	0	—	A	2
66/40/1	F_2(DXR)	selfed	"	+	F_3	1	0		A	3
66/41/3	F_1(DXR)	selfed	"	+	F_2	1	0		A	1
67/1/1	R(var. pannon)	XD(66/21/2)	Sep1967	+	F_1	10	0	—		
67/1/2	R "	XD(66/21/5	"	+	F_1	10	0	—		
67/3/1 to 24	F_1(RXR)	to be selfed		+						
67/4/1 to 5	F_1(RXD)	to be selfed								
67/5/1-10	F_1(RXR)	to be selfed								
67/19/1	F_2(DXR)	selfed	Sep1967	+	F_3	2	0	—		

TABLE 2

NUMBER OF RAY FLORETS IN PLANTS PRODUCED BY CONTROLLED CROSSES.

Section A. Rayless (ovules) Xrayed (pollen).

✓ indicates mean of first 15 heads counted in earlier experiment.

Expt. 1. Parents :- N.14.10.K (rayless) x rayed (H) (mean ray number 16).

F1		mean	range
(1)	1.3.0.2.5.2.3.0.0.6.4.3.2.4.	2	0 - 6
(2)	11.1.1.2.3.1.9.7.6.5.4.	5	1 -11
(3)	11.2.4.2.1.3.4.15	4	1 -15
(4)	5.3.7.10.1.1.5.7.7.8.2.1.4.6.6. ✓	5	1 -10
(5)	12.10.7.8.8.8.4.7.8.9.11.3.9.16.0. ✓	8	0 -16
(6)	5.4.3.	4	3 - 5
(7)	7.7.6.12.0.1.9.0.1.11.7.5.0.10.8. ✓	6	0 -12

Plant (3) selfed not in flower. (1 plant 66/41).

Expt. 2. Parents :- N.14.11.K (rayless x rayed (H) (mean 16).

F1			
(1)	o.1.11.8.7.2.6.11.3.1.0.0.	6	0 -11

Selfed - F2 not in flower. (1 plant 66/39).

Expt. 3. Parents :- N.14.12.K (rayless) x rayed (H) (mean 16).

F1				
65/4	(1)	5.4.8.1.8.4.20.14.13.12.14	9	1 -20
"	(2)	1.8.5.7.4.8.5.8.3.4.6.1.2.4.6. ✓	5	1 - 8
"	(3)	17.15.15.18.15.23.15.16.19.18.21.	17	15 -21
	(4)	8.5.13.5.5.5.5.	6	5 -13

Table 2 cont.

		mean	range
	(6) 0.1.0.0.0.0.0.1.0.	0	0 - 1
	(11) 2.0.2.8.4.2.8.4.2.2.0.	3	0 - 8
	(12) 9.6.12.4.5.11.1.2.3.4.1.0.0.1.4. ✓	4	0 -12
	(13) 13.8.11	11	8 -13
	(14) 7.7.9.3.12	7	3 -12
	(15) 17.12.18.15.17.17.16	16	12 -18
	(16) 12.6.7.	8	6 -12
	(17) 18.14.17.15	16	15 -18
	(18) 13.14.13.13.12.12	13	12 -14
	(19) 12.7.7.	9	7 -12
	(20) 8.7.9.11.13.8.6.13.11.8.9.	9	6 -13
	(21) 4.4.6.3.	4	3 - 6
	(24) 5.8.1.10.2.2.18.12.14.15.14	9	1 -18
	(25) 12.12.	12	12
	(26) 10.5.10.0.6.4.6.	5	0 -10
	(27) 0.4.1.0.3.7.	5	0 - 7
	(28) 13.	13	13
	(29) 14.0.10.4.10.9.12.8.7.16.7.5.8.0.6.10.	8	0 -16
	(30) 0.1.3.1.2.4.1.15.9	4	0 -15
	(32) 3.5.4.4.	4	3 - 5
	(36) 11.2.8.7.12.9.4.5.11.8.11.8.13.4.8. ✓	8	2 -13
	(37) 6.5.2.7.	5	2 - 7
<u>F2</u>:-	(1) selfed. (a) 9.2.13.5.6.12.	7	2 -13
F1 (2) Selfed:-			
	(a) o.1.0.0.0.0.0.0.2.	0	0 - 2
	(b) 25.20.19.	21	19 -25
	(c) 12.13.13.20.14.13.6.	13	6 -20
	(d) 0.0.0.0.0.0.0.1.0.0.0.0.0.0.0.0.0. ✓	0	0 - 1
	(f) 0.0.2.	1	0 - 2
	(h) 16.15.17.10.19.18.17.12.18.16.18	16	10 -19
	(i) 18.1.7.4.13.2.5.8.	7	1 -18

Table 2 cont.	mean	range
F_2 (Expt. 3 cont.):-		
F1 (3) selfed:-		
(a) 17.13.12	13	12 -17
F1 (13) selfed:-		
(a) 2.0.3.	2	0 - 3
F1 (19) selfed:-		
(a) 4.5.1.3.4.5.5.3.4.3.6.5.3.12.5.	5	1 -12
F1 (21) selfed:-		
(a) 12.12.13.12.	12	12 -13
(b) 4.5.7.6.1.11.2.3.1.9.5.6.7.1.	5	1 -11
F1 (24) selfed:-		
(a) 20.18.16.18.21.13.	16	13 -21
F1 (27) selfed:-		
(a) 0.0.0.0.0.0.0.0.0.1.2.0.5.	1	0 - 5
F1 (32) selfed:-		
(66/8/1)		
(a) 12.7.5.1.3.	6	1 -12
(b) 4.5.0.6.2.1.8.1.	3	0 - 8
(d) 0.0.0.0.	0	0
(e) 16.12.13.15.	14	12 -16
F3 (24) (a) selfed:-	3	0 -11
(a) 6.4.5.5.4.11.6.1.2.6.7.5.1.2.1.8.2.1.4. 2.2.0.3.1.0.4.2.5.4.6.2.0.6.6.2.4.4.5.4.8.1. 0.1.2.0.3.2.4.3.6.2.3.2.4.1.1.2.3.4.1.2.1.5. 5.7.3.1.1.2.0.0.0.0.		
Test Cross (4) x rayless parent N14.12.K		
(i) o.0.0.0.0.1.0.0.0.0.0.0.0.0.0.	0	0 - 1
(II) x rayless parent N14.12.K		
(i) 7.1.3.	4	1 - 7
(ii) 12.8.4.17.11.6.	10	4 -17

Section B. Rayed (ovules) X rayless (pollen).

Expt. 4. Parents:- N14.1.L
N15.2.L (Rayed mean 16 rays) x rayless
N15.4.M (T). Fruit mixed on sowing.
N15.5.M

Mixed F_1		Mean	range
(1)	8.0.1.0.2.8.1.1.21.8.2.0.17.4.	4	0 -21
(2)	10.2.4.1.1.2.0.10.12.15.3.1.1.1.4.	4	0 -15
(3)	6.5.4.2.1.0.3.5.4.8.1.7.9.5.5.	5	0 - 9
(4)	9.1.0.15.1.3.1.2.4.	4	0 -15
(5)	0.0.2.5.4.3.0.1.10.0.0.4.7.2.6.	3	0 -10
(6)	9.3.13.8.8.5.4.9.12.11.11.7.8.2.11.	8	2 -13
(7)	10.13.17.12.8.2.8.9.16.1.14.2.4.11.5.	10	1 -17
(8)	0.2.0.0.8.4.0.6.8.0.1.0.0.3.8.4.	3	0 - 8
(9)	0.11.1.8.11.7.6.2.0.3.1.0.	6	0 -11
(10)	12.7.11.4.4.5.8.13.2.3.20.1.13.2.7.	7	1 -20

Expt. 5. Parents:- rayed
65/9/1 17 - 20 rays X rayless (65/14/1)

F_1:-	(66/1)	2	0 - 8
(1)	4.1.1.0.3.4.5.0.1.2.3.3.1.1.1.1.2.2.1.0. 4.1.0.3.1.8.1.3.1.2.2.2.0.3.2.1.0.0.1.4.8.7. 0.0.4.8.3.5.6. (50)		
(2)	8.7.2.12.13.14.7.8.5.13.6.15.9.3.6.8.11. 7.3.14.7.7.7.12.15.7.10.7.11.8.15.11.8. 11.13.12.6.15.10.4.7.13.8.11.8. (45)	9	2 -15

F_2:-

F_1/ (2) selfed.

(a)	14.18.15.9.18.14.10.19.20.17.19.18.16. 18.18.14.16.14.16.21.16.13.17.14.18.20. 20.18.17.18.18.20.18.17.16. (35)	17	9 -21

(b) 14 heads with 1 ray, 1 head with 2 rays,

F_2 cont. (b) mean range

41 heads 0 rays (56) 0 0 - 2

(c) 0.3.3.4.2.7.2.4.9.9.2.3.2.0.1.2.2. 3 0
4.2.2.2.0.15.3.8.14.0.0.3.1.3.3.9.
0.2.0.1.3.0.1.0.0.3.5.2.8.0.5.1.15.
3.4.3.2.0.0.2.3.2.1.0.13.2.9.6.6.2.1.2.3.
0.1.7.0.3.0.0.1.0.3.5.2.3.9.9.2.4.8.0.2.
1.1.1.1.0.0.0.0.0.0.0.0.1.7.1.12.0.0.5.
1.1.1.2.0.4.1.0.1.3.0.7.3.0.0.0.3.0.0.2.1.
2.2.3.0.0.0.2.2.0.4.0.1.2.3.0.2.3.5.0.2. (151)

(d) 59 heads all 0. 0 0

Expt. 6. Parents :- 'Fimbriate' rayed.
(65/16/1) 17 - 20 rays x rayless 65/23/1 (Nth. Cotes).
(Not known if all fimbriate).

F_1:- no. of fimbriate rays/head indicated in brackets.

(1) 8(4) 3(2) 12(3) 17(0) 1(1) 3(0) 15(1)
4(0) 12(4) 12(7) 16(1) 15(0) 14(5) 5(3)
14(7) 11(2) 10(3) 15(6) 14(5) 13(8) 3(2)
7(2) 8(2) 11(5) 8(2) 12(3) 6(2) 3(0) 10(5) mean range
6(1) 13(4). (31 heads) 10(3) 1(0) -17(8)
301 rays
90 fimb. about 30% fimb.

Expt. 7. Parents rayed. 66/6/1 x rayless 65/45/8
Mean 15. range 6-19 Bch. Pt.
(Tetney)

F_1

(i) 24 heads rayless - 26 heads 1 ray - 10 heads 2 rays -
10 heads 3 rays- 5 heads 4 rays - 4 heads 5 rays -
2 heads 3 rays - 1 head 9 rays - 1 head 10 rays (total
83 hd's) 151 rays.
mean 2. range 0-10

Section C. rayless x rayless

Expt. 8. Parents :- rayless N.14.2.H x rayless (T)

F1

		mean	range
(1)	28 heads all 0.	0	0
(2)	43 heads 0, 1.2.	0	0 - 2
(3)	17 heads 0, 1	0	0 - 1
(4)	16 heads 0, 1.3.2.1.	0	0 - 3
(5)	22 heads 0, 1	0	0 - 1
(6)	18 heads 0, 1	0	0 - 1
(7)	22 heads 0, 2.2.	0	0 - 2
(8)	6 heads all 0.	0	0
(9)	37 heads all 0.	0	0

Expt. 9. Parents :- rayless x selfed. (65/10/1).

(1)	53 heads 0, 7 heads 1.	0	0 - 1

Expt. 10. Parents :- rayless x selfed. (65/14/1).

(1)	89 heads 0 rays 1.2.2.1.	0	0 - 2

Expt. 11. Parents :- rayless x selfed. (65/15/1).

(1)	116 heads all 0.	0	0

Expt. 12. Parents :- rayless x selfed (65/23/1).

66/7	(1)	24 heads all 0.	0	0
	(2)	127 heads all 0.	0	0

Section D. Rayed x rayed

Expt. 13. Parents H15.9.N
H16.1.P x rayed (T) mean 16.
H16.4.P

F1

(1)	4.15.5.4.16.4.13.6.5.14.	9	4 -16

Expt. 13 cont.

		mean	range
(2)	14.16.17.	16	14-17
(3)	3.6.9.3.8.8.13.9.9.7.8.11.11.5.10	8	3-13
(4)	1.2.0.4.10.0.2.14.7.8.10.4.3.3.15	7	0-15
(5)	9.12.10.10.12.15.12.9.17.10.12.10. 8.9.10.	12	8-17
(6)	17.8.12.11.9.12.8.21.19.10.20.11.12. 10.9.11.18.	12	8-21
(7)	17.4.13.7.11.12.13.16.20.11.12.10.9. 11.18.	12	7-20
(8)	5.11.0.6.7.16.8.7.12.10.9.10.4.0.14.	8	0-16

Expt. 14.

Fimbriate ray
65/16/1
(17-21)

x self

Fimbriate rays indicated in brackets.

(1)	(1) 0 0 (3) 0 0 1 (1) 0 0 0 0 0	0	0- 3

Expt. 15. Rayed plant x self

65/22/3
(m18 r 12-23)

(Seperate flowering stems
in brackets).

66/6 (1) (14.8.6.10.16.12.10.19.16.19.19.15.9.19.15.16.17.19.12.19.16.16.12.)(7.6.4.10.2.6.7.7.10.10.4.10.10.4.9.8.12.7.11.15.10.5.9.14.6.14.10.12).

(mean 15 range 6-19) (mean 8 range 2-15).

(3) 10 heads 0 2.2.1.1. mean 0. range 0-2.

(4) (0.0.7.9.0.0.0.1.8.0.0.1.8.7.4.3.0.0.2.) (7.10.13.12.5.14.14.4.5.7.14.11.12.14.8.12.12 13.9.13.10.13.11)

(mean 3 range 0-9) (mean 11 range 5-14)

(5) 6.6.3.4.9.10.12.4.5.6. mean 6 range 3-12.

Expt. 15 cont.

(6) (5.17.14.3.6.8.17.17.10.10.16.9.2.17.9.11.8.4.5.17.
6.4.12.10.11.6.12.9.18.6.6.13.9.5.15.20.6.6.16.15.
15.15.6.12.15.19.11.12.13.12.15).
(16.7.12.12.8.11.21.11.14.11.9.8.5.13.8.3.)
(mean 11. range 2-20) (mean 11 range 3-21)
(8) (0.1.0.0.1.3.0.)(2.3.2.6.1.2.8.2.1.0.1.0.)
(mean 1 range 0-3) (mean 2 range 0-8)
(9) (4.1.1.0.3.4.)(5.0.1.2.3.3.1.1.1.1.2.2.1,0.4.1.0.3.1.
8.1.3.1.2.2.2.0.3.2.1.0.0.1.4.8.7.0.0.4.8.3.5.6.)
(mean 2 range 0-4) (mean 2 range 0-8)
(11) 1.1.0.5.2.5. mean 2 range 0-5.

APPENDIX VIII

A SIMPLE MODEL OF POPULATION POTENTIAL GROWTH RATE IN A COLONISING SITUATION

This is a method adapted from that of Blower (1968) and described in Blower and Gabbutt (1964) in a study of rates of increase in populations of millipedes. The model, an extension of the work of Birch (1948) and Cole (1954), considers the effect of replacement rate, age at first brood, and the number of broods in successive years on the intrinsic rate of natural increase. Adapting this method to <u>Aster</u> populations, the following parameters will be used; b - the replacement rate (the number of plants which survive to produce fruit), - the age, in years at first flowering, and x - the number of years in which each plant flowers. The intrinsic rates of natural increase can be calculated* for various life cycle types in a situation where no selection occurs. The life cycle types can be coded by the expression $b/\alpha/x$, thus:- 10/1/1 is a hapaxanthic annual producing 10 surviving

---

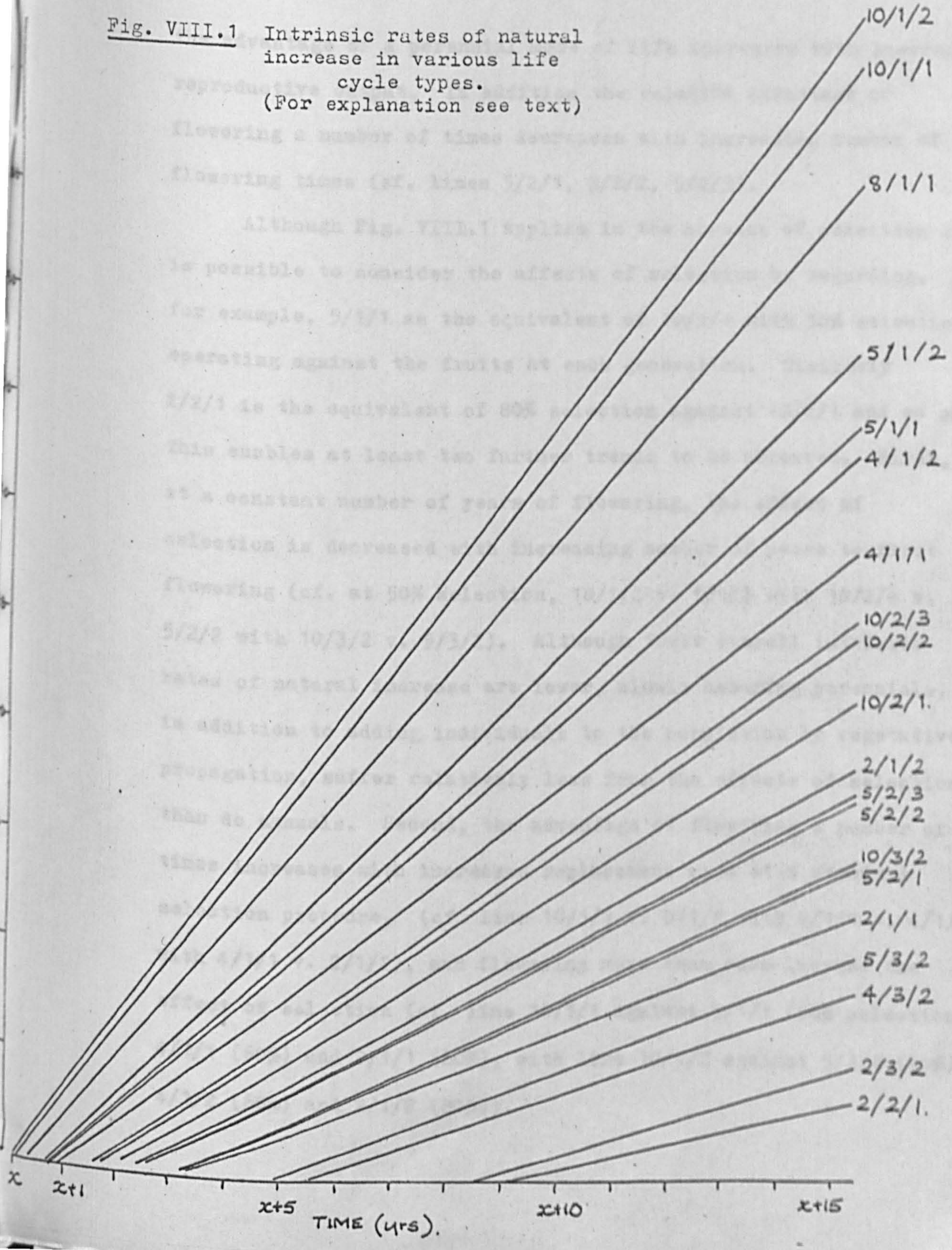
* any term 'n' in the series is obtained by adding together the number of preceding terms equal to the number of flowering times and separated from 'n' by the same number of terms as the number of years taken to flower minus one. The result is then multiplied by the assumed replacement rate. Thus for a plant which has a replacement rate of 1, takes 2 years to flower and flowers 3 times (1/2/3). The series is:-

$$\underbrace{1,1,2},2,\underset{\uparrow}{4},5,\underbrace{8,11,17},24,\underset{\uparrow}{36},52,\ \ldots\ldots\ldots\ldots$$

fruits in the first year, 5/3/2 is a perennial flowering for the first time in its third year, flowering twice and producing 5 surviving fruits at each flowering; and so on. The various rate of increase for a number of types are given in Fig. VIII.1.

This model, although simple and taking no account of selection or of vegetative propagation of individuals, does illustrate some of the effects of variation in reproductive output, year to first flowering and perenniality on an annual to short-lived perennial such as <u>Aster</u> in a colonising situation. (In reality most populations probably remain constant in size over a long period and thus the intrinsic rate of increase is never realised). First it can be seen that, axiomatically, lowered fruit production is offset by flowering in the first year (cf. all 5/1 and 4/1 lines with 10/2 lines and 2/1/2 with 10/3/2) and thus rapid colonisation of a niche is better achieved, in the absence of selection and ignoring the effect of gene flow, by first year flowerers i.e. under equal fruit production annuals exploit a niche more quickly than second-year flowering perennials. Second, it can be seen that the relative advantage of flowering in the first year increases with increased replacement rate (of lines 10/1/1 v. 10/2/1, 5/1/1 v. 5/2/1 and 2/1/1 v. 2/2/1), early flowering being especially important where reproductive output is high. Third, the advantage of flowering a number of times (increasing 'x') decreases with increased replacement rate (cf. lines 10/1/2 v. 10/1/1 with 5/1/2 v. 5/1/1 with 4/1/2 v. 4/1/1 with 2/1/2 v. 2/1/1). Thus, conversely,

Fig. VIII.1 Intrinsic rates of natural increase in various life cycle types. (For explanation see text)



the advantage of a perennial mode of life increases with lowered reproductive output. In addition the relative advantage of flowering a number of times decreases with increasing number of flowering times (cf. lines 5/2/1, 5/2/2, 5/2/3).

Although Fig. VIII.1 applies in the absence of selection it is possible to consider the affects of selection by regarding, for example, 5/1/1 as the equivalent of 10/1/1 with 50% selection operating against the fruits at each generation. Similarly 2/2/1 is the equivalent of 80% selection against 10/2/1 and so on. This enables at least two further trends to be observed. First, at a constant number of years of flowering, the effect of selection is decreased with increasing number of years to first flowering (cf. at 50% selection, 10/1/2 v. 5/1/2 with 10/2/2 v. 5/2/2 with 10/3/2 v. 5/3/2). Although their overall intrinsic rates of natural increase are lower, slowly maturing perennials, in addition to adding individuals to the population by vegetative propagation, suffer relatively less from the effects of selection than do annuals. Second, the advantage of flowering a number of times increases with increased replacement rate at a standard selection pressure, (cf. line 10/1/1 v. 5/1/2 with 8/1/1 v. 4/1/2 with 4/1/1 v. 2/1/2), and flowering more than once lessens the effect of selection (cf. line 10/1/1 against 5/1/1 (50% selection) 4/1/1 (60%) and 2/1/1 (80%), with line 10/1/2 against 5/1/2 (50%) 4/1/2 (60%) and 2/1/2 (80%)).

Adams, D. A. (1963) Factors Influencing Vascular Plant Zonation in North Carolina Salt Marshes. *Ecology* 44 : 445-456.

Admiralty Tide Tables (1967) European Waters, Admiralty, London.

Adriani, E. D. (1945) Sur la Phytosociologie, la Synecologie et le bilan d'eau de Halophytes de la Mediterranee francaise. *S.I.G.M.A.* 88 : 1-217.

Anderson, E. (1929) Variation in *Aster anomalus*. *Ann. Mo. Bot. Gard.* 16 : 129-144.

Antonovics, J. (1968a) Evolution in closely adjacent Plant populations V. Evolution of self-fertility. *Heredity Lond.* 23 : 219-238.

Antonovics J. (1968b) Evolution in closely adjacent plant populations VI. Manifold Effects of Gene Flow. *Heredity Lond.* 23 : 507-524.

Aston, J. L. and Bradshaw, A. D. (1966) Evolution in closely adjacent plant populations II. *Agrostis stolonifera* in maritime habitats. *Heredity, Lond.* 21 : 649-664.

Avers, C. J. (1953) Biosystematic studies in Aster. II Isolating mechanisms and some phylogenetic considerations. *Evolution, Lancaster Pa.* 7 : 317.

Babcock, E. B. (1947) The Genus Crepis. Part One : The Taxonomy, Phylogeny and Evolution of Crepis. *Univ. Calif. Publ. Bot.* 21.

Baker, H. G. (1951) Hybridisation and Natural Gene-Flow Between Higher Plants. *Biol. Rev.* 26 : 302-337.

Baker, H. G. (1953) Race formation and reproductive method in Flowering Plants. *Symp. Soc. exp.Biol.* 7 : 114-145.

Baker H. G. (1953a) Dimorphism and Monomorphism in the Plumbaginaceae. III The Genus *Limonium* *Ann. Bot. N.S.* 17 : 433-445.

Baker, H. G. (1954) Abstract in *J. Ecol.* 42 : 571.

Baker, H. G. (1955) Self-Compatibility and Establishment after "Long-Distance" Dispersal. *Evolution Lancaster Pa* 9 : 347-349.

Baker, H. G. (1959) Reproductive Methods as Factors in Speciation in Flowering Plants. *Cold. Spring Harb. Symp. Quant. Biol.* 24 : 177-191.

Bakker, D. (1960a) A comparative life-history study of *Cirsium arvense* (L) Scop. and *Tussilago farfara L.* the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee in Harper J. L. (ed) The Biology of Weeds. Oxford : 205-222.

Bakker, D. (1960b) Senecio congestus (R.Br.) DC. in the Lake Yssel polders. Act. Bot. Neerl. 9 : 235-259.

Bakker, D., Jonker, J. J. and Smits, H. (1960) Land reclamation in Holland. Shell Public Health and Agricultural News 3 : 143-151.

Bakker, D. Borg. S. J., Ter, and Otzen, D. (1966) Ecological Research at the Plant ecology Laboratory, State University, Groningen. Wentia 15 : 1-24.

Ball, P. W. (1960) The experimental taxonomy of Salicornia. Ph.D. Thesis, University of Leicester.

Ball, P. W. and Brown, K. G. (1970) A Biosystematic and Ecological Study of Salicornia in the Dee Estuary. Watsonia, 8 ; 27-40.

Bange, G. G. J. and van Vliet, E. (1961) Traslocation of Potassium and Sodium in intact Maize seedlings. Pl. Soil 15 : 312.

Barnes, F. A. and King, C. A. M. (1951) A preliminary survey at Gibraltar Point, Lincolnshire. Rep.Bird.obs. and Field Res. Sta. Gib.Pt. Lincs. (1951) : 41-59.

Barnes, F. A. and King, C. A. M. (1955) Beach changes in Lincolnshire since the 1953 storm surge. E. Midl.Geogr. 4 : 18-28.

Barnes, F. A. and King, C. A. M. (1957) The Spit at Gibraltar Point, Lincolnshire. E.Midl. Geogr. 8 : 22-31.

Barnes, F. A. and King, C. A. M. (1961) Salt marsh development at Gibraltar Point, Lincolnshire. E.Midl.Geogr. 15:20-31.

Barton, L. V. (1965) Seed dormancy : general survey of dormancy types in seeds, and dormancy imposed by external agents. Encyc. Plant Physiology. 15 : 699-720.

Battaglia, B. (1958a) 'Balanced polymorphism in Tisbe reticulata, a marine copepod'. Evolution Lancaster pa. 12 : 358-368.

Battaglia, B. (1958b) Ecological differentiation and incipient intraspecific isolation in marine Copepods. Ann.Biol. 33 : 259-268.

Baumeister, W. and Schmidt, L. (1962) Über die Rolle des Natriums im pflanzlichen Stoff wechsel. Flora.Allg.Bot.Zeitung. 152 : 24-56.

Berg, R. L. (1959) A general evolutionary principle underlying the origin of developmental homeostasis. Am.Nat. 93 : 103-105.

Bernstein L. and Hayward, H. E. (1958) Physiology of Salt Tolerance. A.Rev.Pl.Physiol. 9 : 25-46.

Bertolani-Marchetti, D. (1953) Il Popolamento vegetale Nelle Stazioni Salse delle valle Padini. Webbia 9 : 511-622.

Binet, P. (1965) Action de la temperature et de la Salinite sur la germination des graines de Cochlearia anglica L. Rev.Gen. Bot. 72 : 221-236.

Birch, L. C. (1948) The intrinsic rate of increase of a population of insects. J.anim. Ecol. 17 : 15-26.

Black, J. N. (1958) Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterranean L.) with particular reference to leaf area and light microclimate. Aust.J.agric.Res. 9 : 299-318.

Black, J. N. (1960) The significance of petiole length, leaf area and light interception in competition between strains of subterranean clover (Trifolium subterranean L.) grown in swards. Aust. J. agric.Res. 11 : 277-291.

Black, R. F. (1960) Effects of NaCl on the ion uptake and growth of Atriplex vesicaria Heward. Aust.J.biol.Sci. 13 : 249-66.

Blower, J. G. (1968) The age structure of millipede populations in relation to activity and dispersion. In The Soil Ecosystem Publication No.8. London, Systematics Association.

Blower, J. G. and Gabbutt, D. D. (1964) Studies in the millipedes of a Devon Oak wood. Proc.Zool.Soc.Lond. 143 : 143-176.

Bocher, T. W. (1949) Racial divergencies in Prunella vulgaris in relation to habitat and climate. New Phytol. 48 : 285-324.

Bocher, T. W. (1963) The study of ecotypical variation in relation to experimental morphology. Regnum vegetabile 27. Symposium on Biosystematics. Montreal.

Bocher, T. W., Larsen, K, and Rhan, K., (1955) Experimental and Cytological studies on plant species. II. Trifolium arvense and and some other pauciennial herbs. Dan. Biol.Skr. 8 : 3-31.

Bollard, E. G. and Butler G. W. (1966) Mineral nutrition of plants. A.Rev.Pl.Physiol 17 : 77-112.

Boorman, L. A. (1966) Experimental studies in the genus Limonium D.Phil.Thesis, University of Oxford.

Boorman, L. A. (1968) Some aspects of the reproductive biology of Limonium vulgare and L. humile. Ann.Bot.(N.S.) 32 : 803-824.

Botanical Exchange Club, Reports of (1915, 1923, 1931, 1945) various notes - Authors or page refs. in text.

Bracher, R. (1929) The ecology of the Avon Banks at Bristol. J.Ecol. 17 : 35-80.

Bradshaw, A. D. (1952) Populations of Agrostis tennis resistant to lead and zinc poisoning. Nature, Lond. 169 : 1098.

Bradshaw, A. D. (1960) Population differentiation in Agrostis tennis Sibth. III Populations in varied environments. New Phytol. 59 : 92-103.

Bradshaw, A. D. (1962) The taxonomic problems of local geographical variation in plant species. Systematics Assocs. Pub. 4 : 7-16.

Bradshaw, A. D. (1965) Evolutionary Significance of Phenotypic Plasticity in Plants. Adv.Genet. 13 : 115-155.

Bradshaw, A. D., McNeilly T. S., and Gregory, R. P. G. (1965) Industrialisation, Evolution and the development of heavy metal tolerance in plants. In Goodman G. T., Edwards, R. W. and Lambert, J. M. (Eds.) Ecology and the Industrial Society. Brit.Ecol. Soc.Sympl 5 : 327-343.

Britton, C. E. (1932) The Naturalised and Alien Asters of the British plant list. Bot.Soc. and Exch.Club.Brit. Isles. 9 : 710-718.

Brouwer, R. (1965) Ion absorption and transport in plants. A.Rev.Pl. Physiol. 16 : 241-266.

Brownell, P. F. (1965) Sodium as an essential micronutrient element for a higher plant (Atriplex vesicaria) Pl.Physiol. Lancaster. 40 : 460-468.

Burchell, J. P. T. (1935) Some Pleistocene Deposits at Kirmington and Crayford. Geol.Mag. 72 : 327.

Burke, F. (1943) Occurrence of halophytes in inland Cheshire. N.W.Nat. 18 : 183-5.

Cavers, P. B. and Harper, J. L. (1964) Biological flora of the

British Isles: Rumex obtusifolius L. and R. Crispus L. J.Ecol. 52 : 737-66.

Cavers, P. B. and Harper, J. L. (1966) Germination polymorphism in Rumex crispus and Rumex obtusifolius. J.Ecol. 54 : 367-382.

Cavers, P. B. and Harper, J. L. (1967a) Studies in the dynamics of plant populations. I The fate of seed and transplants introduced into various habitats. J.Ecol. 55 : 59-72.

Cavers, P. B. and Harper, J. L. (1967b) The comparative biology of closely related species living in the same area. IX. Rumex : the nature of adaptation to a sea-shore habitat. J.Ecol. 55 : 73-82.

Chapman, V. J. (1938) Studies in salt marsh ecology. Sections I-III. J.Ecol. 26 : 144-179.

Chapman, V. J. (1939) Studies in salt marsh ecology. IV-V. J.Ecol. 27 : 160-201.

Chapman, V. J. (1940) Studies in salt marsh ecology. VI-VII. J.Ecol. 28 : 118-152.

Chapman, V. J. (1941a) Studies in salt marsh ecology. Section VIII. J.Ecol. 29 : 69-82.

Chapman, V. J. (1941b) The zonation of marine algae on the shore. Proc.Linn.Soc.Lond. 154 : 239-253.

Chapman, V. J. (1942) The new perspective in the Halophytes. Q.Rev.Biol. 17:291-311.

Chapman, V. J. (1959) Studies in salt marsh ecology. IX changes in the vegetation at Scolt Head Island. J.Ecol. 47 : 619-626.

Chapman, V. J. (1960) Salt Marshes and Salt Deserts of the World. London and New York.

Chapman, V. J. (1960a) The Plant Ecology of Scolt Head Island in Steers, J. A. (ed.) 1960. Scolt Head Island. Cambridge : 85-163.

Chapman, V. J. (1964) Coastal Vegetation. Oxford and London.

Chapman, V. J. (1966) Vegetation and Salinity, in Boyko, H. (Ed.) Salinity and aridity. The Hague : 23-42.

Chesters, C. G. C. (1951) A preliminary account of the vegetation of the foreshore from Seacroft to Gibraltar Point. Rep.Bird. Obs. and Field Res.Sta. Gib.Pt.Lincs. (1950) : 48-57

Clapham, A. R., Pearsall, W. H., and Richards, P. W. (1942)

Biological Flora of the British Isles. Aster tripolium. J.Ecol. 30 : 385-395.

Clapham, A. R., Tutin, T. G., and Warburg, E. F. (1962) Flora of the British Isles. London and New York.

Clarke, P. (1902) Note in 'Essex Naturalist', 12 : 237.

Clausen J. (1951) see Clausen (1962). Clausen J. (1962) Stages in the Evolution of Plant Species. New York.

Clausen, J., Keck, D. D., and Hiesey, W. M. (1947) Heredity of geographically and ecologically isolated races. Am.Nat. 81 : 114-133.

Clements, F. E., Weaver, J. E. and Hanson, H. C. (1929) Competition in cultivated crops. Publs. Carnegie Inst. Wash. 398 : 202-233.

Cole, C. (1954) Population consequences of life history phenomena. Q. Rev.Biol. 29 : 103-137.

Colman, J. (1933) The nature of the intertidal zonation of plants and animals. J.Mar.biol.Ass. U.K. 18 : 435-476.

Colyer, C., and Hammond, C. (1951) Flies of the British Isles. London.

Cooper, J. P. (1964) Climatic variation in forage grasses I leaf development in climatic races of Lolium and Dactylis. J. Appl.Ecol I :45-61.

Coste H. L'abbe (1903) 'Flore descriptive et illustree de la France' (p.294) Paris.

Cronquist, A. (1955) Phylogeny and taxonomy of the Compositae. Am.Midl.Nat. 53 : 478-511.

Danser, B. H. (1929) Über die Begriffe Komparium, Kommiskuum und Konvivium und über die Entstehungsweise der Konvivien. Genetica, 11 : 399-450.

Dalby, D. H. (1962) The nature of variation in the British Glassworts (Salicornia spp.). Ph.D.Thesis. University of London.

Dalby, D. H. (1963) Seed dipersal in Salicornia Pusilla. Nature Lond. 199 : 197-198.

Darlington, C. D. and Wylie, A. P. (1955) Chromosome Atlas of Flowering Plants.

Davis, P. H., and Heywood, V. H. (1963) Principles of Angiosperm Taxonomy, London.

Davison, A. (1964) Some factors affecting seedling establishment on calcareous soils.Ph.D.Thesis, University of Sheffield.

Donald, C. M. (1963) Competition among crop and pasture plants. Advan.Agron 15 : 1-118.

Doty, M. S. (1946) Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27 : 315.

Doty, M. S. and Archer, J. G. (1950) An experimental test of the tide factor hypothesis. Am.J.Bot. 37 : 458-464.

Drummond, D. C. (1960) The food of Rattus norvegicus Berk. in an area of sea wall, salt marsh and mudflat. J.Anim.Ecol. 29 : 341-347.

Evans, H. J. and Sorger, G. J. (1966) Role of mineral elements with emphasis on the univalent cations. A.Rev.Pl.Physiol. 17 : 46-76.

Evans, R. G. (1947a) The intertidal ecology of Cardigan Bay. J.Ecol. 34 : 273-309.

Evans, R. G. (1947b) The intertidal ecology of selected localities in the Plymouth neighbourhood. J.mar.biol.Ass.U.K. 27 : 173-218.

Evans, R. G. (1957) The intertidal ecology of some localities on the Atlantic coast of France. J.Ecol. 45 : 245-271.

East, E, M. (1940) The distribution of self-sterility in the flowering plants. Proc.Am.Phil.Soc. 82 : 449-518.

Eijk M. van (1938) Einfluss der Salzaufnahme auf die Wurzelatmung bei Aster tripolium. Proc.Kon.Nederl.Akad.Wetens. 10 : 2-8.

Epstein, E. and Jefferies, R. L. (1964) The genetic basis of selective ion transport in plants. A.Rev.Pl.Physiol. 15 : 169-184.

Falconer, D. S. and Robertson, A. (1956) Selection for environmental variation of body size in mice. Z.I.A.V. 87 : 385-391.

Ferguson, I. K. (1964) Notes on the stigma morphology and flowering behaviour in British Salicorniae. Watsonia 6:25-27.

Fisher, R. A. and Yates, F. (1963) Statistical Tables for Biological, Agricultural and Medical Research. 6th. Edn. London.

Ford, E. B. (1940) Polymorphism and Taxonomy in 'The New Systematics (ed. Huxley, J.) Oxford : 493-513.

Ford, E. B. (1945) Plymorphism. Biol.Rev., 20 : 73-88.

Ford, E. B. (1964) Ecological Genetics. London.

Fryxell, P. A. (1957) Mode of reproduction of higher plants. The Botanical Review 23 : 125-233.

Gajewski, W. (1963) The heredity of seed-dispersing mechanisms in Geum. Genetics Today. Proc. XI Int. Congr. Genetics : 465-482.

Gauch, H. G. and Wadleigh, C. H. (1944) Effects of high salt concentrations on growth of bean plants. Bot.Gaz. 105 : 378-387.

Gilmour, J. S. L., and Gregor, J. W. (1939) Demes : a suggested new terminology. Nature, Lond. 144 : 333.

Gilmour, J. S. L. and Heslop-Harrison, J. (1954) The deme terminology and the units of micro-evolutionary change. Genetica, 27 : 141-161.

Godwin, H. (1956) The History of the British Flora. Cambridge.

Goldsmith, F. B. (1967) Some aspects of the vegetation of sea cliffs. Ph.D.Thesis, University of Wales.

Goodman, P. J., Braybrooks, E. M., and Lambert, J. M. (1959) Investigations into 'Die-Back' in Spartina townsendii agg. I The present status of Spartina townsendii in Britain. J.Ecol. 47 : 651-677

Gray. A. J. (1959) Spartina townsendii - its role in the colonisation and development of Tetney Haven salt marsh. Trans.Lincs.Nat. Union 1959.

Gray, S. F. (1821) A Natural Arrangement of British Plants (according to their relations to each other ....). Vol.I. London.

Greenway, H., and Rogers, A. (1963) Growth and ion uptake of Agropyron elongatum on saline substrates, as compared with a salt tolerant variety of Hordeum vulgare. Pl.Soil 18:21-30.

Gregor, J. W. (1938) Experimental taxonomy, II initial population differentiation in Plantago maritima L. of Britain. New Phytol. 37 : 15-49.

Gregor, J. W. (1939) Experimental taxonomy. III: Population differentiation in North American and Euopean Sea plantains allied to Plantago maritima L. New Phytol. 38 : 293-322.

Gregor, J. W. (1944) The ecotype. Biol.Rev. 19 : 20-30.

Gregor, J. W. (1946) Ecotypic differentiation. New Phytol. 45 : 254-270.

Gregor, J. W. (1956a) Genotypic-environmental interaction and its bearing on a practical problem of international interest. Proc.Intern.Grassland Congr., 7th. Palmerston, New Zealand : 202-211.

Gregor, J. W. (1956b) Adaptation and ecotypic components. Proc. Roy.Soc.B145 : 333-337.

Gregor, J. W., and Watson, J. P. (1961) Ecotypic differentiation : observations and reflections. Evolution, Lancaster, Pa. 15 : 166-173.

Grigson, G. (1955) The Englishman's Flora. London.

Guppy, H. B. (1906) Observations of a Naturalist in the Pacific between 1896 and 1899. 2 vols. London.

Hannon, N. and Bradshaw, A. D. (1968) Evolution of salt tolerance in two coexisting species of grass. Nature, Lond. 220 : 1342-1343.

Harberd, D. J. (1957) The within population variance in genecological trials. New. Phytol. 56 : 269-280.

Harberd, D. J. (1958) Progress and prospects in Genecology. Rep. Scott.Plant Breed Sta. : 52-60.

Harberd, D. J. (1961) The case for extensive rather than intensive sampling in genecology. New Phytol. 56 : 269-280.

Harberd, D. J. (1967) Observations on natural clones in Holcus mollis. New Phytol. 66 : 401-408.

Harper, J. L. (1959) The ecological significance of dormancy and its importance in weed control. Proc. IVth Inter.Cong. Crop Protection, Hamburg. 1 : 415-420.

Harper, J. L. (1961) Approaches to the study of Plant competition. Symp. Soc. expt. Biol. 15 : 1-39.

Harper, J. A. (1963) 'The nature and consequence of interference amongst plants'. Genetics Today (1964) London, and New York : 465-482.

Harper, J. L. (1965) Establishment, aggression and cohabitation in Weedy species. in The Genetics of Colonising species. 1st. I.V.B.S. symposium. New York and London : 243-268.

Harper, J. L. (1966) The reproductive Biology of the British Poppies in Hawkes (Ed.). Reproductive Biology and Taxonomy of Vascular Plants London: 26-39.

Harper, J. L., and Chancellor, A. P. (1959) The comparative biology of closely related species living in the same area. IV. Rumex : interference between individuals in populations of one and two species. J.Ecol. 47 : 679-695.

Hayward, H. E. (1956) Plant growth under saline conditions. In "Utilization of Saline water". UNESCO Reviews Res, Arid Zone Research, IV : 37-72.

Hayward, H. E., and Bernstein, L. (1958) Plant-growth relationships on salt-affected soils. Bot.Rev. 24 : 584-635.

Hegi, G. (1906) Illustriete Flora von Mittel-Europa. Vol VI (1) Munchen.

Heimann, H. (1966) Plant growth under Saline Conditions and the Balance of the Ionic Environment. in Boyko, H. (Ed.) 'Salinity and Aridity' The Hague : 201-213.

Heslop-Harrison, J. (1964) Forty Years of Genecology. Adv.Ecol.Res. 2 : 159-247.

Heslop-Harrison, J. W. (1948) Proc U. Durham Phil.Soc. 10 : 506.

Heslop-Harrison, J. W. (1951) Proc.U.Durham Phil.Soc. 11 : 4.

Heywood, V. H. (1959) The taxonomic treatment of ecotypic variation. Systematics Assocn. Pub., 3 : 87-112.

Hiesey, W. M. (1963) The genetic-physiologic structure of species complex in relation to environment. Genetics Today. Proc. XI Int. Congr. Genetics : 437-445.

Hinde, H. P. (1954) The vertical distribution of salt marsh phanerogams in relation to tide levels. Ecol.Monogr. 24 : 209-225.

Hodgson, G. L., and Blackman, G. E. (1956) An analysis of the influence of plant density on the growth of *Vicia faba* 1, The influence of density on the pattern of development. *J.exp.Bot*. 7 : 147-165.

Holmes, M. G. (1960) Salt marsh ecology. *J. Durham Coll. Nat.Hist.Soc*. 7 : 31-37.

Howitt, R. C. L., and Howitt, B. M. (1963) *A Flora of Nottinghamshire*. Nottingham.

Hubbard, C. E. (1968) *Grasses*. London.

Hubbard, J. C. E. (1969) Light in relation to tidal immersion and the growth of *Spartina townsendii* (s.l.) *J.Ecol*. 57 : 795-804.

Hubbard, J. C. E., and Stebbings, R. E. (1967) Distribution, Dates of origin and acreage of *Spartina townsendii* (s.l.) marshes in Great Britain. *Proc.bot.Soc.Br.Isl*. 7 : 1-7.

Huffaker, R. C., and Wallace, A. (1959a) Sodium absorption by different plant species at different potassium levels. *Soil Sci*. 87 : 130-134.

Huffaker, R. C., and Wallace, A. (1959b) Effect of potassium and sodium levels on sodium distribution in some plant species. *Soil Sci*. 88 : 80-82.

Hutchinson, T. C. (1967) Ecotypic differentiation in *Teucrium scorodonia* with respect to susceptibility to lime-induced chlorosis and to shade factors. *New. Phytol*. 66 : 439-453.

Huxley, J. S. (1938) Clines : an auxiliary taxonomic principle *Nature, Lond*. 142 : 219.

Huxley, J. S. (1955) Morphism and Evolution. *Heredity* 9 : 1-52.

Huziwara, Y. (1959) "Chromosomal evolution in the subtribe Asterinae". *Evolution, Lancaster Pa*. 13 : 188-194.

Imms, A. D. (1951) '*A general textbook of Entomology*'. London.

Jain, S. K., and Bradshaw, A. D. (1966) Evolutionary divergence among adjacent plant populations I. The evidence and its theoretical analysis. *Heredity Lond*. 21 : 407-441.

Jinno, T. (1956) On the relation between the chromosome numbers and the flora growing in the inland sea in Japan. *Jap.J.Genet*. 13 : 147-150.

Kettlewell, H. B. D. (1955) Selection experiments on industrial melanism in the Lepidoptera. Heredity, Lond. 9 : 323-342.

Kettlewell, H. B. D. (1956) Further selection experiments on industrial melanism in the Lepidoptera. Heredity, Lond. 10 : 287-301.

Khan, M. A. (1963) Physiologic and genetic analysis of varietal differences within Linum usitatissimum (flax and linseed). Ph.D. Thesis, University of Wales.

Khan, M. I. (1967) The genetic control of canalisation of seed size in plants. Ph.D. Thesis, University of Wales.

King, C. A. M. (1959) Beaches and Coasts. London.

Knuth, P. (1908) Handbook of Flower Pollination Vol.11. (Trans. Ainsworth-Davis) Oxford.

Langlet, O. (1963) Patterns and terms of intraspecific ecological variability. Nature, Lond. 200 : 347-348.

Lees, F. A. (1888) The Flora of West Yorkshire. London.

Lewis, J. R. (1964) The Ecology of Rocky shores. London.

Linne K. von. (1753) 'Species Plantarum' Ray Soc. Facsimile (1959) p 872.

Löve, A. and Löve, D. (1944) Cyto-taxonomical studies on Boreal plants III Some new chromosome numbers of Scandanavian plants. Arkiv For Botanik 31A : 1-22.

Löve, A. and Löve, D. (1961) Chromosome numbers of Central and Northwest European plant species. Opera Botanica 5. Lund.

Luxton, M. (1964) Some aspects of the biology of salt-marsh Acarina. Acarologia (C.R.Ier Congres Int. d'Acarologie Fort Collins, Col., U.S.A. 1963) : 172-182.

Marker, M. E. (1967) The Dee estuary : its Progressive Silting and Salt Marsh Development. Trans.Inst.Br. Geogr. 41 : 65-71.

Mason, W.W. (1925) Manuscript register of Lincolnshire plants. Unpublished m/s.

Mayer, A. M., and Poljakoff-Mayber, A. (1963) The Germination of Seeds. Oxford.

McNeilly, T. (1967) Evolution in closely adjacent populations III Agrostis tenuis on a small copper mine. Heredity Lond. 23 : 99-108.

McNeilly, T. and Antonovics (1968) Evolution in closely adjacent populations IV. Barriers to gene flow. Heredity Lond. 23 : 205-218.

Melderis, A. and Bangerter, E. B. (1955) 'A Handbook of British Flowering Plants'. London.

Milton W. E. J. (1939) The occurrence of buried viable seeds in soils at different elevations and on a salt marsh. J.Ecol. 27 : 149-159.

Montfort, C. and Brandup, W. (1927) Physiologische und pflanzengeographische Seesalzwirkungen. II : Okologische Studien uber Keimung und erste Entwicklung bei Halophyten. Jb.Wiss.Bot 66 : 902-946.

Montfort, C, and Brandup, W. (1928) Physiologisches und pflanzengeographische Seesalzwirkungen. III Jb.Wiss.Bot.: 67-105.

Myerscough, P. J., and Whitehead, F. H. (1967) Comparative biology of Tussilago farfara L., Chamaenerion angustifolium (L) Scop., Epilobium montanum L., and Epilobium adencaulon Hausskn. II Growth and Ecology. New Phytol 66 : 785-823.

Nees, von Esenbeck. (1818) 'Index seminum quae in horto bot. Vratislaviense prostant'. Breslau.

Nees, von Esenbeck (1832) Genera et species Asterearum. Vratislaviae.

Negodi, G. (1941) Cariologia dei generi Aster, Agathaea, Boltonia ed alcuni dati sui generi Felicia ed Erigeron (Asteraceae sez. Astereae subsez. Asterinae). Bull.Soc.Adriat.Sci.Nat.Trieste 39 : 27-38.

Nicholson, W. A. (1914) A Flora of Norfolk. London.

Perring, F. H. (1968) (Ed) . Critical Supplement to the Atlas of the British Flora. London.

Perring, F. H. and Walters, S. M. (1962) Atlas of the British Flora. B.S.B.I. London.

Perring, F. H., Sell, P. D., and Walters, S. M. (1964) A Flora of Cambridgeshire. Cambridge.

Petch, C. P., and Swann, E. L. (1962) 'West Norfolk Plants Today' Suppl. B.S.B.I. Proceedings.

Petch, T. (1905) Notes on Aster tripolium. Naturalist, Hull 1905. 50-54.

Pigott, C. D. (1969) Influence of mineral nutrition on the zonation of flowering plants in coastal salt-marshes. Ecological Aspects of the Mineral Nutrition of Plants. Brit. Ecol. Soc. Symp. 9 : 25-35.

Polya, G. (1948) Chromosome numbers of certain alkali plants. Archiva Biologica Hungarica. 18 : 145-148.

Poma, G. (1922) L'influence de la salinite de l'eau sur la germination et la croissance des plantes halophytes. Acad. Roy. Belg. Bull. Class. Sci. 5th ser., 8 : 81.

Praeger, R. L. (1913) On the Bouyancy of the Seeds of some Britannic Plants. Scient. Proc. R. Dubl.Soc. 14 : 13-62.

Quinlan, J. D. and Sagar, G. R. (1965) Grain yield in two contrasting varieties of Spring Wheat. Ann.Bot. (N.S.) 29 : 683-698.

Rahn, K. (1954) Experimental and cytological studies in Plantago media. Bot. Tidsskr. 51 : 300-307.

Rains, D. W. and Epstein, E. (1967) Preferential absorption of potassium by leaf tissue of the mangrove, Avicennia marina : an aspect of the halophytic competence in coping with salt. Aust. J. biol. Sci. 20 : 847-857.

Ranwell, D. S. (1968) Coastal marshes in perspective. University of Strathclyde Regional Studies Group Bulletin. 9 : 1-26.

Ranwell, D. S., Bird, E. C. F., Hubbard, J. C. E. and Stebbings, R. E., (1964) Spartina salt marshes in southern England.V. tidal submergence and chlorinity in Poole Harbour. J. Ecol 52 : 627-641.

Ratter, J. A. (1959) A cytogenetic study of Spergularia Ph.D. Thesis. University of Liverpool.

Rees, T. K. (1940) Algal colonisation at Mumbles Head J. Ecol. 28 : 403-437.

Reid, C. (1899) The Origin of the British Flora. Dulav & Co.

Richards, F. J. (1934) The salt marshes of the Dovey Estuary. IV. The rates of vertical accretion, horizontal extension and scarp erosion. Ann.Bot. N.S. 48 : 225-259.

Ridley, H. N. (1930) The Dispersal of Plants Throughout the World. Ashford.

Rikli, M. (1943) Das Pflanzenkleid der Mittelmeerlander. Vol.I Bern.

Robinson D. N. (1956) The N. E. Coast of Lincolnshire, a study in Coastal Evolution. M Sc. thesis, University of Nottingham.

Rodrigues, J. E, de. (1953) 'Contribuicao para o conheeimento cariologica das halofitas e psamofitas literais'. Diss. Univ. Coimbra 1953.

Roy, S. K. (1963) The variation of organs of individual plants. J. Genet. 58 : 147-176.

Salisbury, E. J. (1929) The Biological Equipment of Species in relation to competition. J. Ecol. 17 : 198-222.

Salisbury, E. J. (1942) 'The Reproductive Capacity of Plants'. London.

Saunders, E. (1896) The Hymenoptera aculeata of the British Isles. London.

Savulescu. T. (Ed) (1955) Flora republicii Populare Romane. Vol. IX. Bucuresti.

Schmalhausen, LI (1949) 'Factors of Evolution'. New York.

Scholander, P. F. (1968) How Mangroves Desalinate Seawater. Physiol. Plant 21 : 251-261.

Schratz, E. (1936) Beiträge zur Biologie der Halophyten (III). Jb. Wiss. Bot. 83 : 133-189.

Scott, G. A. M. (1960) Shingle beach plants. Ph.D. Thesis. University of Wales.

Sharrock, J. T. R. (1967) A study of morphological variation in Halimione portulacoides (L) Aell. in relation to variations in the habitat. Ph.D. Thesis. Southampton University.

Shimotomai N. and Huzimara Y. (1942) Zytologische Untersuchungen Uber Aster, Gymnaster, Kalimeris und Heteropappus aus Japan. Cytologia 12 : 206-218.

Shirley, H. L. (1943) Is tolerance the capacity to endure shade? J.For. 41 : 339-345.

Sinskaya, E. N. (1958) Investigations on the composition of ecotypical and varietal populations. Rep.Scot.Plant Breed Stat. 1958 : 31-40.

Skalinska, M, Szapik, R., Piotrowicz, M. (et al) (1959) Further studies in chromosome numbers of Polish angiosperms (Dicotyledons) Acta Soc. Bot. Polon., 28 : 487-529.

Sorensen, T. (154) Adaptation of small plants to deficient nutrition and a shart growing season. Illustrated by Cultivation experiments with Capsella bursa-pastori (L) Med. Bot. Tidsskr. 51 : 339-361.

South, R. (1947) 'The Butterflies of the British Isles'. London.

Stebbins, G. L. (1950) Variation and Evolution in Plants. New York.

Stebbins, G. L. (1958) Longevity, habitat and release of genetic variability in the higher plants. Cold Spring Harb. Symp. Quant. Biol. 23 : 365-378.

Steers, J. A. (1960) Scolt Head Island, Cambridge.

Stephenson, T. A. and Stephenson, A. (1949) The universal features of zonation between tide-marks on rocky coasts. J. Ecol. 37 : 289-305.

Sterk, A. A. (1968) Een studie van de variabiliteit van Spergularia media en Spergularia marina van Nederland. Doctoral Thesis. University of Utrecht.

Stocker, O. (1928) 'Das Halophyten problem. Ergebrisse der Biologie. 3 Bd. : 265-354.

Stopford, S. C. (1951) An ecological survey of the Cheshire foreshore of the Dee Estuary. J.Anim. Ecol. 20 : 103-122.

Styles, B. T. (1962) The taxonomy of Polygonum aviculare and its allies in Britain. Watsonia 5 : 177-214.

de Tabley, Lord (1899) Flora of Cheshire.

Tahara, M., and Shimotomai, N. (1926) Chromosompolyploidie bei Aster und Dessen Verwandten Gattungen. Bot.Mag. Tokyo 60(471) : 132-136.

Thoday, J. M. (1958) Homeostasis in a selection experiment. Heredity. Lond. 12 : 401-415.

Thomas, R. L. (1966) The Influence of Seed Weight on Seedling Vigour in Lolium perenne. Ann. Bot. (N.S.) 30 : 111-121.

Timson, J. (1965) Fruit variation in Polygonum persicaria L. Watsonia 6 : 106-108.

Trow, A. H. (1912) On the inheritance of certain characters in the common groundsel Senecio vulgaris Linn. and its segregates. J. Genet. 2 : 1-12.

Tsopa, E. (1939) La Vegetarion des Halophytes du Nord de la Roumanie en connexion avec celle du reste du pays. S.I.G.M.A. 70 : 1-22.

Turesson, G. (1920) The cause of plagiotrophy in maritime shore plants. Lunds. Univ. Arsskr. Adv. 2 (N.F.) 16 : 1-33.

Turreson, G. (1922) The genotypical response of the plant species to the habitat. Hereditas 3 : 211-350.

Turesson, G. (1925) The plant species in relation to habitat and climate. Hereditas 6 : 147-236.

Umamaheswararao M. and Sreeramulu T. (1964) An ecological study of some intertidal algae of the Visakhapatnam coast. J. Ecol. 52 : 595-616.

Uphof, J. C. Th. (1941) Halophytes. Bot.Rev. 7 : 1.

Verrall, G. H. (1901) Platypezidae, Pipunculidae and Syrphidae of Gt. Britain. London.

de Vries, H. (1901) The law of separation of characters in crosses. Jl. R. hort. Soc. 25 : 243-249.

Wareing, P. F. (1966) Ecological aspects of seed dormancy and germination. In Hawkes J. G. (ed). Reproductive Biology and Taxonomy of Vascular Plants. Oxford.

Webb, D. A. (1966) Dispersal and establishment: What do we really know? in Hawkes J. G. (Ed). Reproductive Biology and Taxonomy of Flowering Plants (1966) : 93-102.

Wendelberger, Von. (1950) Zur Soziologie der kontinentalem Halophytenvegetation Mitteleuropas. Ost. Akad. Wiss. Mat.-Natur. Klasse. 108 : 1-180.

Wetmore, R. H. and Delisle, A. L. (1939) Studies in the genetics and cytology of two species in the genus Aster and their polymorphy in nature. Am.J.Bot. 26 : 1-12.

Wiehe, P. O. (1953) A quantitative study of the influence of the tide upon populations of Salicornia europaea. J. Ecol. 23 : 323-333.

Wild, Rev. J. (1900) Tetney, Lincolnshire. A History. Grimsby.

Wilkins, D. A. (1959) Sampling for Genecology. Rep.Scott. Plant Breed Sta. : 92-96.

Wilkins, D. A. (1960a) Recognising adaptive variants. Proc.Linn. Soc. Lond. Session. 171 : 122-126.

Wilkins, D. A. (1960b) The measurement and genetical analysis of lead tolerance in Festuca ovina. Rep.Scott.Plant. Breed. Sta. 1960 : 85-98.

Wilkins, D. A. and Lewis, M. C. (1969) An application of ordination to genecology. New Phytol. 68 : 861-872.

Williams, M. C. (1960) Effect of sodium and potassium salts on growth and oxalate content of Halogeton. Plant. Physiol. Lancaster. 35 : 500-505.

Williams W. T. and Lambert, J. M. (1959) Multivariate methods in plant ecology. I. Association-analysis in plant communities. J. Ecol. 47 : 83-101.

Williams, W. T., and Lambert, J. M. (1960) Multivariate methods in plant ecology II. The use of an electronic digital computer for association analysis. J. Ecol. 48 : 689-710.

Woodell, S. R. J. (1965) Natural hybridisation between the cowslip (Primula veris L.) and the Primrose (P.vulgaris Huds.) in Britain. Watsonia 6 : 190-202.

Wulff, H. D. (1937) Karyologische untersuchungen an der Halophytenflora Schleswig-Holstein. Jb. Wiss.Bot. 84 : 182.

Yapp, R.H., Johns, D, and Jones, O. T. (1917) The salt marshes of the Dovey Estuary II : The salt marshes. J. Ecol. 5 : 65-103.

Zohary, M. (1950) Evolutionary trends in the fruiting head of Compositae. Evolution, Lancaster Pa. 4 : 103-109.