

THE SALT MARSHES OF MILFORD HAVEN, PEMBROKESHIRE

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The main flowering plant communities of the Milford Haven salt marshes are described, using data from about 16 marshes situated at different distances from the sea. The main physical features of the marshes are discussed and, together with the tidal régime, are related to plant distribution. The paper concludes with a short description of the biotic influences which may change the plant communities in the future.

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INTRODUCTION

SALT marshes may be defined as the vegetation (normally dominated by flowering plants) which develops on muddy shores between approximately mean sea level and the highest high waters of the spring tides. Although in the present paper most algae are excluded, they may be very important ecologically, especially at the lower levels, and a fully comprehensive account of salt marsh plants would certainly include the algae as well.

The marshes studied are shown (together with their Grid References) on the map of Milford Haven in Fig. 1. By levelling from the nearest Ordnance Survey bench marks, I have established secondary marks on almost all these marshes. Heights throughout the paper, derived from these secondary marks, are given in metres above Milford Haven chart datum (CD), which is -3.17 m. OD (Newlyn). Tidal predictions are extracted from the Admiralty Tide Tables, where Milford Haven features as a Standard Port.

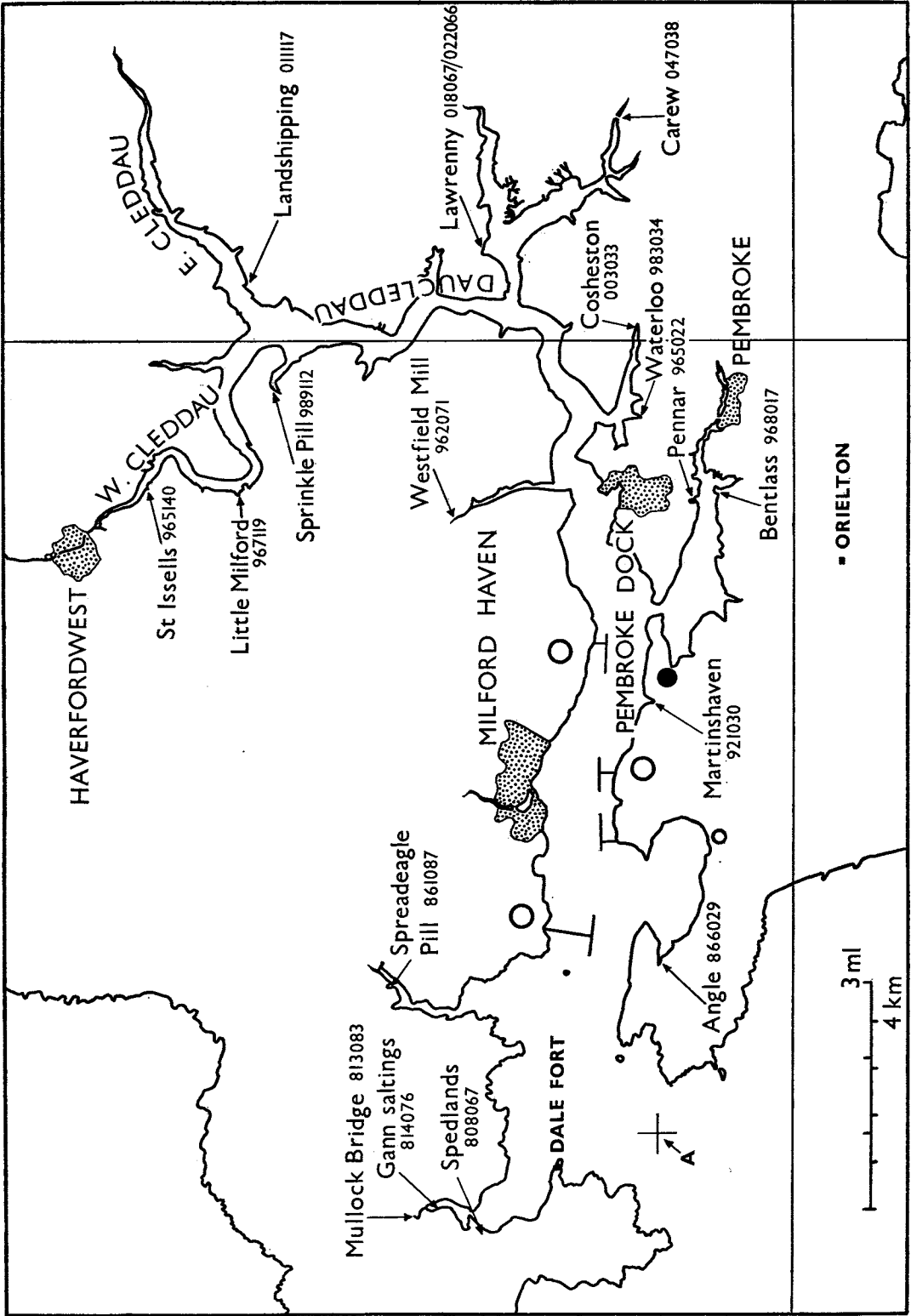


Fig. 1.
Map of Milford Haven. Large rings: oil tank farms and refineries. Small ring: tank farm. Solid spot: oil-fired power station. A: arbitrary point at entrance to Haven (grid ref. 12/830030), used in Fig. 22.

Where appropriate, plant names follow Clapham, Tutin and Warburg (1962). Many genera are represented by only a single species on most marshes, to save space they are usually referred to by their generic names only. These species are:

<i>Agrostis stolonifera</i>	<i>Plantago maritima</i>
<i>Armeria maritima</i>	<i>Puccinellia maritima</i>
<i>Aster tripolium</i>	<i>Schoenoplectus tabernaemontani</i>
<i>Cochlearia anglica</i>	<i>Scirpus maritimus</i>
<i>Festuca rubra</i>	<i>Spergularia media</i>
<i>Glaux maritima</i>	<i>Suaeda maritima</i>
<i>Halimione portulacoides</i>	<i>Triglochin maritima</i>
<i>Limonium humile</i>	

The common allotetraploid *Spartina* "townsendii" is referred to as *Spartina* (see discussion, p. 314), whilst no attempt has been made to distinguish the annual *Salicornia* spp., apart from the very distinct *S. pusilla*. Both *Zostera marina* and *Z. angustifolia* are recorded for Milford Haven by Perring and Walters (1962), but material from Sandyhaven, illustrated in Fig. 14, has the split leaf sheath of *Z. noltii* (Clapham, Tutin and Warburg, 1962, p. 942). My records may, in fact, relate to either or both of the latter two species.

MARSH PHYSIOGRAPHY

Introduction

The Milford Haven marshes are situated in sheltered inlets and along the tidal stretches of lateral streams, unlike those which have been most extensively studied elsewhere in Britain (e.g. at Blakeney and Scolt Head in Norfolk, and the Dyfi in Merioneth) which have developed in the shelter of off-shore shingle bars. The Milford Haven type is thus more akin to the marshes of the Exe estuary, Poole Harbour and Southampton Water.

I have not been able to visit all the Haven marshes, and there are certainly a few small ones (especially in the E. Cleddau) which are consequently not considered. Along most of the Haven shores, there is a sudden and steep erosion cliff perhaps 3 to 5 metres high, whose base lies approximately at extreme high water springs (EHWS), and which could not possibly be formed by wave action at the present time. The upper edge of the wave-cut platform corresponding to this cliff has, in the past, been much used locally as a cart track, providing a firmer route just above the intermittent muddy stretches. In many places there is a narrow fringe of salt marsh below this level, at times so eroded as to consist of no more than isolated relict fragments of stratified mud with the normal salt marsh flora growing on top. In yet other places (as at Bentlass and Lawrenny), wave action and water currents keep the stony shore clear of all sediments apart from a thin and discontinuous layer of mud which may support little beyond scattered plants of *Limonium humile* and *Puccinellia maritima*.

Sediment deposition

Deposition of sediments is a complex process, involving both coarse and fine material. Some of this is sorted by water currents, and in the neighbourhood of creeks or streams (where sand banks may accumulate) markedly stratified sediments may be seen. These are usually clearly visible in the eroding banks of the Gann at

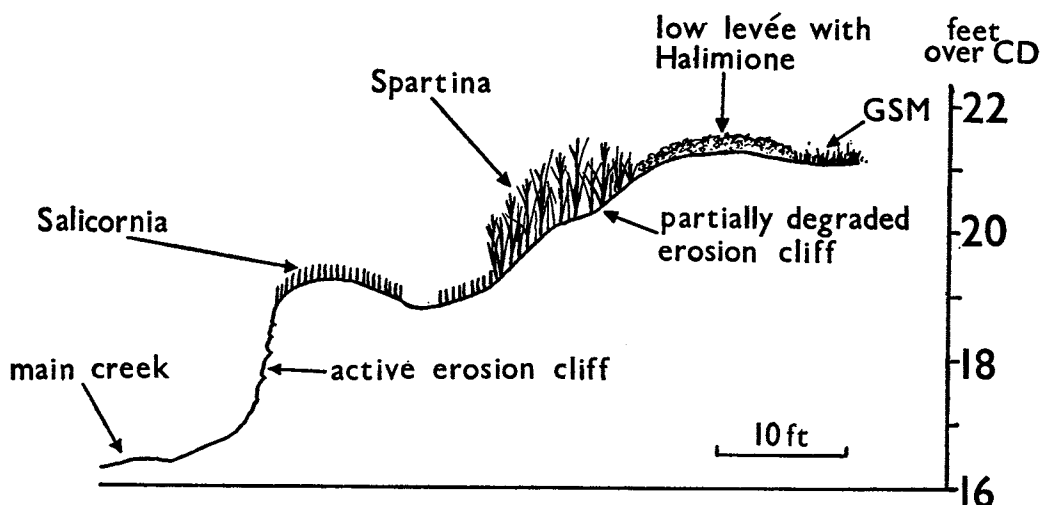


FIG. 2.
Section through creek bank, Gann saltings.

approximately 816077. In this same area, low levées (up to 5 cm. high) build up along the creek edges (see Fig. 2). However, over most of the salt marsh surface deposition is of fine mud particles, probably mostly redistributed from near or below low-water. Jakobsen (1961) comments that in the marshes near Esbjerg in W. Denmark, the mud is not derived locally, stream action there being negligible and redistribution of inshore sediments insufficient to explain marsh build-up. The mud is apparently brought in from the open sea during westerly gales. An equivalent explanation cannot be true for Milford Haven, and I suspect that the poor development of salt marshes in this area is because there is little by way of a "mud reservoir" in the vicinity. Posford, Pavry and Partners have kindly shown me borehole data obtained prior to the straightening of the deep-water channel giving access to the oil terminals in the lower parts of the Haven (see Fig. 1). Most of these records show that there is relatively little evidence of sedimentation in mid-channel (often no soft sediments, and rarely more than one metre.) Nelson-Smith (1965) gives some figures for materials in suspension, a typical one being about 23.5 ppm., which is very much less than in most other estuaries. Appreciable mudbanks accumulate only to the sides of the main channel in sheltered sites, but are much more common in the Dauceddau and its tributaries. This mud, however, appears not to be transported any distance, but to circulate locally between the marshes and nearby low-level mud banks. Clearly an explanation of the origin of these mud banks requires further work, but the picture of material being carried down the streams in suspension and then being deposited and in the process progressively raising the salt marsh surface, may be misleading in its apparent simplicity.

During 1969 I made some field measurements on accretion rates at Bentlass and Angle, the results being shown in Fig. 3. Considerable variation is seen between marshes, but for any single transect there is an almost linear relationship between elevation and amount deposited, at least down to the *Spartina* stands. These figures for the middle marsh are similar to those from other marshes in Britain. The wholly unconsolidated material in the *Spartina* stands represent smaller figures for actual accretion (after allowing for consolidation and water loss) but it will still be more

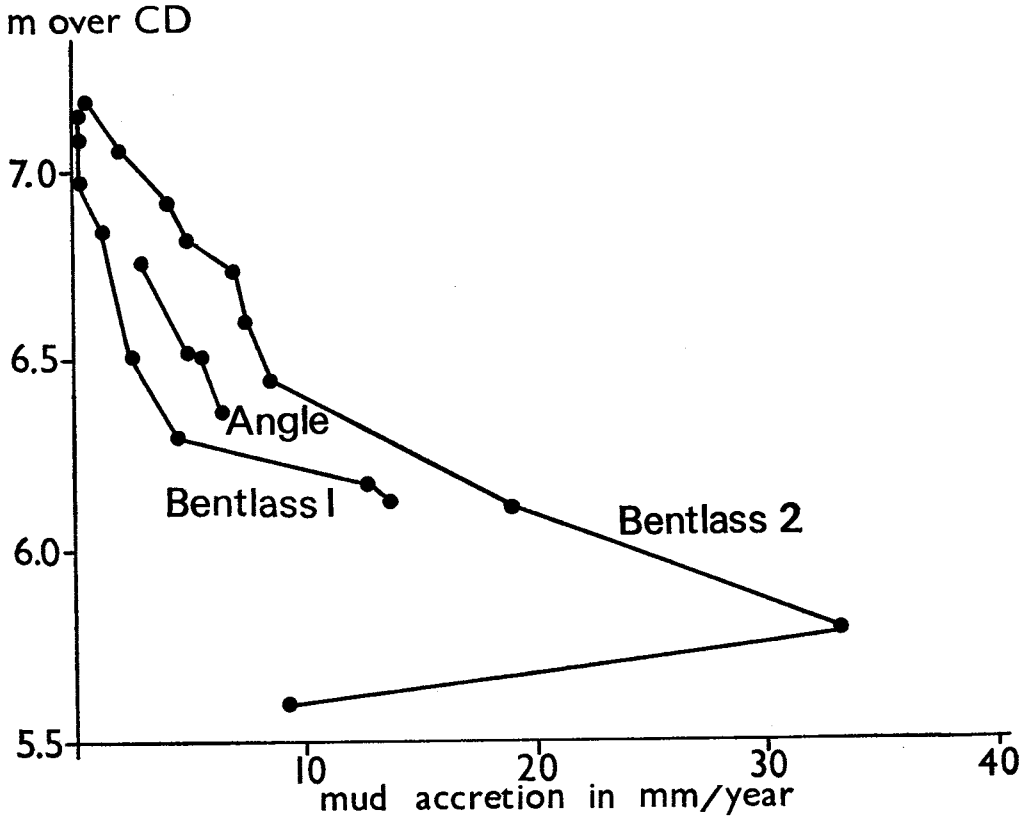


FIG. 3.
Mud accretion rates on two salt marshes in 1969.

than on the middle marsh. Jakobsen (1961) states that only about 50 per cent of the material in suspension is actually caught by salt marsh vegetation, but his reference is to a marsh dominated by *Puccinellia*. *Spartina* has remarkable powers of catching sediments (see the figures (Ranwell, 1964) of 8 to 10 cm. per year in high-level *Spartina* marsh at Bridgwater Bay, Somerset), whilst its ability to trap floating oil has been noted in Poole Harbour by Ranwell and Hewett (1964) and in Milford Haven by Dalby (1969a). Accretion in *Spartina* stands can quickly lead to a general raising of the ground level at a rate which, at a rather later stage, is somewhat out of phase with the slower upward growth associated with *Puccinellia*. The ultimate fate of elevated *Spartina* swards is not yet known, but in the short term there are no species that can compete successfully with it unless it is weakened in some way (though Gillham (1957) has noted *Juncus maritimus* crowding out *Spartina* on the Exe marshes). Some dense stands may develop "die-back" (Goodman *et al.*, 1959), apparently as a result of reducing conditions round the roots, especially in pans on the sward and at its outer edge. I have seen what appears to be "die-back" at the outer edges of a dense sward at Waterloo, at a height of about 5.35 m. CD. Normally the habit on soft level mud is that of annular clumps, mostly growing outwards, but with some rhizomes running back to the centre to produce new growths there. In this way concentric rings can be formed (Caldwell, 1957) as can be seen in many parts of the Haven.

Erosion cycle

On the smaller marshes, where the slope is greater, build-up (apart from the action of *Spartina*) probably proceeds in a manner closely analogous to that described by Jakobsen (1954) in Denmark. When mud-banks close inshore reach about 5.9 to 6.1 m. CD, *Puccinellia* becomes established, and the small vegetated mounds increase in size. These mounds coalesce in front of the earlier erosion cliffs, and gradually form a low marsh front which gains new species (especially *Limonium* and *Aster*) as its level rises. As the new frontal marsh gives increasing protection to the cliff behind, erosion there by wave action decreases and finally virtually ceases. But by this time erosion has begun at the new marsh edge, and a new cliff is formed there (Fig. 4). In this way the small fringing marshes develop through a balance between

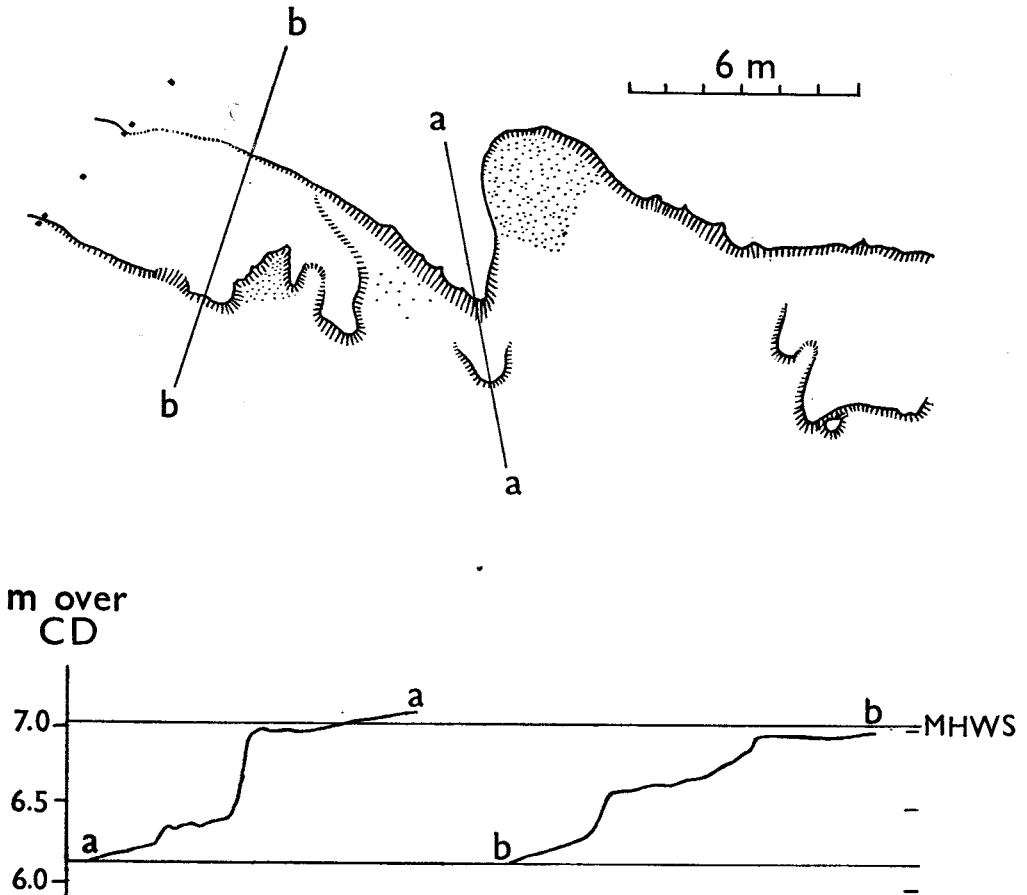


FIG. 4.

Terrace features at edge of marsh, Bentlass. Plan above, two sections along labelled lines below.

erosion and deposition, with the sediment involved not necessarily having travelled very far. The coarser material may, in fact, move only a few feet this: is especially true for the small stones sorted by wave action in small rapidly eroding bays on erosion cliffs. These bays are cut back very fast by the channelling of oncoming waves and stones accumulate on the upwardly sloping floor forming a characteristic site for

almost pure stands of *Suaeda*. Where there is more mud held by *Puccinellia*, small unbranched forms of *Salicornia* may be very common.

In the upper stretches of the estuary (e.g. at Little Milford and at Uzmaston) the erosion cliffs often form three or four terraces, each being of short lateral duration at any particular site. They presumably result from erosion by river currents, possibly during spring tides, but it should be noted that such erosion cliffs are common features on many marshes, especially along their outer edges, and they have variously been explained as being due to wave action on flood tides, erosion following the meandering of river channels and the results of land level rising relative to sea level (see Chapman, 1960b, pp. 158–159). On the Gann saltings there are miniature features which result from the drainage of pans when the heads of creeks cut back and drain them, whilst steep banks there and, for example, at Bentlass, are the remains of artificial earth walls built at some time in the past for land reclamation purposes.

Salt marsh pans

The small pools on the marsh surface, known as pans, are typically developed on horizontal marsh surfaces, and in Milford Haven are probably mostly due to initial irregularities of surface persisting for many years. Water stands for a long time after tidal cover or heavy rain, and seedling establishment is prevented. Complete drying during summer neap tides causes high salinities in the surface soil, which again restricts the chances of colonization. The factors controlling the physical and chemical conditions in pans are fully discussed by Nicol (1935). Once a pan is

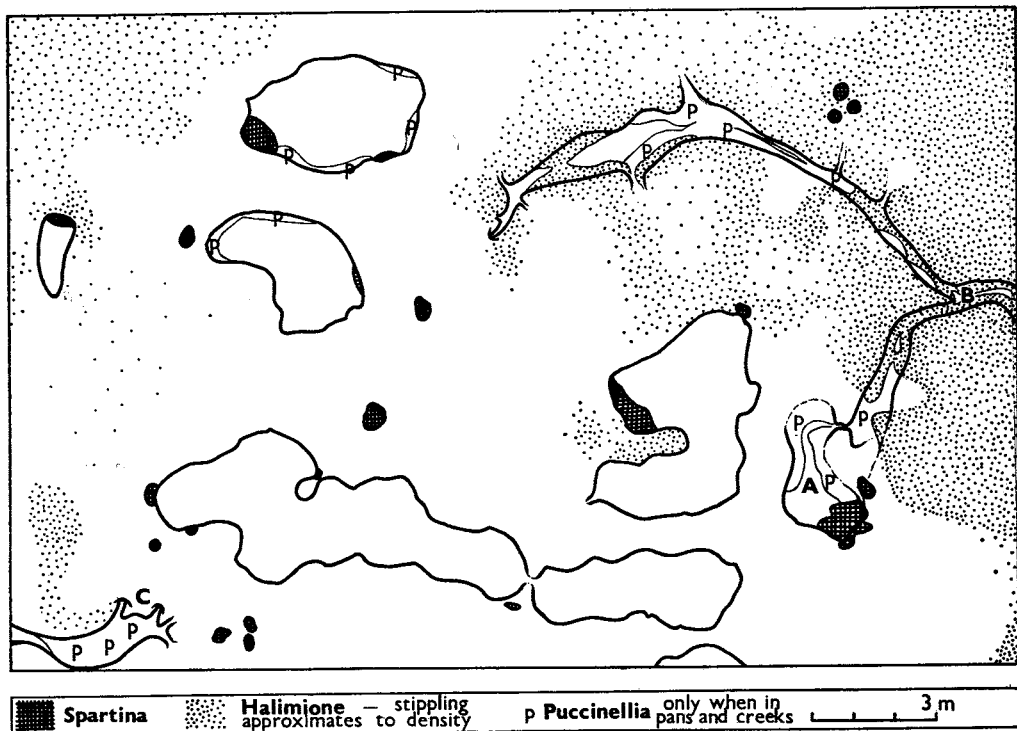


FIG. 5.

Area of pans and creeks on wild marsh, Gann saltings. A: pan recently drained by cutting-back of creek. B: creek overhung by *Halimione*. C: region of active erosion at creek head. *Puccinellia* occurs throughout most of the area depicted, except where there is a dense cover of *Halimione*.

formed, with standing water, wave action undercuts the edges and there is slow increase in size as the banks erode. Even with a fetch of only a few metres this erosion can be considerable. Primary pans of this kind are numerous on parts of the Gann saltings (see Fig. 5), especially on the unreclaimed wild marsh, whilst there are a few at Angle, Bentlass and Little Milford. In Fig. 5, the pan marked A has been drained by a creek cutting back. When this happens on the Gann saltings, the pan floor is colonized by *Puccinellia*, and then the normal primary marsh sequence follows (unless the site is overwhelmed by *Halimione*). The earlier seral stages than occur at about 30 cm. higher over CD than would be expected at the marsh front, because of the general raising of the marsh surface where the pans are situated.

Elevation and slope

Most of the marshes slope downwards towards the main drainage channels, as shown in Fig. 6, the surface following a gentle graded curve in those sites so far studied. The curve is presumably at least partially determined by the differential accretion rates discussed earlier, but is sharply interrupted at Lawrenny by the erosion cliff. A few marshes show appreciable horizontal stretches, but these vary both in elevation and plant cover from marsh to marsh (see Table 1).

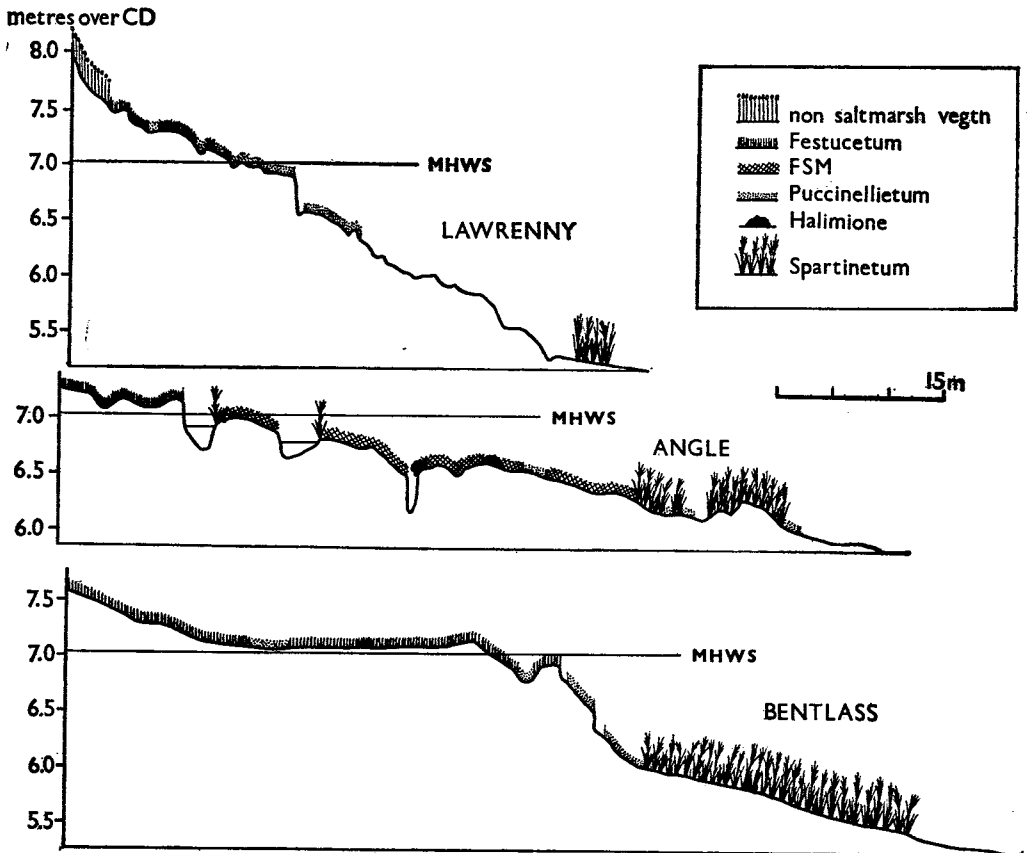


FIG. 6.

Profiles across three salt marshes, showing main communities in relation to height over chart datum.

Table 1. Heights of approximately level salt marshes

Marsh	Community	Approximate height in metres over CD
Gann saltings	Puccinellietum	6.55
Martinshaven	FSM	6.86-6.92
Bentlass	Festucetum	7.01
Little Milford	FSM	7.01

Only on the Gann saltings is there a really large horizontal level marsh surface, where the highest points on the very gently undulating marsh do not fall by more than about 3 to 6 cm. over a horizontal distance of 300 m., though pans and related depressions may fall a further 10 cm.

On the east side of Angle Bay, there is a considerable expanse of sand and mud with a gradient of no more than about 1:330, exposed from ELWS up to about 5.80 m. CD. Though this is mostly below the main salt marsh levels for the Haven, *Zostera* extends much higher than elsewhere, because of poor surface drainage.

FLOWERING PLANT COMMUNITIES

Alternative approaches to the problem

Before adopting a system of classification of the flowering plant communities, a choice had to be made between the commonly employed alternatives. These are firstly, the hierarchical systems based on that of the Montpellier School, founded by Braun-Blanquet, a modified version of which is applied to salt marsh vegetation by Chapman (1960b, p. 275). The second is the traditional British approach employing dominant species (see Tansley, 1949, p. 821), and with the communities named after the dominants. Thus one dominated by *Festuca rubra* is a Festucetum rubrae or simply a Festucetum, and one dominated by *Juncus maritimus* is a Juncetum maritimi. By emphasizing the dominants, considerable variation is permitted in the minor constituents, but at the same time (as Continental botanists quickly point out) we inevitably lose a great deal of information by using units which are so widely defined. The third approach, that of ordination, is quite different in its basic approach. It is usually based on a more rigorous mathematical framework, and seeks to place sample plots (or species) according to one or more scales (usually more or less related to environmental factors), but without the primary objective of producing mutually exclusive categories.

It will be seen that the first two alternatives depend on communities actually existing in nature as more or less homogeneous floristic units, but the third accepts gradients and continuous variation between successive plots. In the present paper I am using a combination of ordination and classification by dominants, because I think this best for a situation where there are undeniable commonly repeated sequences of units defined by a limited number of species (Fig. 7), but where the secondary constituents may show very considerable variation from marsh to marsh. The repeating sequence is, of course, due to elevation and tidal action, and results from each species having its own range of environmental tolerances. These will overlap from species to species (Fig. 8), giving the visual zonation, and may at times blur the boundaries between communities defined by dominants.

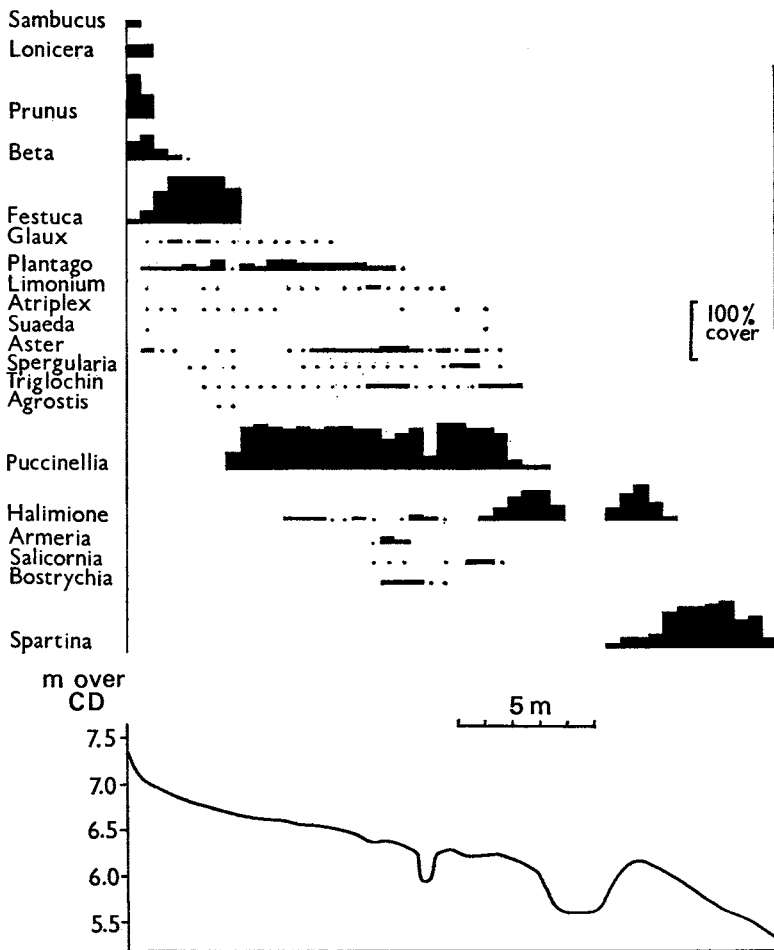


FIG. 7.

Belt transect across narrow marsh at Speadeagle Pill, showing zonation determined by dominant species. Histograms represent percentage cover. The values for *Sambucus nigra*, *Lonicera periclymenum* and *Prunus spinosa* refer to overhanging branches and foliage, and not to plants rooted in the sample areas.

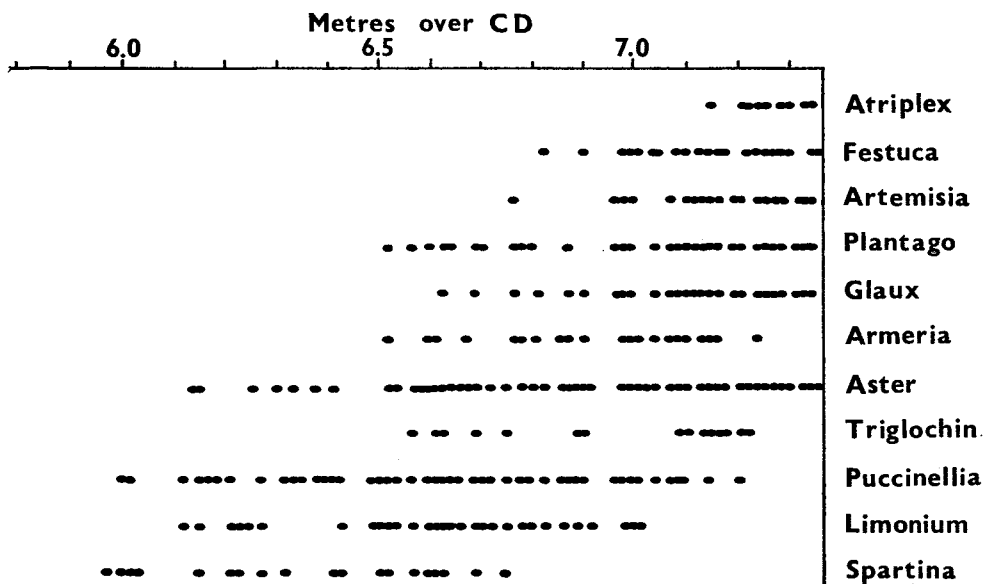


FIG. 8.

Occurrences (irrespective of abundance) of main species at Bentlass in relation to height over chart datum.

Results of ordination and classification

About 200* quadrats (each 0.5 m.²) were scored for species present, using the Domin cover/abundance scale, and the quadrats were ordinated according to the first two components obtained from a principal components analysis.

The application of this kind of analysis to ecological problems is discussed by Orloci (1966) and Austin and Orloci (1966). Each quadrat may be represented by a point in multi-dimensional space, the co-ordinates for fixing its position being, in the present study, the Domin values for each species in turn. The full data will form a multi-dimensional "cloud" in which groups of quadrats which are more or less similar will form denser clusters, separated by less dense regions. The principal components analysis picks out successive components or axes from the "cloud", the first being the axis associated with the maximum variance. The second axis is orthogonal to (and so independent of) the first, and is associated with the maximum variance remaining, and so on with successive axes being associated with smaller and smaller variances. The analysis is thus a kind of analysis of variance, and when all the axes or components are considered together the total variance is accounted for.

In many ecological studies it is possible to equate the components with known environmental factors. This is because the main factors have marked effects and are associated with separate parts of the total variation. It is these portions which are picked out by the principal components analysis. Methods of identifying the components include plotting the attributes used in characterizing the quadrats (species here) and then seeking environmental causes which by one's experience are known to control the distribution of the attributes, or plotting values (e.g. soil pH, depth, etc.) in their appropriate positions, quadrat by quadrat, and then seeking visual patterns and gradients which correlate with the component axes. In the present study, the first axis separates the two species which have the highest scores for both frequency and <omin values. It is possible that this axis has no ecological meaning: Kershaw (1967) has noted that the first axis in the inverse analysis (of species instead of quadrats) usually arranges the species in order of frequency. The second axis appears to parallel a soil moisture gradient (wet extreme rather above its left end in Figs. 9 to 11, drier extreme rather below its right end).

The results of the quadrat ordination are given in Figs. 9 to 11. Axis 1 separates two major groups, those quadrats dominated by *Puccinellia* from those dominated by *Festuca*, whilst quadrats dominated by other species come near the centre. This would appear to mark a primary vegetational boundary, that between Puccinellietum and Festucetum. Axis 2 places *Spartina* stands beyond all others to the left, and those with appreciable *Armeria* and *Plantago* to the right. The recognition of the Spartinetum as distinct is reasonable, provided one remembers that it is a community superimposed on an existing seral pattern, and is not necessarily in equilibrium with it.

Forb salt marsh

The nature of the plots with *Armeria* and *Plantago* is more complex, since on the diagrams they bridge the gap between the two extremes of Axis 1, yet they may lack both grasses entirely. When this is the case, they resemble the Plantaginetum described by Chapman (1960a) from Plantago marsh at Scolt Head. This, he says, is rare in salt marsh successions. I have records of it (or very similar communities) from Angle, Martinshaven, Little Milford, Sprinkle Pill, Spredaeagle Pill and the Gann saltings, so it may be regarded as restricted in extent but not uncommon round Milford Haven. It occurs spatially between the Puccinellietum and the Festucetum, and generally occupies the lower part of the range of the latter, as is shown in Table 2. These figures suggest that *Festuca* is not attaining its potential lower limit in certain sites which, at the same time, are not suitable for *Puccinellia*.

* The actual number of quadrats, 198, was fixed by the storage capacity of the computer used, and the sample was a random selection from a total of 465 taken along 15 transects across 12 different marshes.

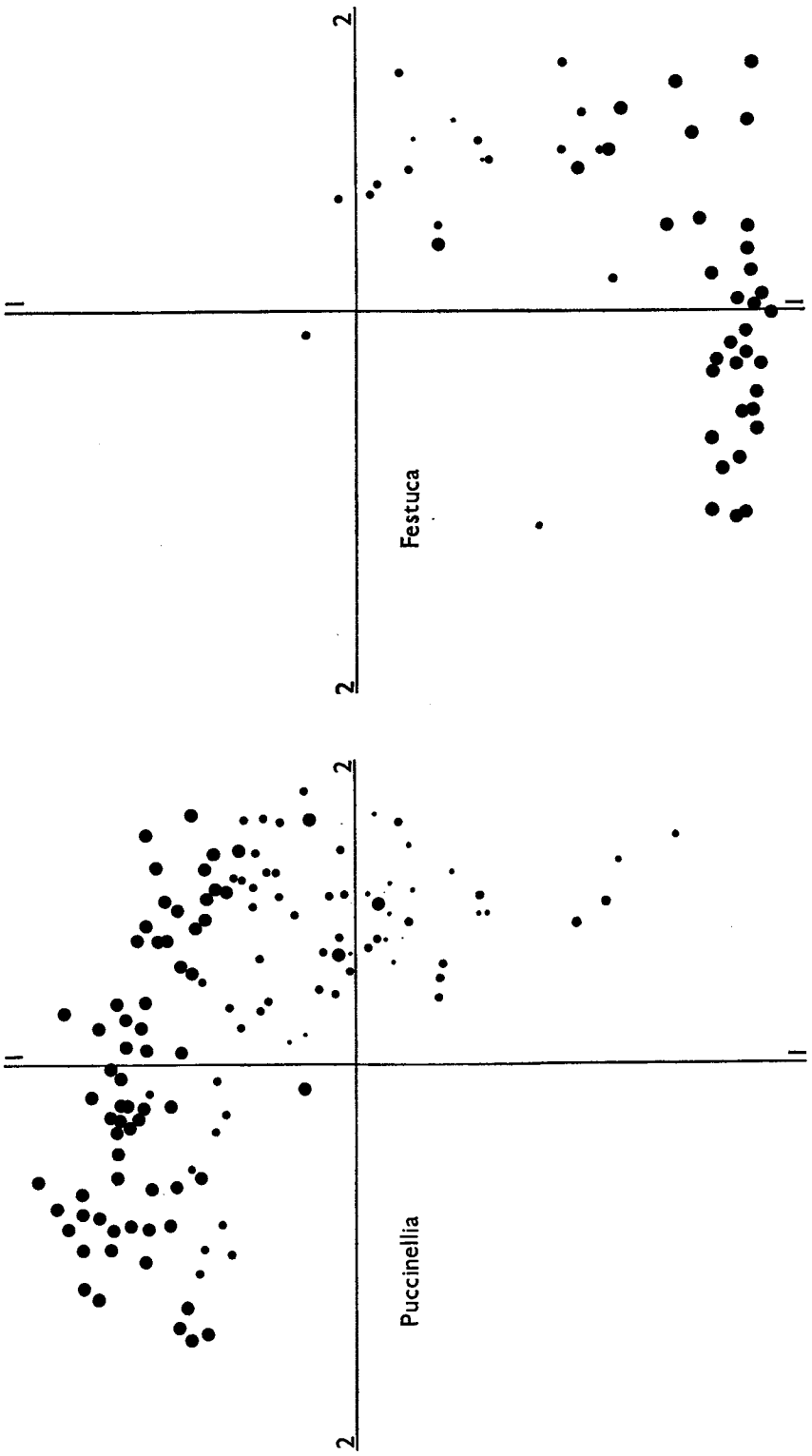


FIG. 9.

FIG. 10.

Figs. 9-11.

These diagrams show the scatter of plots containing the species named, the ordination axes being the first two components of the principal component analysis. In Figs. 9 and 10, large dots represent quadrats with Domin cover 6-10, medium cover 3-5, and small dots 1 or 2. In Fig. 11, the dotted lines enclose areas where the named species have generally high Domin values. The line 0-0 connects assemblages dominated by species other than *Puccinellia* or *Festuca*; it lies almost parallel to the second axis, but the separation between them is probably due to there being more *Puccinellia*-dominated plots than *Festuca*-dominated.

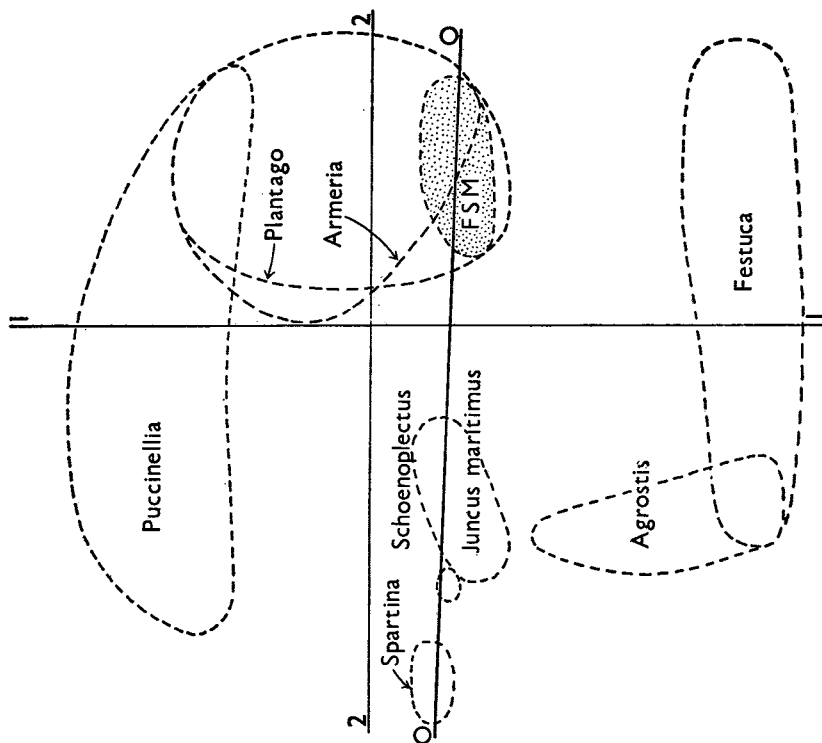


FIG. 11.

At lower levels *Puccinellia* may be present in very small amounts, but in any case the dominants are *Armeria* or *Plantago* or *Juncus gerardii*, or sometimes (and rather strikingly) *Limonium*. The community may thus tentatively be called the forb salt marsh community, or FSM. The dominants in the FSM are also important members of the general salt marsh community (GSM), and may be regarded as a background against which the grasses vary independently. This is represented diagrammatically in Fig. 12. I do not know what factors are responsible for the absence of grasses from

Table 2. Vertical position of the non-grassy general salt marsh community (FSM), given as metres over CD; *Festucetum* defined as quadrats with *Festuca* scoring Domin 6 or more

Marsh	Range of FSM	Lowest <i>Festucetum</i> on same marsh
Gann saltings	6.80-7.13	6.77
Spreadeagle Pill	6.80-6.83	6.68
Angle	6.52-6.89	6.71
Little Milford	7.01	7.28

the FSM, but suspect that it may be the result of interspecific competition. Miss J. M. Baker has told me that *Aster*, *Plantago*, *Armeria*, *Glaux*, *Triglochin* and *Spergularia* are all much more resistant to repeated oil pollution than are *Puccinellia* or *Festuca*, and it may be that in certain natural situations the two latter are at some comparative disadvantage.

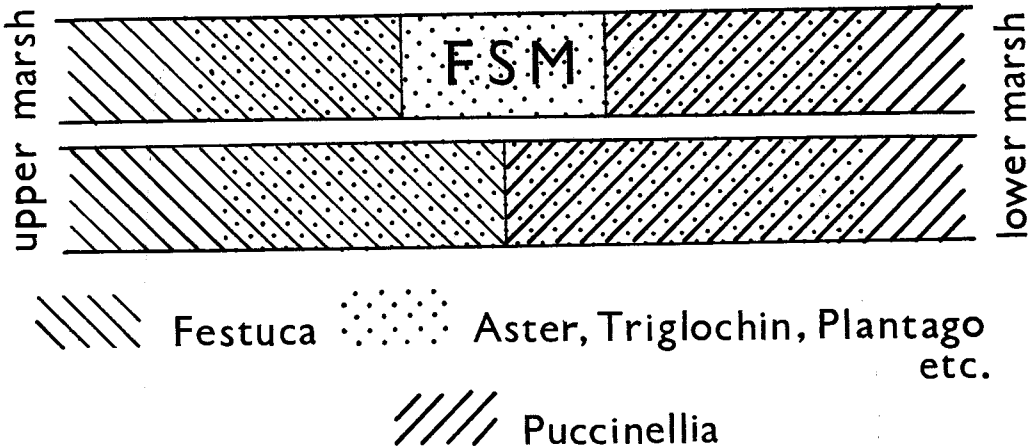


FIG. 12.

Diagram to show floristic relationships between the *Festucetum*, *Puccinellietum* and the non-grassy forb salt marsh (FSM). The normal situation in Milford Haven is that shown in the lower part, where the *Festucetum* is in direct contact with the *Puccinellietum*.

The FSM is not, of course, homogeneous throughout the Haven, and merges with the GSM by way of sites with scattered *Puccinellia*, as at Martinshaven and on low mounds on the Gann saltings, whilst at Little Milford the very flat FSM has both scattered small plants of *Puccinellia*, and spreading tufts of *Festuca*, suggesting a rather unstable balance at present.

Puccinellietum

The lowest *Puccinellietum* is usually composed of the one species only, but is soon invaded by *Limonium*, *Aster* and perhaps *Triglochin*, and then other species are progressively added as the marsh rises in height, leading to a GSM with dominant *Puccinellia* and 5 or 6 secondary species. It is difficult to divide the GSM further, as there is much variation in detail from marsh to marsh (as there is also in the communities called "general salt marsh" by other writers), probably reflecting small differences in drainage, etc.

The absence of *Limonium vulgare* from Milford Haven is noteworthy, and Boorman's comments (1967) on the two *Limonium* spp. should be consulted, since his paper also utilized data from several of the Haven marshes. My figures for the vertical range of *L. humile* are in almost exact agreement with Boorman's, being about one metre (see Fig. 8). In view of his comments on the sensitivity of *Limonium* to pollution near large ports, its distribution in Milford Haven should be carefully watched.

On many marshes in S.E. England, the eradiate form of *Aster tripolium* (var. *discoideus*) is the commonest at low levels in this very variable species. In Milford Haven this does not appear to be true, and plants with different numbers of ray florets seem to be found at all levels. However, Dr. A. J. Gray tells me that although fully rayed and rayless are homozygous states, crosses between them are very variable in ray expression. Intermediate inflorescences (Fig. 13) may thus represent plants of diverse genotype, especially since there can be great variation between inflorescences even on a single plant. Other variants in this species include the var. *crassus* (see Clapham *et al.*, 1942), which occurs on sea cliffs (as, for example, at Barafundle Bay) and is probably an example of ecotypic differentiation.

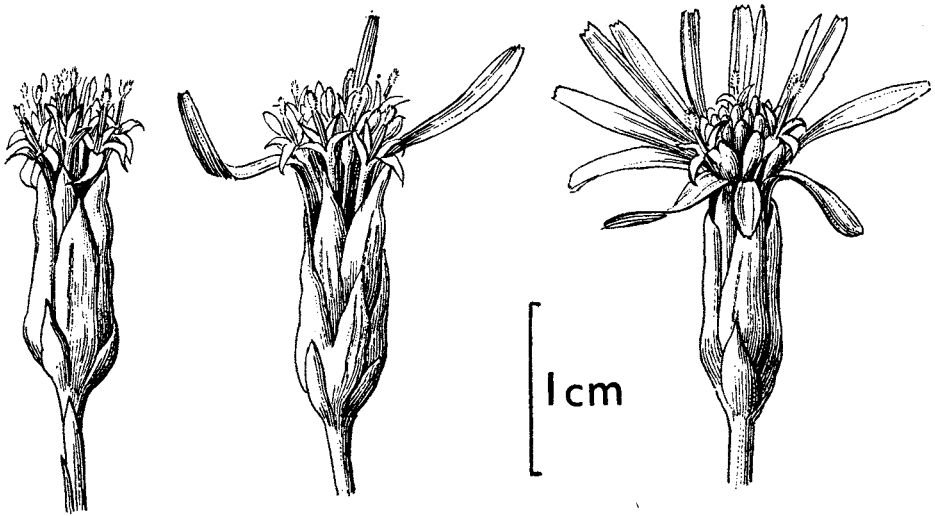


FIG. 13.

Heads of *Aster tripolium*. Left: var. *discoidea*; centre: intermediate form (see text); right: var. *tripolium*.

Festucetum

There is usually an abrupt transition to the *Festucetum*, the lower part of which often contains the main GSM species, apart from *Puccinellia* and *Armeria*. These species are often represented by large well-separated plants, especially when the *Festuca* is rank and ungrazed. The normal transition to non-saline grassland is indicated by the appearance of *Agrostis* (if wetter, and often beside streams) and *Agropyron pungens* (if drier). On a number of marshes there is a conspicuous band of *Artemisia maritima*, flowering in the upper part of the *Festucetum*, but mostly scattered and vegetative lower down.

Lower marsh communities

The communities so far discussed constitute the continuous gradient of environment-and-vegetation which starts with low marsh colonized by *Puccinellia*, and ends with the transition from *Festucetum* to non-saline grassland. It does not start with a *Salicornietum* or *Spartinetum*, and does not normally end with a *Juncetum maritimi* in Milford Haven, in spite of schemes such as those of Chapman (1960b,

pp. 158 and 159). Dense stands of *Salicornia* certainly occur at low levels (often of tetraploid forms, as on the low mud banks of the Gann, shown in Fig. 2), but they play little part in the main succession. The same is true for *Suaeda* on rather stonier ground. Both are opportunist genera, which show enormous variations in population size from year to year. The lowest flowering plant community is that of *Zostera*, which I have seen at Spreading Pill (4·63 to 5·20 m. CD), the east side of Angle Bay (c. 4·88 to c. 5·85 m. CD) and at Bentlass (4·25 to 5·00 m. CD). Mr. T. A. W. Davis also has records from near Pickleridge (grid ref. 812070) and Landshipping, though he believes the species is decreasing at present in Milford Haven. The plant (Fig. 14) grows on very wet substrata, often in shallow pools which persist at low tide. Its branched underground rhizomes are far more substantial than the delicate leaves and may help in stabilizing very fluid mud but, like *Suaeda* and *Salicornia*, I do not think this species is fundamental to the flowering plant succession in Milford Haven.

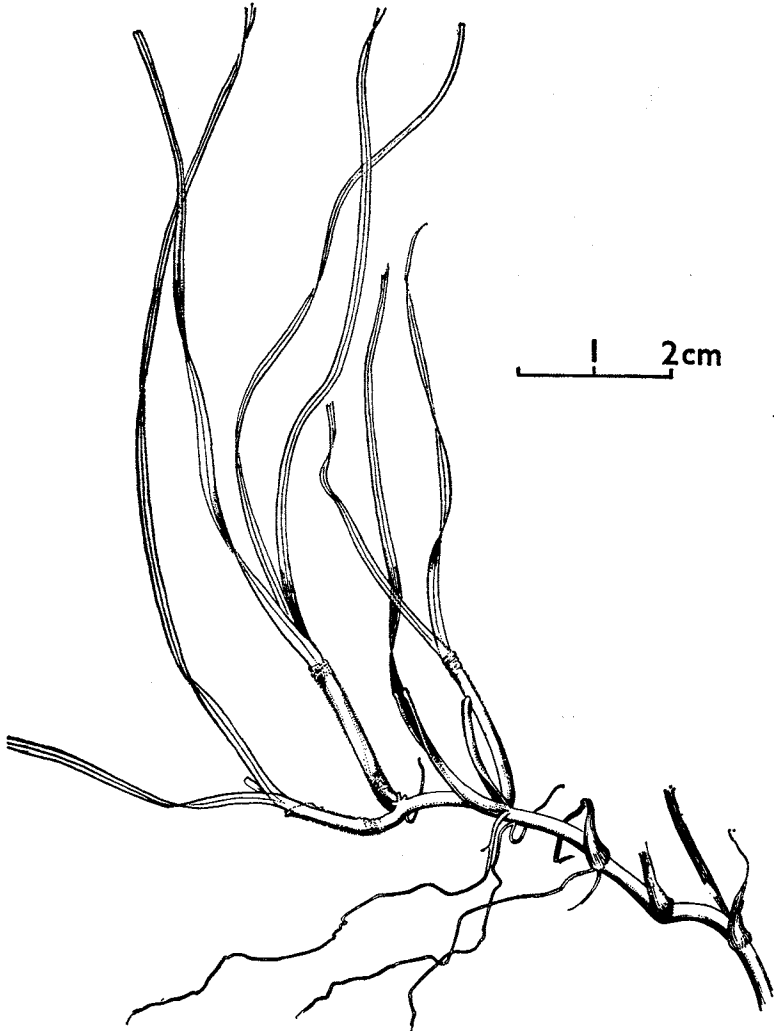


FIG. 14.

Zostera sp. from Sandyhaven. Because the leaf sheaths in this material are split, it should be referred to *Z. noltii*.

Halimionetum and Spartinetum

On the Gann saltings there are well-marked vegetational mosaics which are closely linked with microtopography, both in regard to species composition and total species number, there being little beyond *Puccinellia* in the low areas, and up to 8 or 9 on the higher parts. Using a chi-squared test for interspecific association in 200 6 in. (about 15 cm.) square quadrats, I found that in this mosaic area the species formed 3 groups. (1) *Puccinellia* was present in 95 per cent of the squares, though varying much in abundance. (2) a group of 8 species (*Armeria*, *Aster*, *Cochlearia*, *Limonium*, *Salicornia*, *Spergularia*, *Suaeda* and *Triglochin*) with high chi-squared values, and forming a coherent GSM group, and (3) two species almost totally isolated from the rest, *Halimione* and *Spartina*. These last two grow in pure stands, with almost total exclusion of all other species, and I interpret their lack of association as meaning that they show discordant distribution patterns superimposed on the general vegetation with which they are not in equilibrium.

In the case of *Halimione*, the plant shows signs of recent spread on the Gann saltings. Aerial photographs show annular colonies of this species, behaviour typical of a primary colonizer, and on some salt marshes in southern England it has spread rapidly following artificial draining. Chapman (1950) describes *Halimione* as being sensitive to soil waterlogging, especially in the seedling stage. This suggests that if it has arrived in new areas recently, and conditions there are favourable, it is a species that can spread fast. The enclosing banks of the "inned" marshes on the Gann saltings were breached round about 1920 and have subsequently reverted to secondary marsh, and it is here that *Halimione* is spreading most, although it is also extending its range on the unenclosed wild marsh. On the Gann saltings *Halimione* is particularly conspicuous round the sides and heads of creeks, and its dense growth may completely cover narrow creeks (see Fig. 5). On stonier shores it is also quite common where there is a thin mud coating, but it becomes less common in the upper reaches of the estuary and according to Mr. T. A. W. Davis, reaches its upper limit between Little Milford and St. Issells.

The general history of the origin and spread (mostly by Man) of *Spartina* is now well known, and it is certainly a new arrival in Milford Haven. According to Mr. Davis, it is believed to have been introduced deliberately during the 1939-1945 war, and it was not seen at Sandyhaven or the Gann until about 1952. The widespread plant is the allotetraploid which originated in Southampton Water about 1890, and which has subsequently been distributed from "nurseries" because of its ability to stabilize soft mud. The organization of the rhizome system in rapidly growing clones is described by Caldwell (1957). In Milford Haven its present extension is certainly due to there being a vacant habitat below the *Puccinellietum*, since *Suaeda*, *Salicornia* and *Zostera* can hardly offer any competitive resistance. The lowest level of *Spartina* establishment in Milford Haven is at about 5.0 m. CD, with some evidence of a general rise towards the lower part of the Haven, although there is much scatter, and my record for Angle of 4.94 m. CD is the lowest I have for *Spartina* in the Haven. The isolated plants soon "meadow" to form a sward, and from this sward invasion of higher levels of the marsh takes place. This is mostly by seed, and, although the seed output per plant is generally not very good, their immense numbers ensure that enough seeds are dispersed to permit some to get established, especially beside pans and creeks where there are temporary bared sites. I have

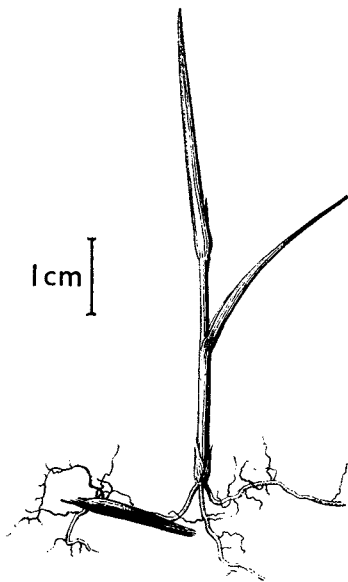


FIG. 15.

Young seedling of *Spartina* with testa still attached. Wet sandy ground near high water mark, Gann saltings.

found many seedlings on rather open stony ground at Lawrenny, and a dense sward of young plants on sand on the outwash deposits from the Dale Sand and Gravel workings at Mullock Bridge. A seedling, with testa still attached, is illustrated in Fig. 15. At the Mullock Bridge site, seedlings have been seen forming an intermittent sward over a distance of about 20 metres, and with a maximum density of 63 per 100 cm.² Although this is a high value for *Spartina* seedlings, Goodman *et al.* (1969) recorded a density twice as high as this for plants on open mud. In conclusion it should be noted that the generally assumed history of the origin of the tetraploid *Spartina* must be inferred to be correct (although it has not been confirmed experimentally), that the original chromosome counts were mostly incorrect, and that the common allotetraploid has no valid Latin binomial name. Strictly, *S. townsendii* should be applied to the diploid, sterile plant only. The allotetraploid has been called *S. anglica* (Hubbard, 1968), but this is not a validly published combination. Marchant (1967 and 1968) should be consulted for details, whilst a general summary of the biology of *Spartina* in Britain is given by Goodman *et al.* (1969).

Upper marsh communities

The remaining salt marsh communities are those which are best developed near the top edges of the marshes, often under the influence of fresh water. These communities often consist of pure stands of *Juncus maritimus*, *Scirpus* or *Schoenoplectus*, and if the fresh water flow is sufficient they may extend low down the marsh. Thus at Martinshaven *Schoenoplectus* goes down to 6.15 m. CD, and at Little Milford *Scirpus* down to 5.5 m. CD, whilst a striking situation is seen west of the marsh by the old quay at Landshipping where there is a diverse assemblage of species including *Iris pseudacorus*, *Oenanthe lachenalii*, *Eleocharis uniglumis*, as well as *Juncus maritimus*, *Scirpus* and *Schoenoplectus*. The last two species extend down to the Spartinetum and merge

with it, all other saltmarsh communities being absent. The zone where the sloping land surface meets the more level marsh, at EHWS, is a tension zone or ecotone between fresh and salt. Several uncommon species are found in this area, such as *Triglochin palustris* and *Althaea officinalis* at Martinshaven, whilst *Carex extensa* and *Parapholis strigosa* occur in the uppermost parts of a few marshes. *Beta maritima* is almost confined to the strand line, where its seeds are carried by the tide, still enclosed in their buoyant perianths. It is commonest on open and rather stony shores where it may reach a very large size. The uncommon glasswort *Salicornia pusilla* also has seeds dispersed by the tide (see Dalby, 1963). It is scattered over several marshes in the upper part of the GSM, being especially common at Angle and on the Gann saltings in places, but goes no further up the Daucleddau than Lawrenny and is more restricted to the lower parts of the Haven than any other salt marsh Angiosperms.

Summary of seral relationships

The seral relationships between the main communities are given by way of a summary in Fig. 16. Their sequence is primarily determined by the height of the

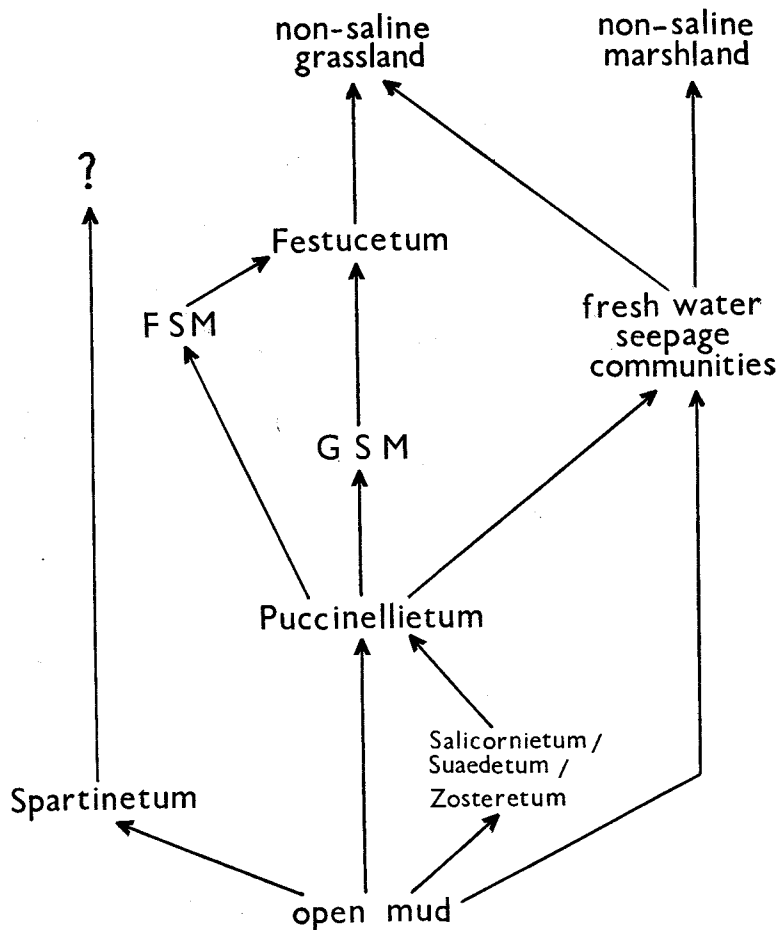


FIG. 16.

Putative seres in Mildford Haven salt marsh communities. Note that local facies and unusual modifications are omitted.

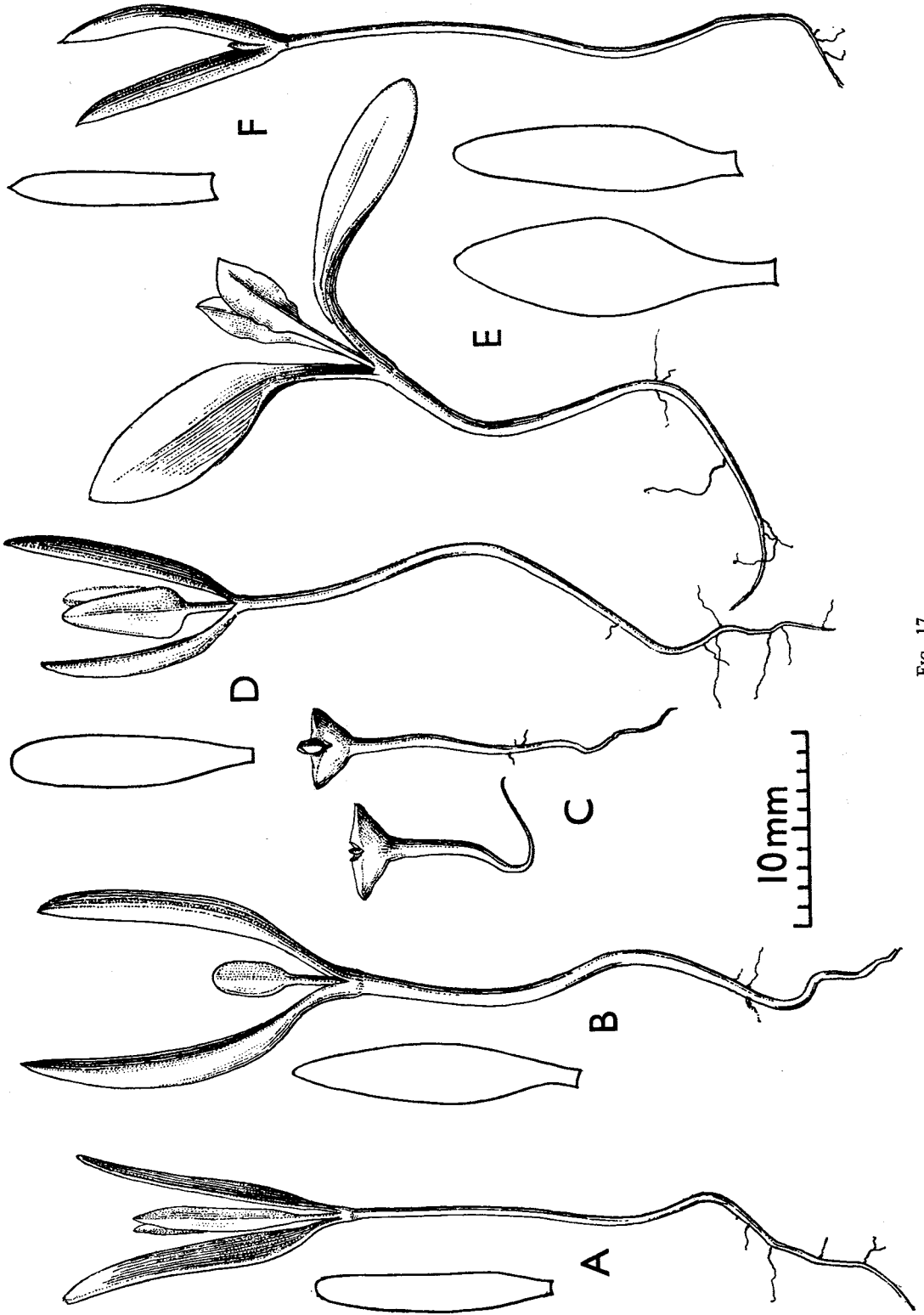


FIG. 17.

Seedlings of salt marsh dicotyledons. I. *Chenopodiaceae*. A: *Atriplex littoralis* B: *Halimione portulacoides* C: *Salicornia* spp. D: *Atriplex hastata* E: *Beta maritima* F: *Suaeda maritima*. Outlines are of cotyledons see from above.

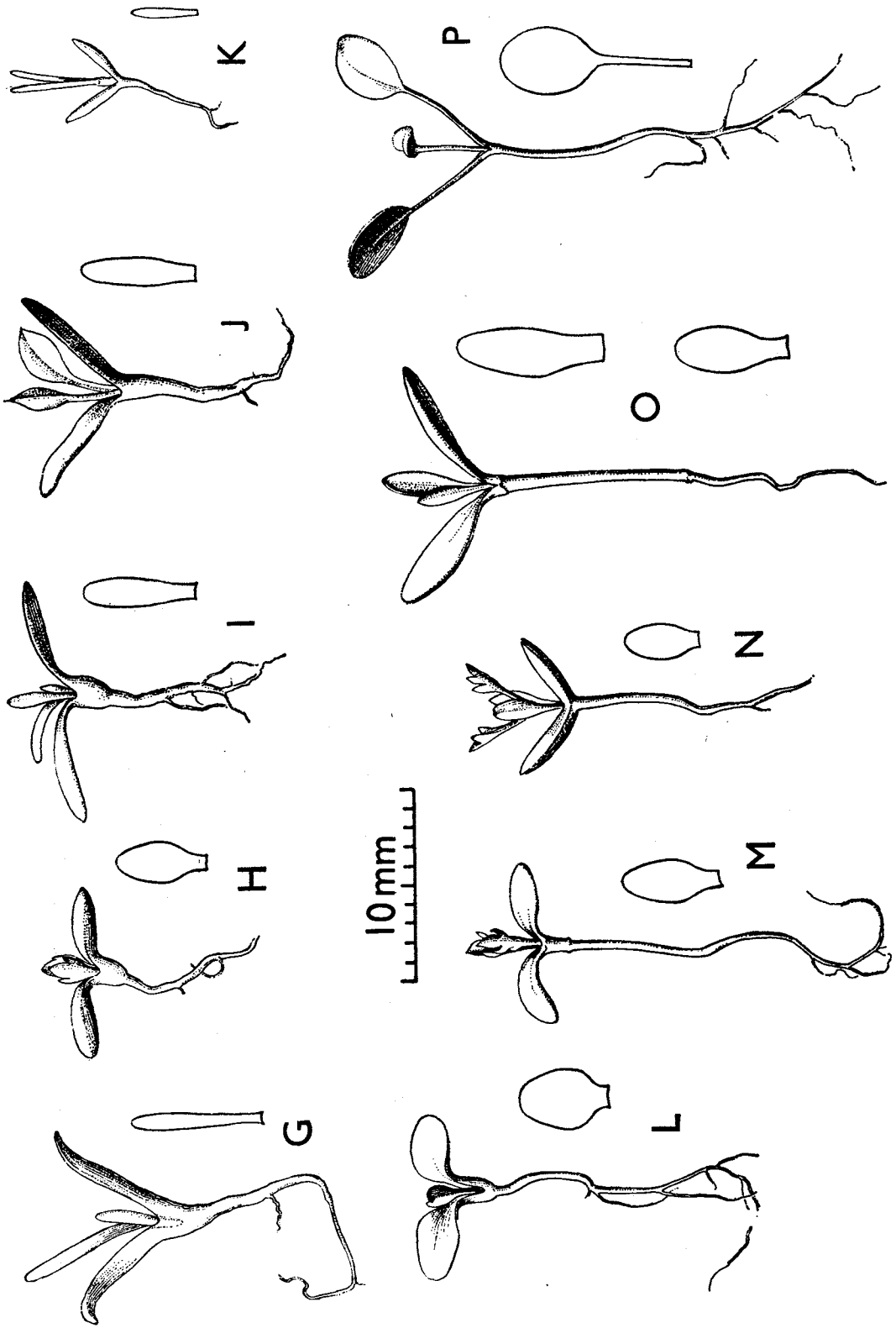


FIG. 18.

Seedlings of salt marsh dicotyledons. II. Other families. G: *Plantago maritima* H: *Plantago maritima* I: *Armeria maritima* J: *Limonium humile* K: *Spergularia media* L: *Sonchus* sp. M: *Tripleurospermum maritimum* N: *Artemisia maritima* O: *Aster tripolium* P: *Cochlearia anglica*. Outlines arc of cotyledons seen from above.

marsh in relation to the annual tide cycle, with local facies caused by variations in soil water content, soil aeration, salinity, etc., and it is impossible to include these variants in a single diagram.

EFFECTS OF ENVIRONMENT ON ESTABLISHMENT

Seed germination and seedling survival

The final plant communities consist of assemblages of species approximately in equilibrium with each other and with the environment, those not suited having either failed to germinate or having died at the seedling stage. Seeds of many salt marsh species become widely distributed (mainly by water currents), and seedlings may be found at levels and in communities where mature plants are rarely or never seen. The factors leading to this considerable death of seedlings are rarely known, and much more field and experimental study is needed. In order to facilitate such studies, drawings are provided in Figs. 17 and 18 of almost all the dicotyledons to be found on the Milford Haven salt marshes. Apart from *Glauca*, the only species omitted are some such as *Samolus valerandii* which are found only at the extreme tops of a few marshes.

Notes on seedling identification

Some species (e.g. *Artemisia* and *Glauca*) are very rarely seen as seedlings, since most apparent seedlings prove to be surfacing shoot apices. Others, such as *Limonium humile*, seem to be thinned out rapidly, since whilst seedlings are locally common in May, young plants are difficult to find later in the year.

Seedlings of most species can vary considerably in size of cotyledons and length of hypocotyl, and in the development of brownish or red pigments. Etiolated growth (very marked at times in *Aster* and *Cochlearia*) may follow germination in the shade of *Halimione*. Many species also vary in the succulence of their cotyledons, this being most marked in *Aster* and *Atriplex hastata*, although there is a general tendency for succulence to increase with age.

Atriplex littoralis. First leaves narrow, parallel-sided, upper surface with few globular hairs; very rare in Milford Haven (see Dalby, 1969b).

Halimione. Cotyledons usually clearly unequal in size, shiny above and usually olive green.

Salicornia. Cotyledons triangular and very succulent; seedlings very variable in size and colour, this variation partly resulting from several species being present in Milford Haven, even though they are not distinguished in this study.

Atriplex hastata. Cotyledons usually rather glaucous and with a matt surface, though shiny if very succulent; first leaves widest at base, upper surface with numerous globular hairs.

Beta. Cotyledons robust, shining and spreading; hypocotyl and lower surface of cotyledons usually bright red; strand line.

Suaeda. Cotyledons nearly circular in section, apiculate at apex.

Plantago maritima. Cotyledons divergent and straight with slightly recurved tips; first leaves very unequal in size, straight.

P. coronopus. Cotyledons fairly fleshy; first leaves lobed, lobes relatively broad (and lacking the minute colourless apiculus seen in *Matricaria*).

Armeria. Cotyledons stiff-looking, and usually red beneath, sometimes persisting until at least five leaves have developed; hypocotyl usually bright red; first leaves narrow and parallel sided; autumn.

Limonium. Very similar to *Armeria*, though hypocotyl possibly slightly less swollen; first leaves wider and shortly acuminate; spring.

Spergularia. Seedlings very numerous and "grass-like"; cotyledons and hypocotyl pale green; leaves brighter green and with small pointed stipules at their bases.

Sonchus sp. Cotyledons glaucous and markedly water-repellent above; first leaves with multicellular hairs on concave inner surface; strand line.

Matricaria maritima. Cotyledons slightly less fleshy than in *Plantago coronopus*, deep green with minute shining spots on upper surface; first leaves lobed, lobes relatively narrow and with minute colourless apiculus at tips; strand line.

Artemisia. Cotyledons succulent; first pair of leaves undivided, subsequent leaves pinnately lobed and grey green; rare.

Aster. Cotyledons somewhat fleshy, olive green or brownish if unshaded; first leaves fleshy and markedly concave.

Cochlearia. Extremely variable in size; the only species with very distinctly petiolate cotyledons; autumn.

Glaux. No seedlings seen.

Most salt marsh species germinate best in fresh water (or, according to Boorman (1967), in fresh water after pre-treatment with salt water for *Limonium*), and in nature these conditions will be caused by rain during periods of non-tidal exposure. The time of year for germination varies with the species, thus I have observed the following in Milford Haven: *Cochlearia anglica* and *Spergularia*, mostly in the autumn (a few in the spring), *Beta*, January to March, whilst the majority of species germinate in April and May. The first are likely to be *Suaeda* and *Salicornia*, followed by *Atriplex* spp., *Halimione* and *Artemisia*, and *Limonium* and *Armeria* in early May. Variations are marked from year to year, whilst delayed germination is common in rather drier sites. Several days are needed following germination to allow the seedlings to develop roots long enough to draw on nutrients in the soil, and to give physical support. Weihe (1935) showed that in the Dovey estuary *Salicornia* needs 2–3 days for establishment, so attention should be given to the duration and time of year of periods of non-tidal exposure.

Physiology

Although salt marsh plants can obviously endure saline conditions, most actually grow better (i.e. attain a greater size) in non-saline soils (see Chapman, 1947, for *Suaeda*, and Chapman *et al.*, 1942, for *Aster*), whilst Gillham (1957) reports on the good growth of some 16 species in non-saline conditions, provided that the plants are kept weeded in cultivation. From such observations, one may adopt the simple classification into (1) obligate halophytes, which must have a saline environment in order to survive (marine algae, *Zostera*), (2) facultative halophytes, which can endure salt conditions (most salt marsh plants), and (3) glycophytes, which are killed by salt at concentrations encountered inter-tidally. Seedlings of glycophytes are often seen along the drift line, but are later eliminated after spring tides. No easy definitions are really satisfactory, however: a tidal covering which affects foliage may have no effect on the root system, whilst cliff ecotypes of, say, *Armeria maritima* are sometimes damaged by spray during storms. Also, the fluctuating salinities in estuaries lead to problems in defining categories.

Halophytes do not live in conditions of "physiological drought" as they prove to have transpiration rates as high as glycophytes, and can absorb water from high salinities in the soil solution, and in some instances directly from sea water during tidal cover (see discussion in Chapman, 1960b, p. 311). Vigour of growth is, however, reduced at very high salinities resulting in stunting of the whole shoot.

Salinity and tidal cover

Variations in salt marsh soil salinities have been studied by Chapman (1938) for Scolt Head, and by Ranwell *et al.* (1964) for Poole Harbour. Chapman (1960b) lists the

factors controlling soil salt content (p. 84) and water content (p. 110). No detailed studies have been carried out to my knowledge on the Milford Haven marshes, but the little data that there is show that there are marked gradients up the shore, that towards EHWS surface salinities are much affected by recent tide and weather conditions, and that at depth in the soil the salinity often falls due to percolation of fresh water. Ranwell (1964) argues that, whilst salinity may be the limiting factor for *Phragmites communis* in Poole Harbour, it is submergence time that controls the lower limits for *Spartina* (6 hrs./tide, with up to 9 hrs./tide out of the growing season). Some comparable figures are given in Table 3 for three species in Poole Harbour and Milford Haven.

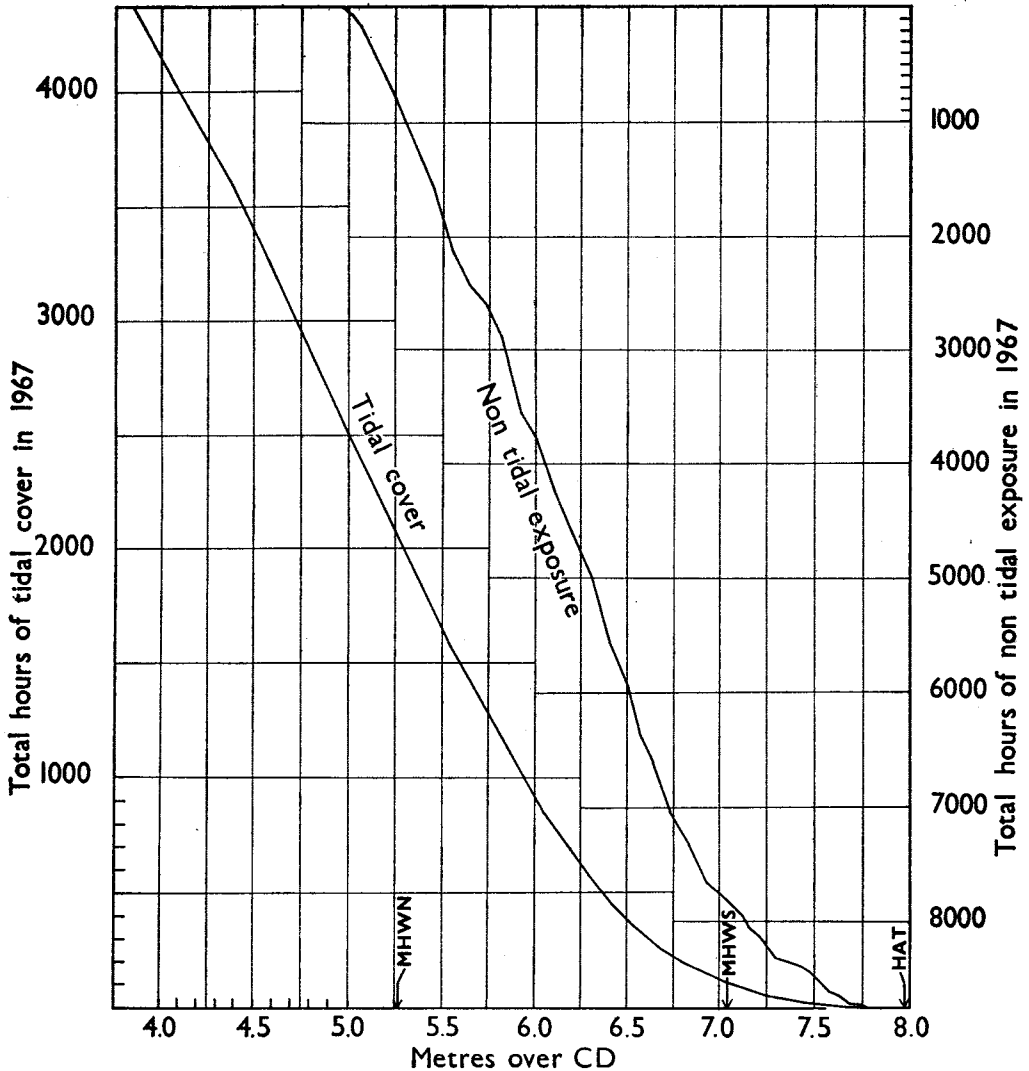


FIG. 19.

Total annual tidal cover and total non-tidal exposure (more than two days without tidal cover) in relation to height over chart datum. Based on tide tables for Milford Haven, 1967.

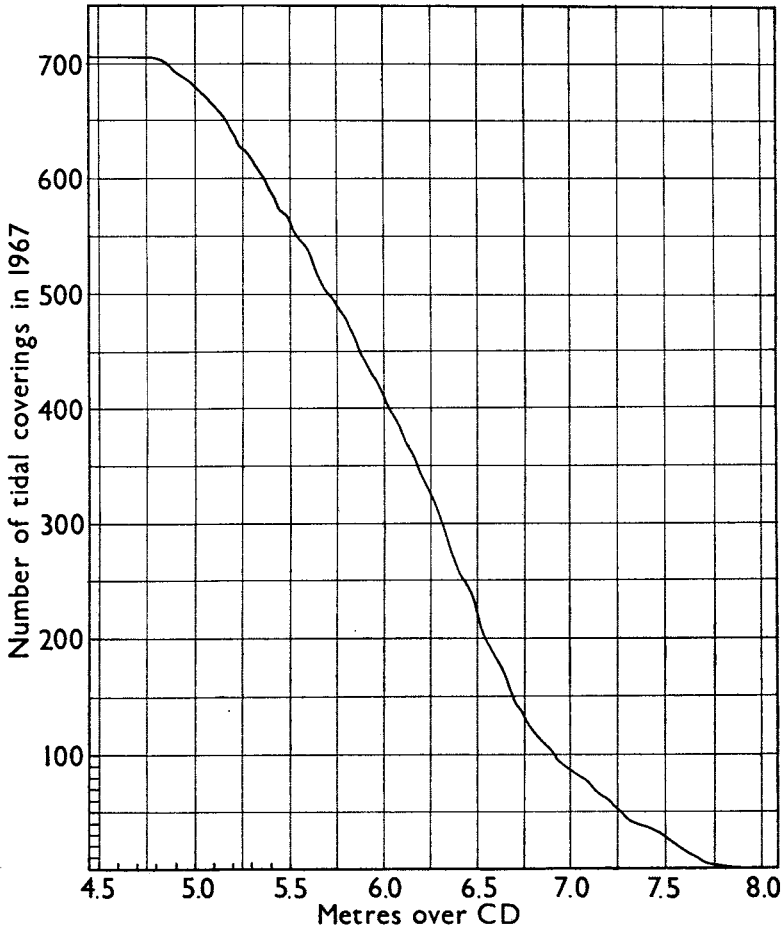


FIG. 20.

Number of tidal coverings in relation to height over chart datum. Based on tide tables for tidal predictions for Milford Haven, 1967.

Table 3. Total annual submergence for three species at their lower limits

Species	Lower limit, Poole Harbour (Ranwell, 1964)	Lower limit, Milford Haven
<i>Agrostis stolonifera</i>	250 hrs./yr.	200 hrs./yr.
<i>Festuca rubra</i>	1,260 hrs./yr.	400 hrs./yr.
<i>Spartina</i> "townsendii"	5,800 hrs./yr.	5,200 hrs./yr.

My figures are obtained from a curve for total tidal cover based on the tidal prediction for Milford Haven in the Admiralty Tide Tables for 1967. This curve, together with that for non-tidal exposure (in this instance, more than 2 days continuous exposure), is given in Fig. 19. The total number of submergences at different levels during the same year is given in Fig. 20.

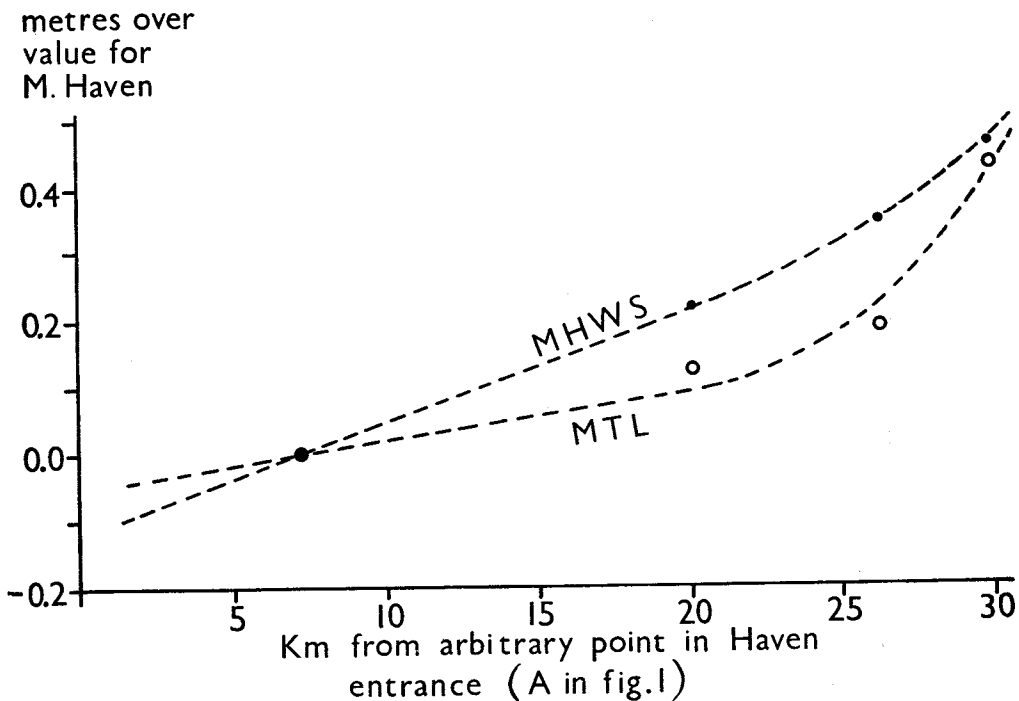


FIG. 21.
Rise in water levels up Milford Haven and the Dauceddau, based on data for mean tide level and mean high water springs.

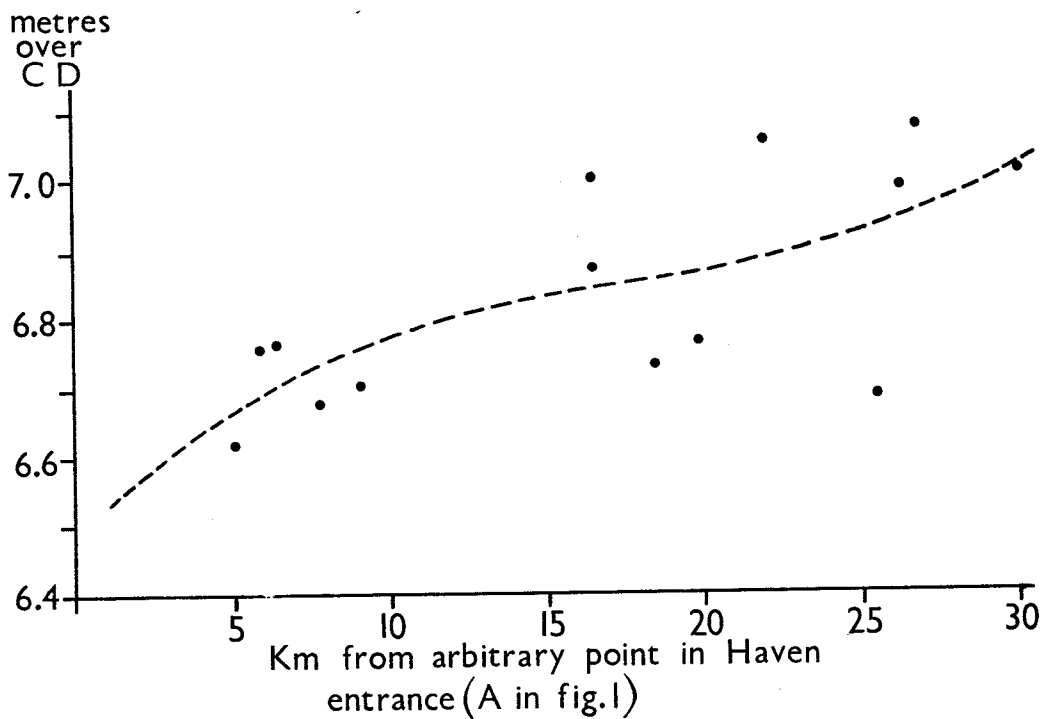


FIG. 22.
Rise in elevation of lowest Festucetum (defined as quadrats with Domin value of 6 or more for *Festuca*) up Milford Haven and the Dauceddau. The dotted line is a fitted third order polynomial regression curve.

Mathematical assumptions made in the preparation of Figs. 19 and 20 are: (1) the time interval between successive high tides is assumed to be constant (12.413 hrs.) throughout the year, (2) the tide curve is assumed to be constant throughout the spring-neap cycle, and I have used a curve drawn midway between the extremes shown in the Admiralty Tide Tables, 1967 (p. 102), and (3) I have had to assume that temporary meteorological disturbances, which cannot be taken into account when preparing the tables, will not cause significant deviations over a long period. Furthermore, any such calculations fail to take into account the time it takes recently covered vegetation or soil to dry out, when the tide ebbs. This is linked with evaporation rates in vegetation of different heights and in different weather conditions. Tidal data are calculated for the port of Milford Haven itself, the recording tide gauge being at Hubberston (grid ref. 893053) on the Milford Haven Conservancy Board's jetty.

High tide and mean water levels may be expected to rise in the upper parts of the estuary due to narrowing of the channel and ponding-back of the river waters. Values for this rise in levels have been kindly given to me by Dr. R. B. Whittington, and I have replotted some of his data (for mean tide level and mean high water spring tides) in Fig. 21. The curves in this diagram are not fitted mathematically. Below, in Fig. 22, are figures for the rise in level of the Festucetum up the estuary. Although the correspondence between the two figures is not exact, there is enough similarity to support the suggestion that vegetation zones rise up the estuary system because the water levels rise. Ranwell *et al.* (1964) note a rise in marsh levels up Poole Harbour, though they give no figures in support.

My use of the lower limit of the Festucetum is to be preferred to that of the upper limit of the Puccinellietum, since *Puccinellia* may grow abnormally high in sites of locally impeded drainage. Examples of this are seen at Mullock Bridge, Pennar, and at Lawrenny (see Fig. 6). In these localities, Puccinellietum may rise as much as 40 cm. above the lowest limits of the Festucetum, suggesting that it is some aspect of soil waterlogging that separates the two species in the field. At Westfield Mill, the Festucetum extends unexpectedly low (6.43 m. CD), and the same is true for the absolute lower limits of *Festuca* and most other species, showing that the whole marsh zonation is depressed at this site. Figures for four species are given in Table 4.

Table 4. *Depression of lower limits at Westfield Mill*

Species	Expected approximate lower limit (metres over CD)	Observed lower limit (metres over CD)
<i>Agrostis stolonifera</i>	7.04	6.43
<i>Atriplex hastata</i>	6.80	6.40
<i>Festuca rubra</i>	6.80	6.43
<i>Glaux maritima</i>	6.64	6.13

This effect is certainly due to lowered salinity in the narrow inlet, especially in times of flood in the stream outflow. During a rising spring tide on 23 November 1969 water extending over the salt marsh one hour before the forecast high tide of 6.77 m. CD had surface salinities of between 2.29‰ and 5.51‰, whilst surface water at Neyland (grid ref. 967053), where the inlet joins the main channel, had a salinity of 26.44‰. One important consequence of this depression of levels is that many species can endure greater lengths and frequencies of tidal cover, provided that the

water salinity is lowered. For *Festuca*, this increase in annual cover is up from 400 to 850 hrs./yr., for *Agrostis* 200 to 850 hrs./yr., for *Atriplex* from 400 to 900 hrs./yr., and for *Glaux* from 540 to 1,500 hrs./yr.

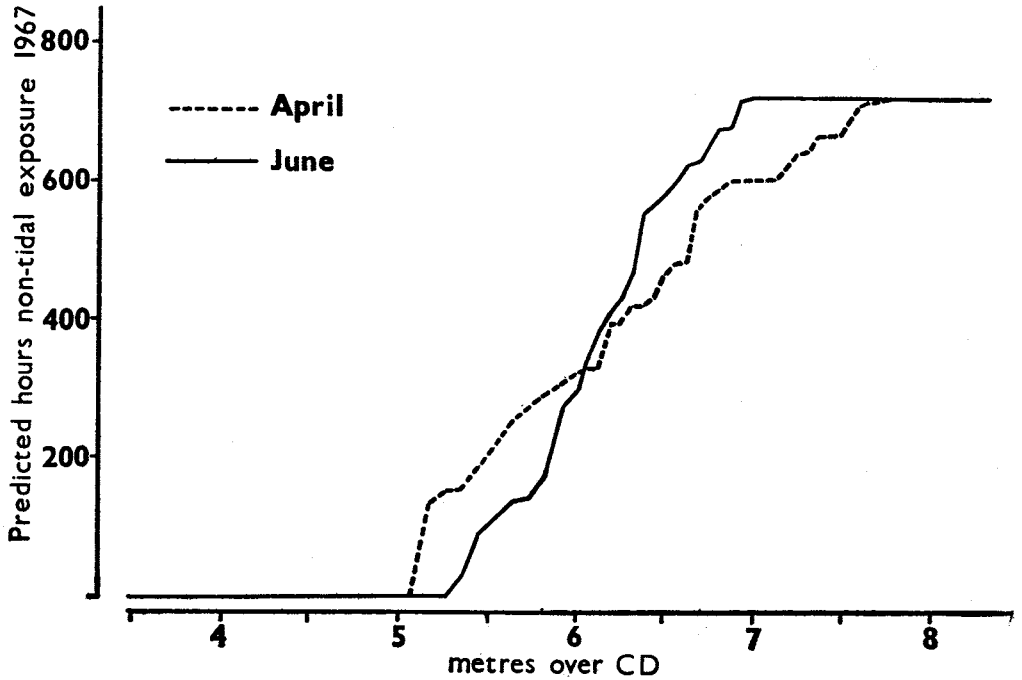


FIG. 23.

Total non-tidal exposure (more than two days exposure without tidal cover) in relation to height over chart datum for two different months in 1967. Based on tidal predictions for Milford Haven.

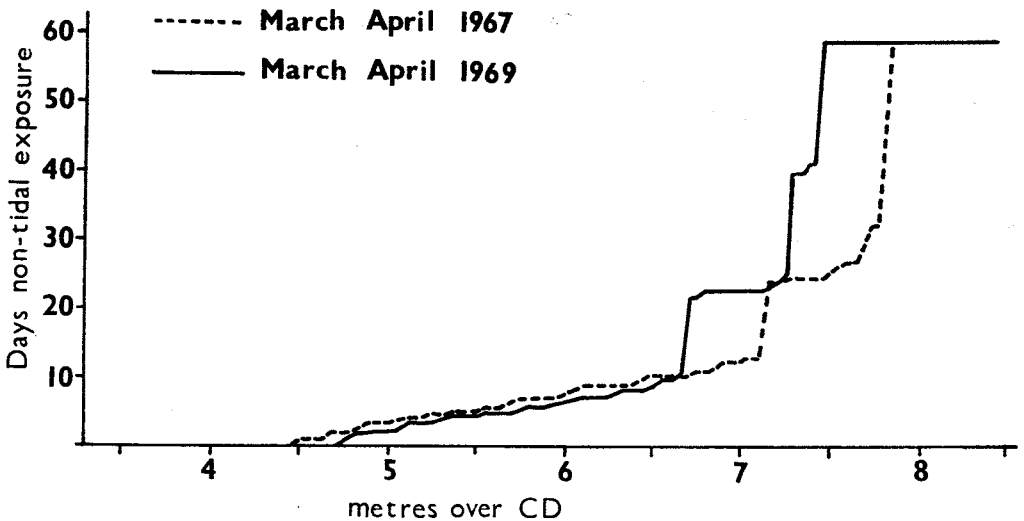


FIG. 24.

Longest period of continuous non-tidal exposure (more than two days without tidal cover) in relation to height over chart datum, for the same period in two different years. Based on tidal predictions for Milford Haven, 1967 and 1969.

Tide factors and critical levels

Various authors have attributed visible zonations of plants and animals, especially on rocky shores, to what have been termed "tide factors" (see discussion in Evans, 1957), where there are critical levels at which there is a sudden change in the times or frequency of non-tidal exposure or tidal cover. Reference to Fig. 23 shows that there can be marked changes in the position of critical levels from month to month, depending mostly on the heights of the spring tides, whilst Fig. 24 shows that there can also be variations from one year to another. From such data I feel that critical levels determined from one year's figures alone may be misleading, and that one should bear in mind longer term variations. A further point is that it may not be clear which of the factors is the one that is actually limiting for a particular species since their significance can vary during a single growing season. Thus tidal cover is only of serious consequence to *Salicornia* during the days before the seedling is fully established, after that it may be covered frequently or not at all, and still proceed to maturity.

BIOTIC EFFECTS

Introduction

The salt marshes may be regarded as showing several contemporary changes, proceeding at different rates. Some (like those resulting from accretion and erosion) are wholly natural, whilst others are due to the activities of Man either directly or indirectly. The changes following the introduction and spread of *Spartina* have been mentioned, but their full scale is not yet known, and *Spartina* meadows may well engulf many salt marsh areas, as well as possibly causing major changes to sedimentation and current patterns in the Dauceddau and its branches. The changes due to Man may be grouped under the headings of grazing and trampling by animals, land reclamation and oil pollution.

Grazing

Unlike marshes on more sandy substrata, those in Milford Haven are not heavily grazed by cattle, although animals have access to many for short periods. This is particularly true of land in the upper parts of the estuary branches (e.g. at Mullock Bridge and near St. Issells), though cattle are also sometimes seen grazing on small areas of *Festucetum* at Bentlass and Lawrenny. Grazing may be expected to favour the increase of *Festuca*, and the decrease of fleshy species unless they possess a rosette habit close to the ground. A comparison of two stretches of shore at Lawrenny, at approximately 7.25 m. CD, separated until 1968 by an electric fence showed a clear difference in general vegetation height between grazed and ungrazed (approx. 10–12 cm., as against 10–20 cm.), but the only statistically significant floristic difference was the reduction in *Aster* in the former. On intensively grazed turfs, it may often be difficult to separate the two dominant grasses *Festuca rubra* and *Puccinellia maritima* since, whilst they are quite distinct in habit when growing normally, grazed *Puccinellia* on relatively dry ground looks very similar to *Festuca*. Ligule and leaf sheath characters will always distinguish them, however, and illustrations are provided in Figs. 25 and 26.

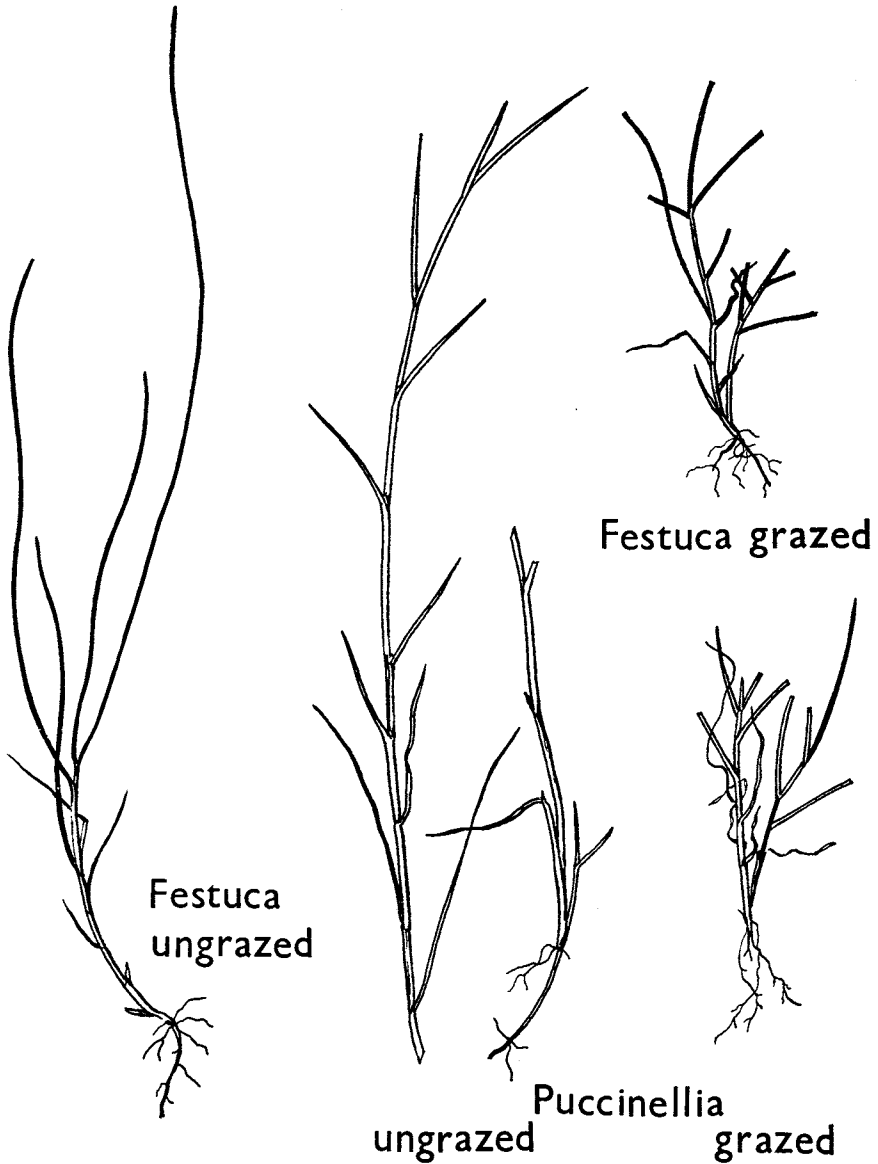


FIG. 25.
Grazed and ungrazed *Festuca rubra* and *Puccinellia maritima* from Bentlass.

Trampling

Heavy trampling on soft ground leads to much disturbance, with holes between tussocks. On the sides of these holes (which are often water filled) opportunist species like *Cochlearia anglica* (and sometimes *C. danica*) may be established, whilst diploid *Salicornia*, and *Suaeda*, grow in saline hollows.

Human trampling is not so frequent now as formerly, as there is much less use of the upper marsh tracks, but the use of wheeled vehicles produces sharply defined ruts in which water can stand, and if disturbance is excessive (as it was in places on the Bentlass foreshore during cable-laying in 1968) the vegetation cover can be locally destroyed. Fortunately it was possible on that occasion to avoid damage to

the most interesting part of the marsh. Repeated foot pressure will eliminate succulents, especially *Aster*, and by physically depressing the surface cause water to stand longer and so favour the increase of *Puccinellia* and temporary stands of diploid *Salicornia*. But much repeated foot pressure will ultimately destroy *Puccinellia* also, as may be seen in the lower parts of the main transect worked by students at Bentlass. From the conservation point of view it seems desirable to restrict trampling on salt marshes (especially just after spring tides) as much as possible and to have alternative areas for intensive working. This, of course, is the reason for the second marked transect at Bentlass.

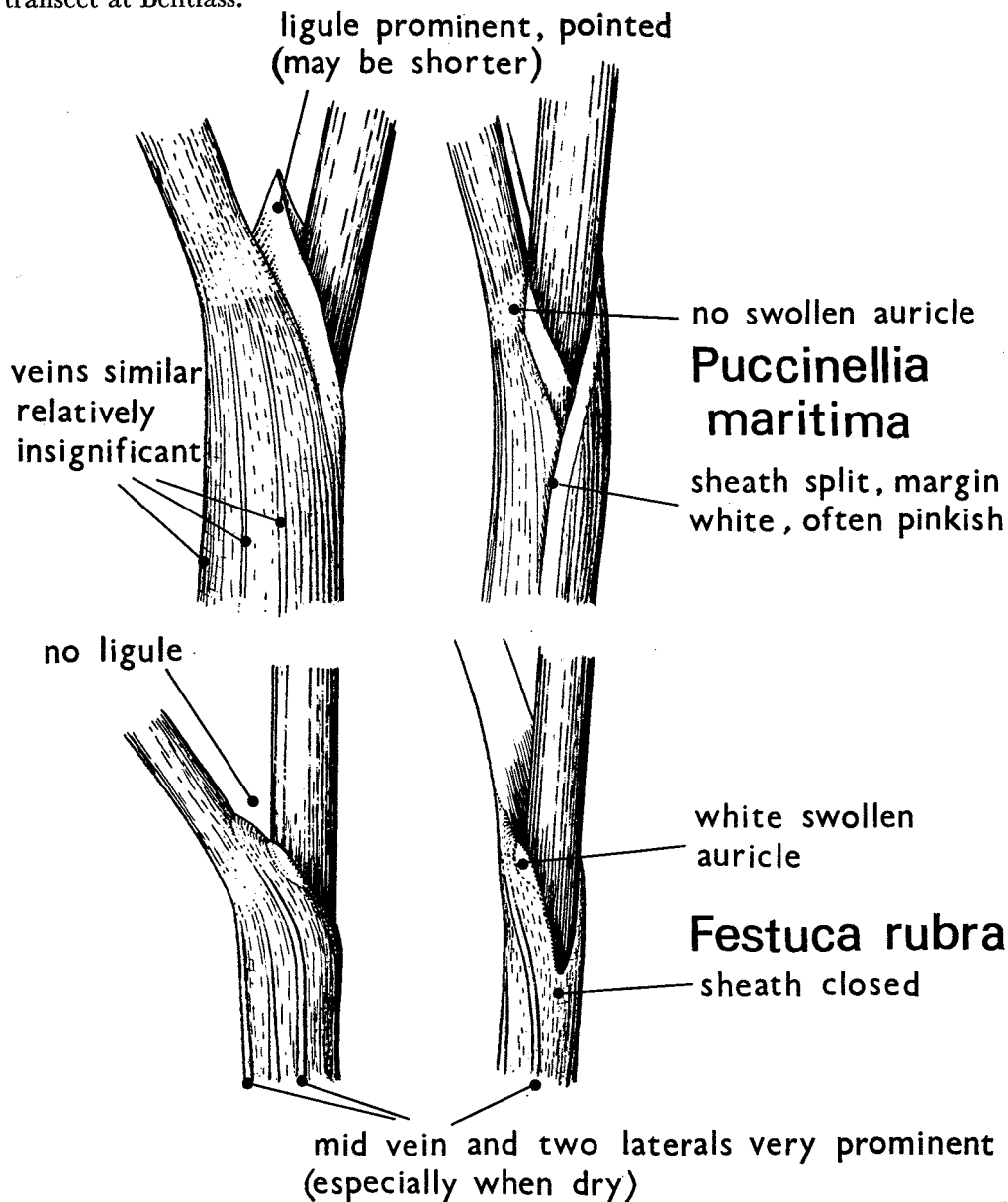


FIG. 26.

Diagnostic characters for separating vegetative material of *Festuca rubra* and *Puccinellia maritima*.

Land reclamation

Land reclamation by "inching" salt marshes will lead to major changes. In Milford Haven it is likely that any future reclamation will be for housing or industrial purposes, but in the past it has been to provide grazing land for farm stock. The ultimate breaching of the banks on the Gann saltings, followed by the formation of secondary marsh there, shows that changes due to reclamation of that kind are not necessarily irreversible. A much more serious change was that proposed as an alternative to the high-level bridge being constructed east of Neyland, with a barrage to take traffic and the progressive replacement of salt by fresh water upstream of the barrage. This barrage project has now been abandoned, and the consequent drastic changes in the Dauceddau prevented.

Oil pollution

The final and, in the long run, potentially most serious threat to the Haven marshes at the present time is that of chemical pollution. Milford Haven is now Britain's largest oil port, and is the site of a very considerable transference of crude oil from ocean-going tankers to shore installations, and of refined products from there to smaller vessels. It is during this transference of oil that spills are most likely to occur, because, as Dudley (1968) points out, however good the equipment may be there is always a slight chance of human error. The problems facing the harbour authorities and the oil companies are well summarized by Dudley, whilst the impact of oil pollution on estuarine life is discussed by Crapp (1969) and Cowell and Baker (1969). The following summary of the effects of crude oil pollution on salt marsh vegetation is based on information very kindly given to me by Miss J. M. Baker of the Field Studies Council Oil Pollution Research Unit.

It is generally true that a single oil spill will not alone cause lasting damage to salt marsh vegetation, unless an exceptionally large amount is involved. Damaged areas recover in anything from three months to two years, either by immigrant seeds or by the regeneration from undamaged and protected growing points. Repeated pollution, however, even involving quite small amounts of oil, will ultimately lead to the complete destruction of all vegetation. Furthermore, attempts at removing oil with detergents (emulsifiers, surfactants) are generally more harmful to the vegetation than is the oil itself.

Annuals such as *Suaeda* and *Salicornia* (and possibly most other species at the seedling stage) are very susceptible, and populations may be totally killed. However, they are adapted to temporary sites and recovery is rapid in subsequent years. Perennials show a range of responses, varying from the main grasses *Festuca*, *Puccinellia* and *Spartina* (which are all capable of limited regeneration but are killed by repeated oilings), through the main GSM species such as *Armeria*, *Aster*, *Plantago* and *Triglochin* (whose rosettes are much more resistant to repeated oilings) to *Agrostis stolonifera* and *Oenanthe lachenalii* which survive the best. Many plants of *Agrostis* are, in fact, killed, but survivors show considerable vigour in vegetative reproduction whilst *Oenanthe* is truly resistant, and has even flowered after 14 successive monthly experimental oilings.

The harmful effects of oil on plants are partly physical (e.g. by stomatal blocking), but are mainly physiological through interference with basic processes such as transpiration, respiration and photosynthesis. Many show inhibition of flowering

if oiling occurs during the preceding photoinductive period, but oiling during the winter when most species have died down or are showing little growth does the least harm. Grasses may show some temporary stimulation of vegetative growth and appear lusher and darker green, but the cause is not yet known.

The future

The threat of oil pollution has directed attention again towards the part that salt marsh vegetation plays in the complex estuarine ecosystem, and Milford Haven seems an ideal area for detailed studies on the impact of industry on natural communities.

Further purely natural changes are possible though, apart from the impact of *Spartina*, they are not likely to introduce situations not already present in some part of the Haven. The main uncertainty concerns oil pollution, and here we must hope that the compromise plans drawn up by the Milford Haven Conservancy Board, in full co-operation with the oil companies and the natural history conservation groups, will restrict harm as far as possible.

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REFERENCES

- ADMIRALTY TIDE TABLES. (1967). Vol. 1. Hydrographer of the Navy, London.
- BOORMAN, L. A. (1967). Biological flora of the British Isles, No. 106. *Limonium vulgare* Mill. and *L. humile* Mill. *J. Ecol.*, **55**, 221-232.
- CALDWELL, P.-A. (1957). The spatial development of *Spartina* colonies growing without competition. *Ann. Bot. N.S.*, **21**, 203-214.
- AUSTIN, M. P. and ORLOCI, L. (1966). Geometric models in ecology. II. An evaluation of some ordination techniques. *J. Ecol.*, **54**, 217-227.
- CHAPMAN, V. J. (1938). Studies on salt-marsh ecology. Sections I to III. *J. Ecol.*, **26**, 144-179.
- CHAPMAN, V. J. (1947). Biological flora of the British Isles, No. 21. *Suaeda maritima* (L.) Dum. *J. Ecol.*, **35**, 293-302.
- CHAPMAN, V. J. (1950). Biological flora of the British Isles, No. 30. *Halimione portulacoides* (L.) Aell. *J. Ecol.*, **38**, 214-222.

- CHAPMAN, V. J. (1960a). *The Plant Ecology of Scolt Head Island*. Chap. VIII in *Scolt Head Island*. ed. J. A. Steers. 2nd edn. W. Heffer & Sons: Cambridge.
- CHAPMAN, V. J. (1960b). *Salt Marshes and Salt Deserts of the World*. Leonard Hill: London.
- CLAPHAM, A. R., PEARSALL, W. H., and RICHARDS, P. W. (1942). Biological flora of the British Isles, No. 8. *Aster tripolium* L. *J. Ecol.*, **30**, 385–395.
- CLAPHAM, A. R., TUTIN, T. G., and WARBURG, E. F. (1962). *Flora of the British Isles*. 2nd edn. University Press: Cambridge.
- COWELL, E. B., and BAKER, J. M. (1969). Recovery of a salt marsh in Pembrokeshire, south-west Wales, from pollution by crude oil. *Biol. Cons.*, **1**, 291–295.
- CRAPP, G. B. (1969). Oil pollution in Milford Haven. *Nature in Wales*, **11**, 131–137.
- DALBY, D. H. (1963). Seed dispersal in *Salicornia pusilla*. *Nature (Lond.)*, **199**, 197–198.
- DALBY, D. H. (1969a). Some observations on oil pollution of salt marshes in Milford Haven. *Biol. Cons.*, **1**, 295–296.
- DALBY, D. H. (1969b). A further note on *Atriplex littoralis* in Milford Haven. *Nature in Wales*, **11**, 141–142.
- DUDLEY, G. (1968). The problem of oil pollution in a major oil port in *The Biological Effects of Oil Pollution on Littoral Communities*, eds. J. D. Carthy and D. R. Arthur, *Fld Stud.*, **2**, suppl.
- EVANS, R. G. (1957). The intertidal ecology of some localities on the Atlantic coast of France. *J. Ecol.*, **45**, 245–271.
- GILLHAM, M. E. (1957). Vegetation of the Exe estuary in relation to water salinity. *J. Ecol.*, **45**, 735–756.
- GOODMAN, P. J., BRAYBROOKS, E. M., and LAMBERT, J. M., (1959). Investigations into “dieback” in *Spartina townsendii* agg. I. The present status of *Spartina townsendii* in Britain. *J. Ecol.*, **47**, 651–677.
- GOODMAN, P. J., BRAYBROOKS, E. M., LAMBERT, J. M. and MARCHANT, C. J. (1969). Biological Flora of the British Isles, No. 116. *Spartina* Schreb. *J. Ecol.*, **57**, 285–313.
- HUBBARD, C. E. (1968). *Grasses*. 2nd ed. Penguin Books, Harmondsworth, Middlesex.
- JAKOBSEN, B. (1954). The tidal area in south-western Jutland and the process of the salt marsh formation. *Geog. Tidsskr.*, **53**, 49–61.
- JAKOBSEN, B. (1961). Vadehavets sedimentomsaetning belyst ved kvantitative målinger. *Geogr. Tidsskr.*, **60**, 87–103.
- KERSHAW, K. A. K. (1967). Ecological methods and computers. *Sci. Prog., Oxf.* (1967), **55**, 437–451.
- MARCHANT, C. J. (1967). Evolution in *Spartina* (Gramineae) I. The history and morphology of the genus in Britain. *J. Linn. Soc. (Bot.)*, **60**, 1–24.
- MARCHANT, C. J. (1968). Evolution in *Spartina* (Gramineae) II. Chromosomes, basic relationships and the problem of *S. x townsendii* agg. *J. Linn. Soc. (Bot.)*, **60**, 381–409.
- NELSON-SMITH, A. (1965). Marine biology of Milford Haven: the physical environment. *Fld Stud.*, **2**, 155–188.
- NICOL, E. A. T. (1935). The ecology of a salt-marsh. *J. mar. biol. Assoc. U.K.*, **20**, 203–261.
- ORLOCI, L. (1966). Geometric models in ecology. I. The theory and application of some ordination methods. *J. Ecol.*, **54**, 193–215.
- PERRING, F. H., and WALTERS, S. M. (1962). *Atlas of the British Flora*. T. Nelson & Sons: London.
- RANWELL, D. S. (1964). *Spartina* salt marshes in southern England. II. Rate and seasonal pattern of sediment accretion. *J. Ecol.*, **52**, 79–94.
- RANWELL, D. S., BIRD, E.C.F, HUBBARD, J.C.E., and STEBBINGS, R.E. (1964b). *Spartina* salt marshes in southern England. V. Tidal submergence and chlorinity in Poole Harbour. *J. Ecol.*, **52**, 627–641.
- RANWELL, D. S. and HEWETT, D. (1964). Oil pollution in Poole Harbour and its effect on birds. *Bird Notes*, **31**, 192–197.
- TANSLEY, A. G. (1949). *The British Islands and their Vegetation*. 2nd edn., University Press: Cambridge.
- WIEHE, P. O. (1935). A quantitative study of the influence of tide upon populations of *Salicornia europaea*. *J. Ecol.*, **23**, 323–333.