

**Edited by  
J. S. Rodwell**

# **British Plant Communities Volume 5**



## **Maritime communities and vegetation of open habitats**

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## British Plant Communities 5



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# British Plant Communities

VOLUME 5

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## MARITIME COMMUNITIES AND VEGETATION OF OPEN HABITATS

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## PREFACE AND ACKNOWLEDGEMENTS

The appearance of this fifth volume of *British Plant Communities* brings to a close the publication of the National Vegetation Classification and, as Coordinator of the project, it is my privilege to put on record the gratitude of the whole research team and my own personal thanks to all who have been instrumental in the completion of the work.

For this volume, we were extremely fortunate in having access from the outset to the data which Dr Paul Adam had energetically assembled for his postgraduate research at Cambridge University into British salt-marsh vegetation. Extensive in its coverage and already developed into a classification scheme with highly informative vegetation descriptions, this work obviated the need for any further detailed survey on our part and more than laid a foundation for our own scheme. Such additional data as we did collect to fill any gaps was also supplemented by local surveys by Dr Pat Doody and Margaret Hill of the then NCC, Dr Malcolm Carter and Dr Judith Roper-Lindsay. In integrating this into the NVC framework and reviewing the progress of our synthesis Paul Adam continued to give of his time and expertise without demur.

For sea-cliffs we were equally blessed in inheriting large quantities of data from Andrew Malloch whose geographical and floristic coverage of this difficult and neglected habitat was adventurously wide and whose knowledge of the plant communities and their environmental relationships was second to none. For this section of the volume, Andrew generously provided the bulk of the material and commented on the final version of the community descriptions.

With sand-dunes, by contrast, we were more or less starting from scratch and the four research assistants, Jacqui Huntley (née Paice), Elaine Radford (née Grindey), Paul Wilkins, Martin Wigginton and myself, collected as broad a spread of data as we could from around the coasts of England and Wales. For Scotland, we were especially grateful here, as with other vegetation types covered by the project, for unhindered access

to data collected by Eric Birse and James Robertson, then of the Macaulay Institute in Aberdeen. More locally, but extremely helpful too, were data from Welsh dune slacks being assembled by Dr Peter Jones at Cardiff University. As Andrew Malloch developed the preliminary descriptions of the vegetation types, we were greatly assisted by comments from Drs Pat Doody and Geoff Radley, Imogen Crawford and Dr Tom Dargie and others involved in the country agencies' application of the NVC in their extensive survey and mapping of dune systems.

Also included in this volume are weed communities and other vegetation types of more open habitats like screes, rock outcrops, spoil, walls and pavement cracks, together with communities of periodically-inundated river banks, shoals, lake margins and trackways. For weeds of arable land and gardens, we were very grateful for access through David Shimwell to the data collected by Dr Alan Silverside, now of Paisley University, for his doctoral thesis at Durham. David Shimwell and Elaine Radford were responsible for the preliminary characterisation of most of the vegetation types in this section of the work and Elizabeth Cooper, then at Lancaster University, gave sterling help with the later stages of data analysis.

As with the other volumes of *British Plant Communities* then, there are many and diverse debts to acknowledge here. From the start, the NVC has been very much a collaborative effort and, in addition to the particular thanks paid above and in other volumes, I would like here to mark some of the more substantial contributions to the overall success of the project through the years.

First among them, I want to record my debts to Donald Pigott and Derek Ratcliffe, the two prime movers of the project and an inspiration throughout. The long progress of the work has seen the retirement of both from their final professional appointments but, in their continuing busy lives, they have gone on supporting the project and my own part in it with their concern

and encouragement. The significance of their contributions to ecology and conservation are much wider, of course, than the NVC but their commitment to this particular task and their belief in the value of the work have been immensely sustaining and its results will stand especially as a testament to their role in the whole venture.

Continuously close at hand in Lancaster, always willing to help and support, even in the midst of his own heavy academic burdens, has been Andrew Malloch. Quite apart from his supervision of the project in the north-west of England and substantial contributions to this volume, Andrew has played a very significant role in developing the software used for much of the data analysis in the project, has provided welcome assistance, always patient and thoughtful, with the processing of numerous data sets and, throughout, has retained his original conviction of the worthwhile character of our task. Though also retired now, he has gone on gently pressing his concern for its success.

Among others in the team, Michael Proctor has been especially valuable in his contribution to the work on mires and tall-herb fens, but his supervision of the project field work in the south-west of Britain, his comments, always perceptive and enriching, on many sections of the text as they have progressed, and the humour with which he carries his depth of knowledge have been extremely helpful and entertaining.

John Birks provided, from the outset, an inspiration and model for the kind of industrious and painstaking science that we hope we have pursued throughout the project. With his formidable knowledge of the British flora and particular skill with bryophytes, he helped ensure a seriousness in our recording from the start, set a pace for data collection in his supervision of the south-east region of England and contributed especially to the characterisation of woodland and upland communities.

David Shimwell, like others among the team, had been a forerunner in developing a phytosociological approach to British vegetation and, in his oversight of survey in our Midlands region and particular contributions on the classification of heaths, swamps, weed and inundation communities, he played a key role, enlivened by his wry humour, in bringing the whole work to completion.

Under the supervision of this team, the burden of survey for the project fell on the four research assistants and me. The Coordinating Panel are immensely grateful to Jacqui Huntley, Elaine Radford, Paul Wilkins and Martin Wigginton for their energetic commitment to covering the ground in their own regions, their sustained accuracy in collecting samples, the data processing and preliminary characterisation of vegetation types which they carried out with their supervisors and with continuing good humour. From our earliest meeting in the field,

when we gathered in 1975 at Preston Montford Field Centre to agree and test our sampling methodology and survey strategy, there was a lively team spirit which sustained our work to the end.

Particular individuals outside this group have played a variety of essential roles in the work. Katherine Hearn, now of the National Trust, and Ian Rotherham, now at Sheffield Hallam University, supplemented our survey effort in southern Scotland and the Yorkshire Dales. Then, we could never have acquitted ourselves adequately in the accounts for a number of vegetation types without access to substantial quantities of data given so generously by Dr Bryan Wheeler (mires), Dr Martin Page (mesotrophic grasslands), Dr Terry Wells (calicolous grasslands) and Dr Paul Adam (salt-marsh vegetation) and for many plant communities in Scotland by Eric Birse and James Robertson. In data processing, we were particularly indebted to Dr Hilary Birks for her analysis of vast amounts of upland data and to Professor Brian Huntley for his ingenuity in developing software for processing our samples.

In projects of this kind, large, complex and generating substantial amounts of data and material, technical and secretarial assistance are crucial and from start to finish the research team has been admirably served by a series of outstanding colleagues. Philip Harper, Frances Rake, Beryl Fletcher, Sylvia Peglar, Mary Pettit, Margaret Pigott, Steve Ridgill and Joel Miller assisted with the laborious tasks of data coding and analysis and, in the early years, Jennie Ford and Claire Ashworth acted as secretaries to the team.

The bulk of the secretarial work for the project, though, fell on Carol Barlow who typed the great majority of the text, data tables and indexes for *British Plant Communities*, and this in days before the miracles of the word processor, helped prepare much of the manuscript for publication and serviced the operation of the entire task from soon after our start right through the middle years. She did so with unfailing efficiency and attention to detail and I am enormously grateful for the cheerfulness with which she accomplished this job.

Through the final stages of the work, when completion of the task was complicated by other ever-increasing responsibilities on my part, I have had outstanding support and assistance from Michelle Needham whose competence and skills have been vital to bringing the whole enterprise to its conclusion. Juggling this particular secretarial task – completing the typing of text, tables and indexes and helping prepare the last two volumes of *British Plant Communities* for the Press – with the demanding burden of all her other work at Lancaster has never exhausted her energy and ingenuity, nor her spirit.

The Nature Conservancy Council and later the Joint Nature Conservation Committee funded the NVC from

beginning to end and, in these organisations, we had the benefit of a series of committed and enthusiastic staff involved, along with Derek Ratcliffe, in the advocacy and management of the project. Philip Oswald was of great assistance in the process of negotiating the detail of the publication process at the start and, as Chief Scientist of the NCC after Derek Ratcliffe, Professor Peter Bridgewater provided enthusiastic continuity of support. Also of critical importance in the middle years was Dr Tim Bines, whose own involvement with vegetation survey gave him a particular concern to ensure the success of the work. After him, Lynne Farrell and Margaret Palmer served us well as nominated officers and, in the last years, Dr John Hopkins and Debbie Jackson. I am grateful to all of these for their encouragement and patience and particularly to John for his elliptical wit and a kind of friendship which never compromised his professionalism.

At Cambridge University Press, too, we have benefited much from the ministrations of the Science team, first Dr Martin Walters, then Dr Maria Murphy and particularly Dr Alan Crowden – whose encouraging darts via fax and e-mail I shall greatly miss. Especially pleasing, also, is to thank Jane Bulleid, the sub-editor for all the volumes of *British Plant Communities*, whose enormous care in dealing with a vast quantity of complex manuscript and proofs has been greatly reassuring to me.

At Lancaster, the final stages of the project have taken place within the context of the Unit of Vegetation Science, much of whose work has been concerned with applications of the NVC among the now extremely wide and diverse user community. The various members of the Unit team, necessarily coming and going with the vagaries of funding and their own developing commitments, have provided an environment of great intellectual enrichment and entertaining companionship during this work. Among the training team, Kate Steele and Julia Milton have both contributed greatly to dissemination of NVC skills among a variety of environmental organisations and countless individuals; in NVC-related research, Sue Edwards, Sean Cooch, Kath Milnes and a series of masters students have broadened our understanding of vegetation types and their ecology; Deirdre Winstanley and, especially in later years, Julian Dring have put their energy and ingenuity at the service of NVC database development and computerised applications. Most of all, Elizabeth Cooper, in her exemplary NVC surveys and mapping, her determined commitment to applications in landscape characterisation and her energy, way beyond the call of duty, in helping others learn what the NVC is about, has been an inspiration. At Lancaster University but outside the Unit, I am personally grateful to Professors Terry Mansfield and Bill Davies, Robin Grove-White and Claire Waterton. When belief in the value of the work has

wavered at all, companionship from such as these has been a boon.

More widely among the community of NVC users in Britain, the project has been sustained over the years by the continuing interest, goading, impatience and disbelief of an enormous diversity of people. In the country agencies, I want to record my particular gratitude to Dr Keith Kirby, Mike Alexander, Dr Terry Rowell, Jane MacKintosh, Richard Tidswell, Dr Des Thompson, Dr Chris Sydes, David Horsfield, Alan Brown, Dr Wanda Fojt, Derek Wells, Dr Tim Blackstock, Dr David Stevens and Paul Corbett; also Dr Jonathan Mitchley, Jack Lavin, Geoffrey Wilmore, Dr Tony Whitbread, Reverend Gordon Graham and Dr Margaret Atherden. For those many excluded from this list who have made minor contributions that have accumulated in the various volumes to an impressive weight of help, our apologies, for it is not gratitude that is in short supply here.

In 1991, to mark the appearance of the first volume of *British Plant Communities* and the establishment of the Unit of Vegetation Science, we organised at Lancaster a conference on 'The Future of Phytosociology'. With the financial assistance of the British Ecological Society, involved from the start of the NVC in encouraging the funding of the project, and – especially pleasing – the Tansley Fund of the New Phytologist Trust, we were able to celebrate before an international audience of speakers and participants, the arrival on the European scene, albeit late, of what we hoped was a serious concern to join in the wider phytosociological community. The welcome our appearance received then and the continuing collaboration and friendship of colleagues across Europe and beyond has brought a rare joy and stimulus to the last years of the work and many valuable comments on the developing classification incorporated into the Conspectus included in this Volume. Among these, it is a privilege to single out Dr Joop Schaminée, Professor Sandro Pignatti, Professor Victor Westhoff, Professor Laco Mucina, Professor Hartmut Dierschke, Dr Milan Chytrý, Professor Ayzik Solomeshch, Dr Nikolai Ermakov, Dr Petrit Hoda, Dr Milan Valachovic and Dr Mara Pakalne. My professor at Leeds University, the late (and extraordinary) Irene Manton, who did so much to inspire my early devotion to botany and who was kind enough to support my application to coordinate the National Vegetation Classification, always encouraged me to see the wider world as the proper intellectual framework for research and these new-found fellow-workers have more than borne out that conviction.

In conclusion, I want to go deep and straight in recording the extent of my gratitude to the most personal helpmates in my own contribution to this project. My parents always encouraged my enthusiasm for

plants and, without their inheritance of determination and practicality, I would not have stayed this course. My two sons, Dominic and Peter, have grown up in the project's shadow, helping keep me sane with their devastating insights into my seriousness and their sidelong love. Primarily, though, it is my wife Rosemary who has

borne the chief burden of my commitment to see it all through, shared intimately in the frustrations, exhaustion and excitements of the work and given all that she is to sustain my enthusiasm to the end.

John Rodwell  
*Lancaster*



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# PREAMBLE



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# GENERAL INTRODUCTION

## The background to the work

It is a tribute to the insight of our early ecologists that we can still return with profit to *Types of British Vegetation* which Tansley (1911) edited for the British Vegetation Committee as the first coordinated attempt to recognise and describe different kinds of plant community in this country. The contributors there wrote practically all they knew and a good deal that they guessed, as Tansley himself put it, but they were, on their own admission, far from comprehensive in their coverage. It was to provide this greater breadth, and much more detailed description of the structure and development of plant communities, that Tansley (1939) drew together the wealth of subsequent work in *The British Islands and their Vegetation*, and there must be few ecologists of the generations following who have not been inspired and challenged by the vision of this magisterial book.

Yet, partly because of its greater scope and the uneven understanding of different kinds of vegetation at the time, this is a less systematic work than *Types* in some respects: its narrative thread of explication is authoritative and engaging, but it lacks the light-handed framework of classification which made the earlier volume so very attractive, and within which the plant communities might be related one to another, and to the environmental variables which influence their composition and distribution. Indeed, for the most part, there is a rather self-conscious avoidance of the kind of rigorous taxonomy of vegetation types that had been developing for some time elsewhere in Europe, particularly under the leadership of Braun-Blanquet (1928) and Tüxen (1937). The difference in the scientific temperament of British ecologists that this reflected, their interest in how vegetation works, rather than in exactly what distinguishes plant communities from one another, though refreshing in itself, has been a lasting hindrance to the emergence in this country of any consensus as to how vegetation ought to be described, and whether it ought to be classified at all.

In fact, an impressive demonstration of the value of the traditional phytosociological approach to the

description of plant communities in the British Isles was published in German after an international excursion to Ireland in 1949 (Braun-Blanquet & Tüxen 1952), but more immediately productive was a critical test of the techniques among a range of Scottish mountain vegetation by Poore (1955*a, b, c*). From this, it seemed that the really valuable element in the phytosociological method might be not so much the hierarchical definition of plant associations, as the meticulous sampling of homogeneous stands of vegetation on which this was based, and the possibility of using this to provide a multidimensional framework for the presentation and study of ecological problems. Poore & McVean's (1957) subsequent exercise in the description and mapping of communities defined using this more flexible approach then proved just a prelude to the survey of huge tracts of mountain vegetation by McVean & Ratcliffe (1962), work sponsored and published by the Nature Conservancy (as it then was) as *Plant Communities of the Scottish Highlands*. Here, for the first time, was the application of a systematised sampling technique across the vegetation cover of an extensive and varied landscape in mainland Britain, with assemblages defined in a standard fashion from full floristic data, and interpreted in relation to a complex of climatic, edaphic and biotic factors. The opportunity was taken, too, to relate the classification to other European traditions of vegetation description, particularly that developed in Scandinavia (Nordhagen 1943, Dahl 1956).

McVean & Ratcliffe's study was to prove a continual stimulus to the academic investigation of our mountain vegetation and of abiding value to the development of conservation policy, but their methods were not extended to other parts of the country in any ambitious sponsored surveys in the years immediately following. Despite renewed attempts to commend traditional phytosociology, too (Moore 1962), the attraction of this whole approach was overwhelmed for many by the heated debates that preoccupied British plant ecologists in the 1960s, on the issues of objectivity in the sampling

and sorting of data, and the respective values of classification or ordination as analytical techniques. Others, though, found it perfectly possible to integrate multivariate analysis into phytosociological survey, and demonstrated the advantage of computers for the display and interpretation of ecological data, rather than the simple testing of methodologies (Ivimey-Cook & Proctor 1966). New generations of research students also began to draw inspiration from the Scottish and Irish initiatives by applying phytosociology to the solving of particular descriptive and interpretative problems, such as variation among British calcicolous grasslands (Shimwell 1968a), heaths (Bridgewater 1970), rich fens (Wheeler 1975) and salt-marshes (Adam 1976), the vegetation of Skye (Birks 1969), Cornish cliffs (Malloch 1970) and Upper Teesdale (Bradshaw & Jones 1976). Meanwhile, too, workers at the Macaulay Institute in Aberdeen had been extending the survey of Scottish vegetation to the lowlands and the Southern Uplands (Birse & Robertson 1976, Birse, 1980, 1984).

With an accumulating volume of such data and the appearance of uncoordinated phytosociological perspectives on different kinds of British vegetation, the need for an overall framework of classification became ever more pressing. For some, it was also an increasingly urgent concern that it still proved impossible to integrate a wide variety of ecological research on plants within a generally accepted understanding of their vegetational context in this country. Dr Derek Ratcliffe, as Scientific Assessor of the Nature Conservancy's Reserves Review from the end of 1966, had encountered the problem of the lack of any comprehensive classification of British vegetation types on which to base a systematic selection of habitats for conservation. This same limitation was recognised by Professor Sir Harry Godwin, Professor Donald Pigott and Dr John Phillipson who, as members of the Nature Conservancy, had been asked to read and comment on the Reserves Review. The published version, *A Nature Conservation Review* (Ratcliffe 1977), was able to base the description of only the lowland and upland grasslands and heaths on a phytosociological treatment. In 1971, Dr Ratcliffe, then Deputy Director (Scientific) of the Nature Conservancy, in proposals for development of its research programme, drew attention to 'the need for a national and systematic phytosociological treatment of British vegetation, using standard methods in the field and in analysis/classification of the data'. The intention of setting up a group to examine the issue lapsed through the splitting of the Conservancy which was announced by the Government in 1972. Meanwhile, after discussions with Dr Ratcliffe, Professor Donald Pigott of the University of Lancaster proposed to the Nature Conservancy a programme of research to provide a systematic and comprehensive classification of British plant communities. The new

Nature Conservancy Council included it as a priority item within its proposed commissioned research programme. At its meeting on 24 March 1974, the Council of the British Ecological Society welcomed the proposal. Professor Pigott and Dr Andrew Malloch submitted specific plans for the project and a contract was awarded to Lancaster University, with sub-contractual arrangements with the Universities of Cambridge, Exeter and Manchester, with whom it was intended to share the early stages of the work. A coordinating panel was set up, jointly chaired by Professor Pigott and Dr Ratcliffe, and with research supervisors from the academic staff of the four universities, Drs John Birks, Michael Proctor and David Shimwell joining Dr Malloch. Later, Dr Tim Bines replaced Dr Ratcliffe as nominated officer for the NCC, then Lynne Farrell, Margaret Palmer and Dr John Hopkins.

With the appointment of Dr John Rodwell as full-time coordinator of the project, based at Lancaster, the National Vegetation Classification began its work officially in August 1975. Shortly afterwards, four full-time research assistants took up their posts, one based at each of the universities: Mr Martin Wigginton, Miss Jacqueline Paice (later Huntley), Mr Paul Wilkins and Dr Elaine Grindey (later Radford). These remained with the project until the close of the first stage of the work in 1980, sharing with the coordinator the tasks of data collection and analysis in different regions of the country, and beginning to prepare preliminary accounts of the major vegetation types. Drs Michael Lock and Hilary Birks and Miss Katherine Hearn were also able to join the research team for short periods of time. After the departure of the research assistants, the supervisors supplied Dr Rodwell with material for writing the final accounts of the plant communities and their integration within an overall framework. With the completion of this charge in 1989, the handover of the manuscript for publication by the Cambridge University Press began.

### **The scope and methods of data collection**

The contract brief required the production of a classification with standardised descriptions of named and systematically arranged vegetation types and, from the beginning, this was conceived as something much more than an annotated list of interesting and unusual plant communities. It was to be comprehensive in its coverage, taking in the whole of Great Britain apart from Northern Ireland, and including vegetation from all natural, semi-natural and major artificial habitats. Around the maritime fringe, interest was to extend up to the start of the truly marine zone, and from there to the tops of our remotest mountains, covering virtually all terrestrial plant communities and those of brackish and fresh waters, except where non-vascular plants were the dominants. Only short-term leys were specifically excluded

and, though care was to be taken to sample more pristine and long-established kinds of vegetation, no undue attention was to be given to assemblages of rare plants or to especially rich and varied sites. Thus widespread and dull communities from improved pastures, plantations, run-down mires and neglected heaths were to be extensively sampled, together with the vegetation of paths, verges and recreational swards, walls, man-made waterways and industrial and urban wasteland.

For some vegetation types, we hoped that we might be able to make use, from early on, of existing studies, where these had produced data compatible in style and quality with the requirements of the project. The contract envisaged the abstraction and collation of such material from both published and unpublished sources, and discussions with other workers involved in vegetation survey, so that we could ascertain the precise extent and character of existing coverage and plan our own sampling accordingly. Systematic searches of the literature and research reports revealed many data that we could use in some way and, with scarcely a single exception, the originators of such material allowed us unhindered access to it. Apart from the very few classic phytosociological accounts, the most important sources proved to be postgraduate theses, some of which had already amassed very comprehensive sets of samples of certain kinds of vegetation or from particular areas, and these we were generously permitted to incorporate directly.

Then, from the NCC and some other government agencies, or from individuals who had been engaged in earlier contracts for them, there were some generally smaller bodies of data, occasionally from reports of extensive surveys, more usually from investigations of localised areas. Published papers on particular localities, vegetation types or individual species also provided small numbers of samples. In addition to these sources, the project was able to benefit from and influence ongoing studies by institutions and individuals, and itself to stimulate new work with a similar kind of approach among university researchers, NCC surveyors, local flora recorders and a few suitably qualified amateurs. An initial assessment and annual monitoring of floristic and geographical coverage were designed to ensure that the accumulating data were fairly evenly spread, fully representative of the range of British vegetation, and of a consistently high quality. Full details of the sources of the material, and our acknowledgements of help, are given in the preface and introduction to each volume.

Our own approach to data collection was simple and pragmatic, and a brief period of training at the outset ensured standardisation among the team of five staff who were to carry out the bulk of the sampling for the project in the field seasons of the first four years, 1976–9. The thrust of the approach was phytosociological in its

emphasis on the systematic recording of floristic information from stands of vegetation, though these were chosen solely on the basis of their relative homogeneity in composition and structure. Such selection took a little practice, but it was not nearly so difficult as some critics of this approach imply, even in complex vegetation, and not at all mysterious. Thus, crucial guidelines were to avoid obvious vegetation boundaries or unrepresentative floristic or physiognomic features. No prior judgements were necessary about the identity of the vegetation type, nor were stands ever selected because of the presence of species thought characteristic for one reason or another, nor by virtue of any observed uniformity of the environmental context.

From within such homogeneous stands of vegetation, the data were recorded in quadrats, generally square unless the peculiar shape of stands dictated otherwise. A relatively small number of possible sample sizes was used, determined not by any calculation of minimal areas, but by the experienced assessment of their appropriateness to the range of structural scale found among our plant communities. Thus plots of  $2 \times 2$  m were used for most short, herbaceous vegetation and dwarf-shrub heaths,  $4 \times 4$  m for taller or more open herb communities, sub-shrub heaths and low woodland field layers,  $10 \times 10$  m for species-poor or very tall herbaceous vegetation or woodland field layers and dense scrub, and  $50 \times 50$  m for sparse scrub, and woodland canopy and understorey. Linear vegetation, like that in streams and ditches, on walls or from hedgerow field layers, was sampled in 10 m strips, with 30 m strips for hedgerow shrubs and trees. Quadrats of  $1 \times 1$  m were rejected as being generally inadequate for representative sampling, although some bodies of existing data were used where this, or other sizes different from our own, had been employed. Stands smaller than the relevant sample size were recorded in their entirety, and mosaics were treated as a single vegetation type where they were repeatedly encountered in the same form, or where their scale made it quite impossible to sample their elements separately.

Samples from all different kinds of vegetation were recorded on identical sheets (Figure 1). Priority was always given to the accurate scoring of all vascular plants, bryophytes and macrolichens (*sensu* Dahl 1968), a task which often required assiduous searching in dense and complex vegetation, and the determination of difficult plants in the laboratory or with the help of referees. Critical taxa were treated in as much detail as possible though, with the urgency of sampling, certain groups, like the brambles, hawkweeds, eyebrights and dandelions, often defeated us, and some awkward bryophytes and crusts of lichen squamules had to be referred to just a genus. It is more than likely, too, that some very diminutive mosses and especially hepatics escaped notice in the field and, with much sampling taking place in summer,

winter annuals and vernal perennials might have been missed on occasion. In general, nomenclature for vascular plants follows *Flora Europaea* (Tutin *et al.* 1964 *et seq.*) with Corley & Hill (1981) providing the authority for bryophytes and Dahl (1968) for lichens. Any exceptions to this, and details of any difficulties with sampling or identifying particular plants, are given in the introductions to each of the major vegetation types.

A quantitative measure of the abundance of every taxon was recorded using the Domin scale (*sensu* Dahl & Hadač 1941), cover being assessed by eye as a vertical projection on to the ground of all the live, above-ground parts of the plants in the quadrat. On this scale:

Cover of 91–100% is recorded as Dominant	10		
76–90%	9		
51–75%	8		
34–50%	7		
26–33%	6		
11–25%	5		
4–10%	4		
<4%	{	with many individuals	3
		with several individuals	2
		with few individuals	1

In heaths, and more especially in woodlands, where the vegetation was obviously layered, the species in the

Figure 1. Standard NVC sample card.

NVC record sheet 10/81			
Location	Grid reference	Region	Author
Site and vegetation description		Date	Sample no.
		Altitude m	Slope °
		Aspect °	Soil depth cm
		Stand area m x m	Sample area m x m
		Layers: mean height m m cm mm	
		Layers: cover % % % %	
		Geology	
		Species list	

different elements were listed separately as part of the same sample, and any different generations of seedling or saplings distinguished. A record was made of the total cover and height of the layers, together with the cover of any bare soil, litter, bare rock or open water. Where existing data had been collected using percentage cover or the Braun-Blanquet scale (Braun-Blanquet 1928), it was possible to convert the abundance values to the Domin scale, but we had to reject all samples where DAFOR scoring had been used, because of the inherent confusion within this scale of abundance and frequency.

Each sample was numbered and its location noted using a site name and full grid reference. Altitude was estimated in metres from the Ordnance Survey 1:50000 series maps, slope estimated by eye or measured using a hand level to the nearest degree, and aspect measured to the nearest degree using a compass. For terrestrial samples, soil depth was measured in centimetres using a probe, and in many cases a soil pit was dug sufficient to allocate the profile to a major soil group (*sensu* Avery 1980). From such profiles, a superficial soil sample was removed for pH determination as soon as possible thereafter using an electric meter on a 1:5 soil:water paste. With aquatic vegetation, water depth was measured in centimetres wherever possible, and some indication of the character of the bottom noted. Details of bedrock and superficial geology were obtained from Geological Survey maps and by field observation.

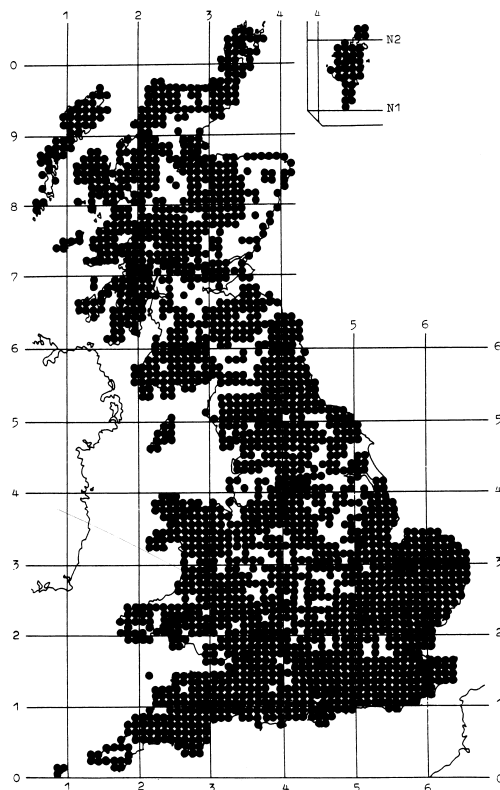
This basic information was supplemented by notes, with sketches and diagrams where appropriate, on any aspects of the vegetation and the habitat thought likely to help with interpretation of the data. In many cases, for example, the quantitative records for the species were filled out by details of the growth form and patterns of dominance among the plants and an indication of how they related structurally one to another in finely organised layers, mosaics or phenological sequences within the vegetation. Then, there was often valuable information about the environment to be gained by simple observation of the gross landscape or microrelief, the drainage pattern, signs of erosion or deposition and patterning among rock outcrops, talus slopes or stony soils. Often, too, there were indications of biotic effects including treatments of the vegetation by man, with evidence of grazing or browsing, trampling, dunging, mowing, timber extraction or amenity use. Sometimes, it was possible to detect obvious signs of ongoing change in the vegetation, natural cycles of senescence and regeneration among the plants, or successional shifts consequent upon invasion or particular environmental impacts. In many cases, also, the spatial relationships between the stand and neighbouring vegetation types were highly informative and, where a number of samples were taken from an especially varied or complex site, it often proved useful to draw a map

indicating how the various elements in the pattern were interrelated.

### The approach to data analysis

At the close of the programme of data collection, we had assembled, through the efforts of the survey team and by the generosity of others, a total of about 35000 samples of the same basic type, originating from more than 80% of the 10 × 10 km grid squares of the British mainland and many islands (Figure 2). Thereafter began a coordinated phase of data processing, with each of the four universities taking responsibility for producing preliminary analyses from data sets crudely separated into major vegetation types – mires, calcicolous grasslands, sand-dunes and so on – and liaising with the others where there was a shared interest. We were briefed in the contract to produce accounts of discrete plant communities which could be named and mapped, so our attention was naturally concentrated on techniques of multivariate classification, with the help of computers to sort the very numerous and often complex samples on the basis of their similarity. We were concerned to employ reputable methods of analysis, but the considerable experience of the team in this kind of work led us to resolve at the outset to concentrate on the ecological

Figure 2. Distribution of samples available for analysis.



integrity of the results, rather than on the minutiae of mathematical technique. In fact, each centre was free to some extent to make its own contribution to the development of computer programs for the task, Exeter concentrating on Association and Information Analysis (Ivimey-Cook *et al.* 1975), Cambridge and Manchester on cluster analysis (Huntley *et al.* 1981), Lancaster on Indicator Species Analysis, later Twinspan (Hill *et al.* 1975, Hill 1979), a technique which came to form the core of the VESPAN package, designed, using the experience of the project, to be particularly appropriate for this kind of vegetation survey (Malloch 1988).

Throughout this phase of the work, however, we had some important guiding principles. First, this was to be a new classification, and not an attempt to employ computational analysis to fit groups of samples to some existing scheme, whether phytosociological or otherwise. Second, we were to produce a classification of vegetation types, not of habitats, so only the quantitative floristic records were used to test for similarity between the samples, and not any of the environmental information: this would be reserved, rather, to provide one valuable correlative check on the ecological meaning of the sample groups. Third, no samples were to be rejected at the outset because they appeared nondescript or troublesome, nor removed during the course of analysis or data presentation where they seemed to confuse an otherwise crisply-defined result. Fourth, though, there was to be no slavish adherence to the products of a single analyses using arbitrary cut-off points when convenient numbers of end-groups had been produced. In fact, the whole scheme was to be the outcome of many rounds of sorting, with data being pooled and reanalysed repeatedly until optimum stability and sense were achieved within each of the major vegetation types. An important part of the coordination at this stage was to ensure roughly comparable scales of definition among the emerging classifications and to mesh together the work of the separate centres so as to avoid any omissions in the processing or wasteful overlaps.

With the departure from the team of the four research assistants in 1980, the academic supervisors were left to continue the preparation of the preliminary accounts of the vegetation types for the coordinator to bring to completion and integrate into a coherent whole. Throughout the periods of field work and data analysis, we had all been conscious of the charge in the contract that the whole project must gain wide support among ecologists with different attitudes to the descriptive analysis of vegetation. Great efforts were therefore made to establish a regular exchange of information and ideas through the production of progress reports, which gained a wide circulation in Britain and overseas, via contacts with NCC staff and those of other research agencies, and the giving of papers at scientific meetings. This meant that, as we

approached the presentation of the results of the project, we were well informed about the needs of prospective users, and in a good position to offer that balance of concise terminology and broadly-based description that the NCC considered would commend the work, not only to their own personnel, but to others engaged in the assessment and management of vegetation, to plant and animal ecologists in universities and colleges, and to those concerned with land use and planning.

### The style of presentation

The presentation of our results thus gives priority to the definition of the vegetation types, rather than to the construction of a hierarchical classification. We have striven to characterise the basic units of the scheme on roughly the same scale as a Braun-Blanquet association, but these have been ordered finally not by any rigid adherence to the higher phytosociological categories of alliance, order and class, but in sections akin to the formations long familiar to British ecologists. In some respects, this is a more untidy arrangement, and even those who find the general approach congenial may be surprised to discover what they have always considered to be, say, a heath, grouped here among the mires, or to search in vain for what they are used to calling 'marsh'. The five volumes of the work gather the major vegetation types into what seem like sensible combinations and provide introductions to the range of communities included: aquatic vegetation, swamps and tall-herb fens; grasslands and montane vegetation; heaths and mires; woodlands and scrub; salt-marsh, sand-dune and sea-cliff communities and weed vegetation. The order of appearance of the volumes, however, reflects more the exigencies of publishing than any ecological viewpoint.

The bulk of the material in the volumes comprises the descriptions of the vegetation types. After much consideration, we decided to call the basic units of the scheme by the rather non-committal term 'community', using 'sub-community' for the first-order sub-groups which could often be distinguished within these, and 'variant' in those very exceptional cases where we have defined a further tier of variation below this. We have also refrained from erecting any novel scheme of complicated nomenclature for the vegetation types, invoking existing names where there is an undisputed phytosociological synonym already in widespread use, but generally using the Latin names of one, two or occasionally three of the most frequent species. Among the mesotrophic swards, for example, we have distinguished a *Centaurea nigra-Cynosurus cristatus* grassland, which is fairly obviously identical to what Braun-Blanquet & Tüxen (1952) called *Centaureo-Cynosuretum cristati*, and within which, from our data, we have characterised three sub-communities. For the convenience of shorthand description and mapping, every vegetation type has been given



a code letter and number, so that *Centaurea-Cynosurus* grassland for example is MG5, MG referring to its place among the mesotrophic grasslands. The *Galium verum* sub-community of this vegetation type, the second to be distinguished within the description, is thus MG5b.

Vegetation being as variable as it is, it is sometimes expedient to allocate a sample to a community even though the name species are themselves absent. What defines a community as unique are rarely just the plants used to name it, but the particular combination of frequency and abundance values for all the species found in the samples. It is this information which is presented in summary form in the floristic tables for each of the communities in the scheme. Figure 3, for example, shows such a table for MG5 *Centaurea-Cynosurus* grassland. Like all the tables in the volumes, it includes such vascular plants, bryophytes and lichens as occur with a frequency of 5% or more in any one of the sub-communities (or, for vegetation types with no sub-communities, in the community as a whole). Early tests showed that records of species below this level of frequency could be largely considered as noise, but cutting off at any higher level meant that valuable floristic information was lost. The vascular species are not separated from the cryptogams on the table though, for woodlands and scrub, the vegetation is sufficiently complex for it to be sensible to tabulate the species in a way which reflects the layered structure.

Every table has the frequency and abundance values arranged in columns for the species. Here, 'frequency' refers to how often a plant is found on moving from one sample of the vegetation to the next, irrespective of how much of that species is present in each sample. This is summarised in the tables as classes denoted by the Roman numerals I to V: 1–20% frequency (that is, up to one sample in five)=I, 21–40%=II, 41–60%=III, 61–80%=IV and 81–100%=V. We have followed the usual phytosociological convention of referring to species of frequency classes IV and V in a particular community as its constants, and in the text usually refer to those of class III as common or frequent species, of class II as occasional and of class I as scarce. The term 'abundance' on the other hand, is used to describe how much of a plant is present in a sample, irrespective of how frequent or rare it is among the samples, and it is summarised on the tables as bracketed numbers for the Domin ranges, and denoted in the text using terms such as dominant, abundant, plentiful and sparse. Where there are sub-communities, as in this case, the data for these are listed first, with a final column summarising the records for the community as a whole.

The species are arranged in blocks according to their pattern of occurrence among the different sub-communities and within these blocks are generally ordered by decreasing frequency. The first group, *Festuca rubra* to *Trifolium pratense* in this case, is made up of the commu-

nity constants, that is those species which have an overall frequency IV or V. Generally speaking, such plants tend to maintain their high frequency in each of the sub-communities, though there may be some measure of variation in their representation from one to the next: here, for example, *Plantago lanceolata* is somewhat less common in the last sub-community than the first two, with *Holcus lanatus* and a number of others showing the reverse pattern. More often, there are considerable differences in the abundance of these most frequent species: many of the constants can have very high covers, while others are more consistently sparse, and plants which are not constant can sometimes be numbered among the dominants.

The last group of species on a table, *Ranunculus acris* to *Festuca arundinacea* here, lists the general associates of the community, sometimes referred to as companions. These are plants which occur in the community as a whole with frequencies of III or less, though sometimes they rise to constancy on one or other of the sub-communities, as with *R. acris* in this vegetation. Certain of the companions are consistently common overall like *Rumex acetosa*, some are more occasional throughout as with *Rhinanthus minor*, some are always scarce, for example *Calliergon cuspidatum*. Others, though, are more unevenly represented, like *R. acris*, *Heracleum sphondylium* or *Poa trivialis*, though they do not show any marked affiliation to any particular sub-community. Again, there can be marked variation in the abundance of these associates: *Rumex acetosa*, for example, though quite frequent, is usually of low cover, while *Arrhenatherum elatius* and some of the bryophytes, though more occasional, can be patchily abundant; *Alchemilla xanthochlora* is both uncommon among the samples and sparse within them.

The intervening blocks comprise those species which are distinctly more frequent within one or more of the sub-communities than the others, plants which are referred to as preferential, or differential where their affiliation is more exclusive. For example, the group *Lolium perenne* to *Juncus inflexus* is particularly characteristics of the first sub-community of *Centaurea-Cynosurus* grassland, although some species, like *Leucanthemum vulgare* and, even more so, *Lathyrus pratensis*, are more strongly preferential than others, such as *Lolium*, which continues to be frequent in the second sub-community. Even uncommon plants can be good preferentials, as with *Festuca pratensis* here: it is not often found in *Centaurea-Cynosurus* grassland but, when it does occur, it is generally in this first sub-type.

The species group *Galium verum* to *Festuca ovina* helps to distinguish the second sub-community from the first, though again there is some variation in the strength of association between these preferentials and the vegetation type, with *Achillea millefolium* being less markedly

## Floristic table MG5

	a	b	c	MG5
<i>Festuca rubra</i>	V (1–8)	V (2–8)	V (2–7)	V (1–8)
<i>Cynosurus cristatus</i>	V (1–8)	V (1–7)	V (1–7)	V (1–8)
<i>Lotus corniculatus</i>	V (1–7)	V (1–5)	V (2–4)	V (1–7)
<i>Plantago lanceolata</i>	V (1–7)	V (1–5)	IV (1–4)	V (1–7)
<i>Holcus lanatus</i>	IV (1–6)	IV (1–6)	V (1–5)	IV (1–6)
<i>Dactylis glomerata</i>	IV (1–7)	IV (1–6)	V (1–6)	IV (1–7)
<i>Trifolium repens</i>	IV (1–9)	IV (1–6)	V (1–4)	IV (1–9)
<i>Centaurea nigra</i>	IV (1–5)	IV (1–4)	V (2–4)	IV (1–5)
<i>Agrostis capillaris</i>	IV (1–7)	IV (1–7)	V (3–8)	IV (1–8)
<i>Anthoxanthum odoratum</i>	IV (1–7)	IV (1–8)	V (1–4)	IV (1–8)
<i>Trifolium pratense</i>	IV (1–5)	IV (1–4)	IV (1–3)	IV (1–5)
<i>Lolium perenne</i>	IV (1–8)	III (1–7)	I (2–3)	III (1–8)
<i>Bellis perennis</i>	III (1–7)	II (1–7)	I (4)	II (1–7)
<i>Lathyrus pratensis</i>	III (1–5)	I (1–3)	I (1)	II (1–5)
<i>Leucanthemum vulgare</i>	III (1–3)	I (1–3)	II (1–3)	II (1–3)
<i>Festuca pratensis</i>	II (1–5)	I (2–5)	I (1)	I (1–5)
<i>Knautia arvensis</i>	I (4)			I (4)
<i>Juncus inflexus</i>	I (3–5)			I (3–5)
<i>Galium verum</i>	I (1–6)	V (1–6)		II (1–6)
<i>Trisetum flavescens</i>	II (1–4)	IV (1–6)	II (1–3)	III (1–6)
<i>Achillea millefolium</i>	III (1–6)	V (1–4)	III (1–4)	III (1–6)
<i>Carex flacca</i>	I (1–4)	II (1–4)	I (1)	I (1–4)
<i>Sanguisorba minor</i>	I (4)	II (3–5)		I (3–5)
<i>Koeleria macrantha</i>	I (1)	II (1–6)		I (1–6)
<i>Agrostis stolonifera</i>	I (1–7)	II (1–6)	I (6)	I (1–7)
<i>Festuca ovina</i>		II (1–6)		I (1–6)
<i>Prunella vulgaris</i>	III (1–4)	III (1–4)	IV (1–3)	III (1–4)
<i>Leontodon autumnalis</i>	II (1–5)	II (1–3)	IV (1–4)	III (1–5)
<i>Luzula campestris</i>	II (1–4)	II (1–6)	IV (1–4)	III (1–6)
<i>Danthonia decumbens</i>	I (2–5)	I (1–3)	V (2–5)	I (1–5)
<i>Potentilla erecta</i>	I (1–4)	I (3)	V (1–4)	I (1–4)
<i>Succisa pratensis</i>	I (1–4)	I (1–5)	V (1–4)	I (1–5)
<i>Pimpinella saxifraga</i>	I (1–4)	I (1–4)	III (1–4)	I (1–4)
<i>Stachys betonica</i>	I (1–5)	I (1–4)	III (1–4)	I (1–5)
<i>Carex caryophylla</i>	I (1–4)	I (1–3)	II (1–2)	I (1–4)
<i>Conopodium majus</i>	I (1–4)	I (1–5)	II (2–3)	I (1–5)
<i>Ranunculus acris</i>	IV (1–4)	II (1–4)	IV (2–4)	III (1–4)
<i>Rumex acetosa</i>	III (1–4)	III (1–4)	III (1–3)	III (1–4)
<i>Hypochoeris radicata</i>	III (1–5)	II (2–4)	III (1–4)	III (1–5)
<i>Ranunculus bulbosus</i>	III (1–7)	II (1–5)	III (1–2)	III (1–7)
<i>Taraxacum officinale</i> agg.	III (1–4)	III (1–4)	III (1–3)	III (1–4)
<i>Brachythecium rutabulum</i>	II (1–6)	III (1–4)	II (2)	III (1–6)
<i>Cerastium fontanum</i>	III (1–3)	II (1–3)	II (1–3)	II (1–3)
<i>Leontodon hispidus</i>	II (1–6)	III (2–4)	III (1–5)	II (1–6)
<i>Rhinanthus minor</i>	II (1–5)	II (1–4)	II (1–3)	II (1–5)
<i>Briza media</i>	II (1–6)	III (1–4)	III (2–3)	II (1–6)
<i>Heracleum spondylium</i>	II (1–5)	II (1–3)	III (1–3)	II (1–5)
<i>Trifolium dubium</i>	II (1–8)	II (1–5)	I (2)	II (1–8)
<i>Primula veris</i>	II (1–4)	II (2–4)	I (2)	II (1–4)
<i>Arrhenatherum elatius</i>	II (1–6)	II (1–7)	I (3–4)	II (1–7)
<i>Cirsium arvense</i>	II (1–3)	II (1–4)	I (1)	II (1–4)
<i>Eurhynchium praelongum</i>	II (1–5)	II (1–4)	I (1–2)	II (1–5)
<i>Rhynchospora squarrosus</i>	II (1–7)	II (1–5)	III (1–4)	II (1–7)
<i>Poa pratensis</i>	II (1–6)	II (2–5)		II (1–6)
<i>Poa trivialis</i>	II (1–8)	I (1–3)	I (1–2)	II (1–8)
<i>Veronica chamaedrys</i>	II (1–4)	I (1–4)	I (1)	II (1–4)
<i>Alopecurus pratensis</i>	I (1–6)	I (1–4)	I (1)	I (1–6)
<i>Cardamine pratensis</i>	I (1–3)	I (1)	I (3)	I (1–3)
<i>Vicia cracca</i>	I (1–4)	I (1–3)	I (1–2)	I (1–4)
<i>Bromus hordeaceus hordeaceus</i>	I (1–6)	I (2–3)	I (3)	I (1–6)
<i>Phleum pratense pratense</i>	I (1–6)	I (1–5)	I (1)	I (1–6)
<i>Juncus effusus</i>	I (2–3)	I (3)	I (1–2)	I (1–3)
<i>Phleum pratense bertolonii</i>	I (1–3)	I (1–3)	I (1)	I (1–3)
<i>Calliergon cuspidatum</i>	I (1–5)	I (2–4)	II (3)	I (1–5)
<i>Ranunculus repens</i>	II (1–7)	I (2)	II (1–4)	I (1–7)
<i>Pseudoscleropodium purum</i>	I (1–5)	I (3–4)	II (2)	I (1–5)
<i>Ophioglossum vulgatum</i>	I (1–5)	I (1)		I (1–5)
<i>Silene silene</i>	I (1–5)	I (1–3)		I (1–5)
<i>Agrimonia eupatoria</i>	I (1–5)	I (1–3)		I (1–5)
<i>Avenula pubescens</i>	I (1–3)	I (2–5)		I (1–5)
<i>Plantago media</i>	I (1–4)	I (1–4)		I (1–4)
<i>Alchemilla glabra</i>	I (2)	I (3)		I (2–3)
<i>Alchemilla filicaulis vestita</i>	I (1–3)	I (3)		I (1–3)
<i>Alchemilla xanthochlora</i>	I (1–3)	I (2)		I (1–3)
<i>Carex panicea</i>	I (1–4)	I (2–4)		I (1–4)
<i>Colchicum autumnale</i>	I (3–4)	I (1–3)		I (1–4)
<i>Crepis capillaris</i>	I (1–5)	I (3)		I (1–5)
<i>Festuca arundinacea</i>	I (1–5)	I (3–5)		I (1–5)

Figure 3. Floristic table for NVC community MG5 *Centaurea nigra*-*Cynosurus cristatus* grassland.

diagnostic than *Trisetum flavescens* and, particularly, *G. verum*. There are also important negative features, too, because, although some plants typical of the first and third sub-communities, such as *Lolium* and *Prunella vulgaris*, remain quite common here, the disappearance of others, like *Lathyrus pratensis*, *Danthonia decumbens*, *Potentilla erecta* and *Succisa pratensis* is strongly diagnostic. Similarly, with the third sub-community, there is that same mixture of positive and negative characteristics, and there is, among all the groups of preferentials, that same variation in abundance as is found among the constants and companions. Thus, some plants which can be very marked preferentials are always of rather low cover, as with *Prunella*, whereas others, like *Agrostis stolonifera*, though diagnostic at low frequency, can be locally plentiful.

For the naming of the sub-communities, we have generally used the most strongly preferential species, not necessarily those most frequent in the vegetation type. Sometimes, sub-communities are characterised by no floristic features over and above those of the community as a whole, in which case there will be no block of preferentials on the table. Usually, such vegetation types have been called Typical, although we have tried to avoid this epithet where the sub-community has a very restricted or eccentric distribution.

The tables organise and summarise the floristic variation which we encountered in the vegetation sampled: the text of the community accounts attempts to expound and interpret it in a standardised descriptive format. For each community, there is first a synonymy section which lists those names applied to that particular kind of vegetation where it has figured in some form or another in previous surveys, together with the name of the author and the date of ascription. The list is arranged chronologically, and it includes references to important unpublished studies and to accounts of Irish and Continental associations where these are obviously very similar. It is important to realise that very many synonyms are inexact, our communities corresponding to just part of a previously described vegetation type, in which case the initials *p.p.* (for *pro parte*) follow the name, or being subsumed within an older, more broadly-defined unit. Despite this complexity, however, we hope that this section, together with that on the affinities of the vegetation (see below), will help readers translate our scheme into terms with which they may have been long familiar. A special attempt has been made to indicate correspondence with popular existing schemes and to make sense of venerable but ill-defined terms like 'herb-rich meadow', 'oakwood' or 'general salt-marsh'.

There then follow a list of the constant species of the community, and a list of the rare vascular plants, bryophytes and lichens which have been encountered in the particular vegetation type, or which are reliably known

to occur in it. In this context, 'rare' means, for vascular plants, an A rating in the *Atlas of the British Flora* (Perring & Walters 1962), where scarcity is measured by occurrence in vice-counties, or inclusion on lists compiled by the NCC of plants found in less than one hundred 10 × 10 km squares. For bryophytes, recorded presence in under 20 vice-counties has been used as a criterion (Corley & Hill 1981), with a necessarily more subjective estimate for lichens.

The first substantial section of text in each community description is an account of the physiognomy, which attempts to communicate the feel of the vegetation in a way which a tabulation of data can never do. Thus, the patterns of frequency and abundance of the different species which characterise the community are here filled out by details of the appearance and structure, variation in dominance and the growth form of the prominent elements of the vegetation, the physiognomic contribution of subordinate plants, and how all these components relate to one another. There is information, too, on important phenological changes that can affect the vegetation through the seasons and an indication of the structural and floristic implications of the progress of the life cycle of the dominants, any patterns of regeneration within the community or obvious signs of competitive interaction between plants. Much of this material is based on observations made during sampling, but it has often been possible to incorporate insights from previous studies, sometimes as brief interpretative notes, in other cases as extended treatments of, say, the biology of particular species such as *Phragmites australis* or *Ammophila arenaria*, the phenology of winter annuals or the demography of turf perennials. We trust that this will help demonstrate the value of this kind of descriptive classification as a framework for integrating all manner of autecological studies (Pigott 1984).

Some indication of the range of floristic and structural variation within each community is given in the discussion of general physiognomy, but where distinct sub-communities have been recognised these are each given a descriptive section of their own. The sub-community name is followed by any synonyms from previous studies, and by a text which concentrates on pointing up the particular features of composition and organisation which distinguish it from the other sub-communities.

Passing reference is often made in these portions of the community accounts to the ways in which the nature of the vegetation reflects the influence on environmental factors upon it, but extended treatment of this is reserved for a section devoted to the habitat. An opening paragraph here attempts to summarise the typical conditions which favour the development and maintenance of the vegetation types, and the major factors which control floristic and structural variation within it. This is followed by as much detail as we have at the present time

about the impact of particular climatic, edaphic and biotic variables on the community, or as we suppose to be important to its essential character and distribution. With climate, for example, reference is very frequently made to the influence on the vegetation of the amount and disposition of rainfall through the year, the variation in temperature season by season, differences in cloud cover and sunshine, and how these factors interact in the maintenance of regimes of humidity, drought or frosts. Then, there can be notes of effects attributable to the extent and duration of snow-lie or to the direction and strength of winds, especially where these are icy or salt-laden. In each of these cases, we have tried to draw upon reputable sources of data for interpretation, and to be fully sensitive to the complex operation of topographic climates, where features like aspect and altitude can be of great importance, and of regional patterns, where concepts like continental, oceanic, montane and maritime climates can be of enormous help in understanding vegetation patterns.

Commonly, too, there are interactions between climate and geology that are best perceived in terms of variations in soils. Here again, we have tried to give full weight to the impact of the character of the landscape and its rocks and superficials, their lithology and the ways in which they weather and erode in the processes of pedogenesis. As far as possible, we have employed standardised terminology in the description of soils, trying at least to distinguish the major profile types with which each community is associated, and to draw attention to the influence of its floristics and structure of processes like leaching and podzolisation, gleying and waterlogging, parching, freeze-thaw and solifluction, and inundation by fresh- or salt-waters.

With very many of the communities we have distinguished, it is combinations of climatic and edaphic factors that determine the general character and possible range of the vegetation, but we have often also been able to discern biotic influences, such as the effects of wild herbivores or agents of dispersal, and there are very few instances where the impact of man cannot be seen in the present composition and distribution of the plant communities. Thus, there is frequent reference to the role which treatments such as grazing, mowing and burning have on the floristics and physiognomy of the vegetation, to the influence of manuring and other kinds of eutrophication, of draining and re-seeding for agriculture, of the cropping and planting of trees, of trampling or other disturbance, and of various kinds of recreation.

The amount and quality of the environmental information on which we have been able to draw for interpreting such effects has been very variable. Our own sampling provided just a spare outline of the physical and edaphic conditions at each location, data which we have summarised where appropriate at the foot of the

floristic tables; existing sources of samples sometimes offered next to nothing, in other cases very full soil analysis or precise specifications of treatments. In general, we have used what we had, at the risk of great unevenness of understanding, but have tried to bring some shape to the accounts by dealing with the environmental variables in what seems to be their order of importance, irrespective of the amount of detail available, and by pointing up what can already be identified as environmental threats. We have also benefited by being able to draw on the substantial literature on the physiology and reproductive biology of individual species, on the taxonomy and demography of plants, on vegetation history and on farming and forestry techniques. Sometimes, this information provides little more than a provisional substantiation of what must remain for the moment an interpretive hunch. In other cases, it has enabled us to incorporate what amount to small essays on, for example, the past and present role of *Tilia cordata* in our woodlands with variation in climate, the diverse effects of dunging by rabbit, sheep and cattle on calcicolous swards, or the impact of burning on *Calluna-Arctostaphylos* heath on different soils in a boreal climate. Debts of this kind are always acknowledged in the text and, for our part, we hope that the accounts indicate the benefits of being able to locate experimental and historical studies on vegetation within the context of an understanding of plant communities (Pigott 1982).

Mention is often made in the discussion of the habitat of the ways in which stands of communities can show signs of variation in relation to spatial environmental differences, or the beginnings of a response to temporal changes in conditions. Fuller discussion of zonations to other vegetation types follows, with a detailed indication of how shifts in soil, microclimate or treatment affect the composition and structure of each community, and descriptions of the commonest patterns and particularly distinctive ecotones, mosaics and site types in which it and any sub-communities are found. It has also often been possible to give some fuller and more ordered account of the ways in which vegetation types can change through time, with invasion of newly available ground, the progression of communities to maturity, and their regeneration and replacement. Some attempt has been made to identify climax vegetation types and major lines of succession, but we have always been wary of the temptation to extrapolate from spatial patterns to temporal sequences. Once more, we have tried to incorporate the results of existing observational and experimental studies, including some of the classic accounts of patterns and processes among British vegetation, and to point up the great advantages of a reliable scheme of classification as a basis for the monitoring and management of plant communities (Pigott 1977).

Throughout the accounts, we have referred to particular sites and regions wherever we could, many of these visited and sampled by the team, some the location of previous surveys, the results of which we have now been able to redescribe in the terms of the classification we have erected. In this way, we hope that we have begun to make real a scheme which might otherwise remain abstract. We have also tried in the habitat section to provide some indications of how the overall ranges of the vegetation types are determined by environmental conditions. A separate paragraph on distribution summarises what we know of the ranges of the communities and sub-communities, then maps show the location, on the  $10 \times 10$  km national grid, of the samples that are available to us for each. Much ground, of course, has been thinly covered, and sometimes a dense clustering of samples can reflect intensive sampling rather than locally high frequency of a vegetation type. However, we believe that all the maps we have included are accurate in their general indication of distributions, and we hope that this exercise might encourage the production of a comprehensive atlas of British plant communities.

The last section of each community description considers the floristic affinities of the vegetation types in the scheme, and expands on any particular problems of synonymy with previously described assemblages. Here, too, reference is often given to the equivalent or most closely-related association in Continental phytosociological classifications and an attempt made to locate each community in an existing alliance. Where the fuller account of British vegetation that we have been able to provide necessitates a revision of the perspective on European plant communities as a whole, some suggestions are made as to how this might be achieved.

Meanwhile, each reader will bring his or her own needs and commitment to this scheme and perhaps be dismayed by its sheer size and apparent complexity. For those requiring some guidance as to the scope of each volume and the shape of that part of the classification with which it deals, the introductions to the major vegetation types will provide an outline of the variation and how it has been treated. The contents page will then give

directions to the particular communities of interest. For readers less sure of the identity of the vegetation types with which they are dealing, a key is provided to each major group of communities which should enable a set of similar samples organised into a constancy table to be taken through a series of questions to a reasonably secure diagnosis. The keys, though, are not infallible short cuts to identification and must be used in conjunction with the floristic tables and community descriptions. An alternative entry to the scheme is provided by the species index which lists the occurrences of all taxa in the communities in which we have recorded them. There is also an index of synonyms which should help readers find the equivalents in our classification of vegetation types already familiar to them.

Finally, we hope that whatever the needs, commitments or even prejudices of those who open these volumes, there will be something here to inform and challenge everyone with an interest in vegetation. We never thought of this work as providing the last word on the classification of British plant communities: indeed, with the limited resources at our disposal, we knew it could offer little more than a first approximation. However, we do feel able to commend the scheme as essentially reliable. We hope that the broad outlines will find wide acceptance and stand the test of time, and that our approach will contribute to setting new standards of vegetation description. At the same time, we have tried to be honest about admitting deficiencies of coverage and recognising much unexplained floristic variation, attempting to make the accounts sufficiently open-textured that new data might be readily incorporated and ecological puzzles clearly seen and pursued. For the classification is meant to be not a static edifice, but a working tool for the description, assessment and study of vegetation. We hope that we have acquitted ourselves of the responsibilities of the contract brief and the expectations of all those who have encouraged us in the task, such that the work might be thought worthy of standing in the tradition of British ecology. Most of all, we trust that our efforts do justice to the vegetation which, for its own sake, deserves understanding and care.



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# SALT-MARSH COMMUNITIES





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# INTRODUCTION TO SALT-MARSH COMMUNITIES

## **The sampling and analysis of salt-marsh vegetation**

The herbaceous vascular vegetation on the intertidal silts and sands of salt-marshes is one of the most frequently used illustrations of ecological pattern but there are considerable difficulties in producing an adequate national classification of the plant communities of this distinctive habitat.

First, much salt-marsh vegetation is species-poor. There is little problem in sampling and sorting monospecific stands but, in many cases, a small number of species occur with varying abundance in a wide variety of combinations on salt-marshes. Early accounts of this vegetation (e.g. Tansley 1911, 1939) relied heavily on dominance in an attempt to make sense of such variation, but, as Dalby (1970) noted, this may obscure patterning among less conspicuous species that it is sensible to try and interpret. Furthermore, there has been a tendency in Britain to lump more complex vegetation, less susceptible to analysis, into a 'general salt-marsh' community. This term has sometimes been applied in its original, broad sense (Tansley 1911) to vegetation 'not dominated by any single species, except locally' and varying 'from place to place according to local conditions and to the accidents of colonisation by different species'; on other occasions (e.g. Chapman 1934), it has been used to denote a more clearly-defined community.

Second, on many salt-marshes there is a site-related element in the floristic variation among the communities which reflects particular local histories of marsh use or unique combinations of environmental conditions. Detailed studies of limited areas of salt-marsh (e.g. Yapp & Johns 1917, Chapman 1934, Dalby 1970, Packham & Liddle 1970, Gray & Bunce 1972) can be particularly valuable in elucidating such local patterns of variation but the use of a single suite of salt-marshes as a reference point for interpreting floristic variation throughout the country can be misleading. The especially attractive and varied salt-marshes of the north Norfolk coast have been frequently employed in such a way and this has bequeathed to us a perspective in which

the salt-marshes of the north and west tend to be underrated. On the other hand, to treat all local variation on an equal level would produce a very cumbersome national classification.

A third point is that 'salt-marsh' is as much a habitat as a group of plant communities and, although the vegetation itself plays some part in salt-marsh development, the physiographic boundaries of the habitat do not exactly coincide with a well-circumscribed range of communities. The salt-marsh flora has two major components: a halophyte element more or less confined to this particular kind of saline environment and an element comprising species which are widespread in inland, non-saline habitats. The latter species are commonly referred to as glycophytes, although it is possible that they include some distinct ecotypes which differ markedly from their inland counterparts in their physiological tolerances. Communities consisting predominantly or entirely of halophytes can sensibly be termed salt-marsh vegetation types but, towards the upper marsh limit and, in some areas (like the grazed marshes of the north and west) more extensively, communities consisting mainly or exclusively of glycophytes also occur in the salt-marsh habitat. These may extend well into the zone of tidal influence but they are often far from the common conception of salt-marsh vegetation. Some are perhaps best seen as highly modified forms of more typical salt-marsh communities produced by specialised treatments. Others probably reflect coincidences of environmental conditions which, though not especially coastal, occur only on salt-marshes. Deciding whether a particular vegetation type is more closely related to a mainstream salt-marsh community or a predominantly inland community is sometimes very difficult.

Finally, algae are often a conspicuous feature of salt-marsh vegetation and a decision has to be taken about whether or not to record them with the vascular flora and employ them in the analysis of data. Although there are some difficulties of identification with these taxa,

especially among the microscopic species, a number of schemes have been proposed for the classification of algal communities on salt-marshes (e.g. Cotton 1912, Carter 1932, 1933*a, b*, Chapman 1974, Polderman 1979, Polderman & Polderman-Hall 1980). These suggest that the concordance of algal assemblages with vascular plant communities may not be precise. In addition, algal communities appear to be subject to greater seasonal changes and, at least where the smaller species are concerned, to be organised on a finer scale. For the most part, therefore, vascular communities appear to be superimposed upon a distinct, more changeable and finer pattern of algal vegetation.

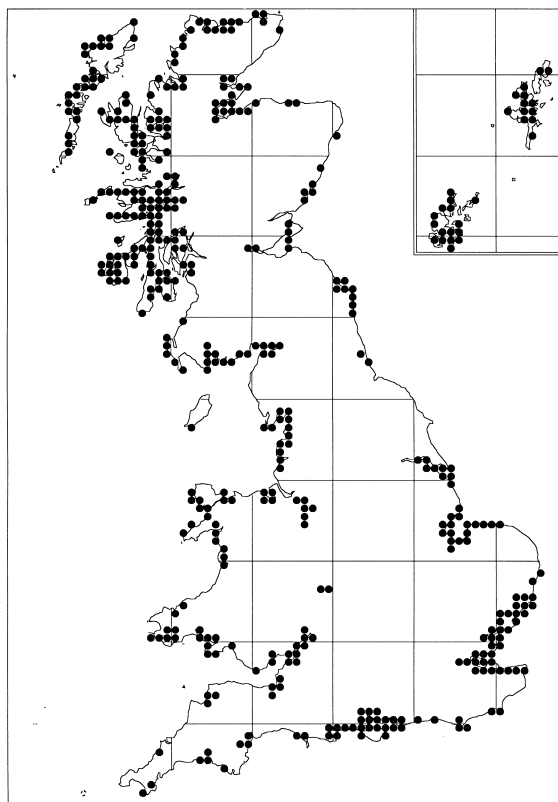
In an attempt to take account of such difficulties, Adam (1976, 1981) collected almost 3000 new samples of vegetation from British salt-marshes and his classification forms the basis of the scheme presented here. Adam's geographical coverage was extensive but some stretches of coastline were sparsely sampled (the Hampshire coast and south-west England) and others unvisited by him (the Thames estuary, the Humber and eastern Scotland). Where possible, this under-representation has been rectified by our own sampling pro-

gramme and by the generous donation of external data, most notably from Birse & Robertson (1976), Hilliam (1977) and Birse (1980), which considerably extended coverage, particularly in eastern Scotland, Orkney and Shetland (Figure 4).

Adam did not include the *Zostera* vegetation of flats in his survey but some very limited sampling by the survey team and a good deal of qualitative information forms the basis of an outline description included here. The work of Lee (1975, 1977) has also enabled a fuller account to be given of those communities represented in inland saline habitats. It has been possible, too, to integrate Adam's data with samples of swamps, mires and mesotrophic grasslands widely distributed inland and so produce a coherent account of some of the communities of the upper salt-marsh. However, the vegetation of brackish pools and ditches and the grassy sea-banks and walls characteristic of many reclaimed sites (Beefink 1975, Gray 1977, Adam & Akeroyd 1978) remains under-sampled.

As with other sections of the National Vegetation Classification, floristic data alone were used to characterise the vegetation types, any available environmental or site information being employed afterwards to help provide an ecological interpretation to the various sample groups distinguished.

Figure 4. Distribution of samples available from salt-marshes.



### The description of salt-marsh communities

Adam warned about the difficulty of generalising from a national scheme to a particular local situation and the same caution should be applied to this expanded and modified classification. Two of the communities distinguished are especially problematic in this respect: the *Puccinellia maritima* salt-marsh (SM13, *Puccinellietum maritimae* (Warming 1906) Christiansen 1927) and the *Festuca rubra* salt-marsh (SM16, *Juncetum gerardi* Warming 1906). These both encompass a very wide range of floristic variation, the internal differences between the sub-communities being almost as great as those features which distinguish these vegetation types from other salt-marsh communities. Although the sub-communities characterised should be useful in discussing national variation, they may well be of less value in local small-scale studies and, in certain cases, it might be appropriate to devise *ad hoc* classifications within these major types for particular sites.

Although Adam's approach was phytosociological, it was an important feature of his work that he classified the samples without prior reference to existing schemes devised for salt-marshes in other parts of Europe (e.g. Beefink 1962, 1965, 1966, Géhu 1975). Nevertheless, there is a striking similarity between many of his final groups and the salt-marsh associations of Continental classifications and much British vegetation of this kind can be seen as extending the known distribution of

previously-described communities. It is less easy to relate the vegetation types characterised here to those in earlier descriptive accounts of British salt-marshes where floristic definition was sometimes vague and units often rather heterogeneous.

A total of 28 communities of salt-marsh vegetation has been characterised from the available data (Figure 5). These can be conveniently reviewed under four main heads: eel-grass and tassel-weed communities of tidal flats, pools and ditches (3 communities), communities of the lower salt-marsh (13), communities of the middle salt-marsh (9) and communities of the upper salt-marsh (3). Brief mention is also made below of vegetation types that are treated in other volumes but which sometimes figure prominently on salt-marshes.

### Eel-grass and tassel-weed communities of tidal flats, pools and ditches

Our three native species of *Zostera* (*Z. marina*, *Z. angustifolia* and *Z. noltii*) are prominent, usually with very few other vascular species but often with abundant algae, in vegetation that occurs on the eu-littoral and sub-littoral zones of sand and silt flats. Without extensive floristic

data, separate communities have not been defined here but these vegetation types are the British representatives of the eel-grass communities of the Mediterranean, west European and Baltic coasts placed in the alliance *Zosterion Christiansen 1934* of the class *Zosteretea marinae*.

*Ruppia maritima* and the much rarer *Eleocharis parvula* can each occur prominently in communities of brackish pools, pans, and creeks and, in certain parts of their ranges in Britain, on the open surface of salt-marshes. Comparable vegetation elsewhere in Europe has been characterised as a *Ruppium maritimae* Hocquette 1927 (SM2) and an *Eleocharietum parvulae* (Preuss 1911/12) Gillner 1960 (SM3) and grouped in the alliance *Ruppion maritimae* Br.-Bl. 1931 of the class *Ruppiaetea maritimae* J. Tüxen 1960.

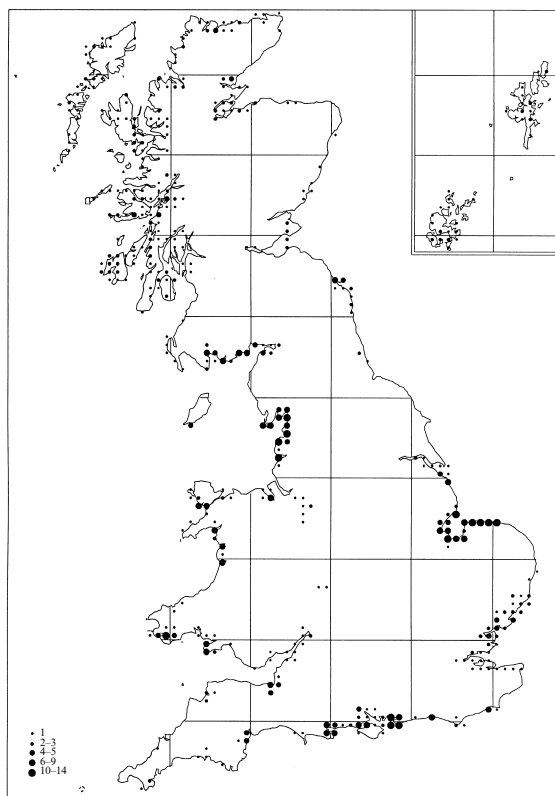
### Lower salt-marsh communities

Although the distinction between low, mid- and upper marsh is not a simple one, it is convenient to group together thirteen communities in which either *Spartina* spp., annual *Salicornia* spp., *Suaeda maritima* and/or *Puccinellia maritima* generally form a prominent component of the vegetation with, more unevenly, *Aster tripolium* and *Halimione portulacoides*.

Three communities dominated by *Spartina* spp. occur in Britain. By far the commonest is the *Spartina anglica* salt-marsh (SM6, *Spartinetum townsendii* (Tansley 1939) Corillion 1953), dominated by *S. townsendii sensu lato* (generally the fertile amphidiploid *S. anglica* but also occasionally with its male sterile F<sub>1</sub> precursor *S. × townsendii*). Although *S. anglica* can be found as a scattered associate in almost every salt-marsh community, the spread over the last 100 years of dense stands of this species is one of the most spectacular recent changes in the vegetation of the maritime zone of Britain. Communities dominated by its presumed parents, the native *S. maritima* (SM4, *Spartinetum maritimae* (Emb. & Regn. 1926) Corillion 1953) and the naturalised alien *S. alterniflora* (SM5, *Spartinetum alterniflorae* Corillion 1953), appear to be declining and are now much restricted in their distribution. Cord-grass vegetation of these types through western Europe and on the east coast of North America has been placed in the alliance *Spartinion* Conrad 1933 of the class *Spartinetea maritimae* R.Tx. 1961.

Annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* occur together in various combinations as colonising vegetation towards the lower limit of salt-marshes and in open and disturbed areas at higher levels. Three communities have been distinguished according to the balance of the various components: the annual *Salicornia* salt-marsh (SM8, *Salicornietum europaeae* Warming 1906), *Suaeda maritima* salt-marsh (SM9, *Suaedetum maritimae* (Conrad 1935) Pignatti 1953) and

Figure 5. Distribution of vegetation types characterised from salt-marshes.



the transitional *Puccinellia-Salicornia-Suaeda* salt-marsh (SM10). Predominantly low-marsh vegetation of these kinds in which annual chenopods are prominent is grouped in the alliance Thero-Salicornion strictae Br.-Bl. 1933 *emend.* R.Tx. 1950 of the class Thero-Salicornietea Pignatti 1953 *emend.* R.Tx. in R.Tx. & Oberdorfer 1958.

The perennial relative of *Salicornia*, now termed *Arthrocnemum perenne*, occurs occasionally in Britain in a variety of salt-marsh communities but locally forms dense stands which are best treated as a distinct vegetation type similar to the *Salicornietum radicans* Br.-Bl. 1931, traditionally separated off from the annual chenopod communities into the *Salicornion fruticosae* Br.-Bl. 1931 alliance of the *Salicornietea fruticosae*.

The five remaining low-marsh communities are all richer and more varied vegetation types than these, composed largely of perennial halophytes and, among these, the grass *Puccinellia maritima* is of prime importance with, less frequently and more unevenly throughout, *Aster tripolium*, *Halimione portulacoides*, *Glaux maritima*, *Plantago maritima*, *Limonium* cf. *vulgare*, *Triglochin maritima*, *Armeria maritima* and *Spergularia media*.

The general relationship of these communities to phytosociological units defined from mainland Europe is fairly clear. They fall within the class *Juncetea maritimae* R.Tx. & Oberdorfer 1958 which also takes in much perennial mid-marsh and sea-cliff vegetation extending from the Arctic to the Mediterranean. West European salt-marsh communities are assigned to the order *Glauco-Puccinellietalia* Beetsink & Westhoff 1962 but, in Britain, the floristic distinction between the two major alliances, the *Puccinellion maritimae* Christiansen 1927 of the low-marsh and the *Armerion maritimae* Br.-Bl. & de Leuw 1936 of the mid-marsh, is not as clear as on the Continent. In this country, *Armeria maritima* and, to a lesser extent, *Glaux maritima*, both considered good diagnostic species for the *Armerion* elsewhere in Europe, extend on to the low marsh and, indeed, are important components of some of the *Puccinellion* communities. Within Britain, a better general distinction between low- and mid-marsh vegetation types is the separation between the dominant role of *Puccinellia maritima* on the one hand and *Festuca rubra* and *Juncus gerardii* on the other, although, in particular situations, this too may be an unclear criterion.

In this scheme, the bulk of this remaining low-marsh vegetation is included in a single large and varied community, the *Puccinellia maritima* salt-marsh (SM13, *Puccinellietum maritimae* (Warming 1906) Christiansen 1927). This is the most widespread of all British salt-marsh vegetation types and it spans swards which grade, in one direction, to the Thero-Salicornion through an increased representation of annual chenopods and, in

another, to the *Armerion* communities with a switch in dominance to *F. rubra*, *J. gerardii* and *Agrostis stolonifera*. As well as some rather species-poor *Puccinellia*-dominated swards, it also includes a variety of richer vegetation types, some previously considered within the ambit of a 'general salt-marsh' community and others representing local variation in which individual species attain prominence.

A second major community, especially on ungrazed sites to the south and east, is the *Halimione portulacoides* salt-marsh (SM14, *Halimionetum portulacoidis* (Kuhnholz-Lordat 1927) Des Abbayes & Corillon 1949). This shares many species with the *Puccinellietum* and grades floristically to it, but it is generally distinct in the partial or total dominance of *H. portulacoides*. Also predominantly on ungrazed south-eastern sites, though somewhat more restricted in its distribution, is the *Aster tripolium* var. *discoideus* salt-marsh (SM11, *Asteretum tripolii* Tansley 1939). Like the *Halimionetum*, this community is often prominent on creek-sides, though it is also frequent low down on salt-marshes and shows some floristic overlap with Thero-Salicornion vegetation. Variation within *A. tripolium* is complex but a provisional community has been erected to contain stands dominated by the rayed form (SM12, cf. *Sociatie van Aster tripolium* Beetsink 1962). This is of local distribution and it shows some affinities with vegetation of brackish waters but further sampling is needed to establish its exact status and relationships. With a similar range and also showing close floristic relationships to the *Halimionetum* is vegetation with a striking local dominance of *Inula crithmoides* (SM26), a plant more geographically confined on salt-marshes than its occurrences on sea cliffs in Britain.

Finally, *Puccinellion* species form an understorey to one of the British salt-marsh communities in which *Juncus maritimus* is a physiognomic dominant. The classification of these vegetation types is problematic (Adam 1977): *J. maritimus* is dominant in certain mid-marsh communities as well as in sub-communities of the *Halimionetum* and the upper-marsh *Atriplici-Elymetum pycnanthi* (see below). However, the *Juncus maritimus*-*Triglochin maritima* salt-marsh (SM15) is a distinct type floristically, is the most widespread of all British *J. maritimus* communities and satisfactorily incorporates those stands in which *J. maritimus* reaches its lowest limit around our coasts. Vegetation of this type has sometimes been separated off into a separate alliance, the Halo-Scirpion (Dahl & Hadač 1971) den Held & Westhoff 1969 *nom. nov.*

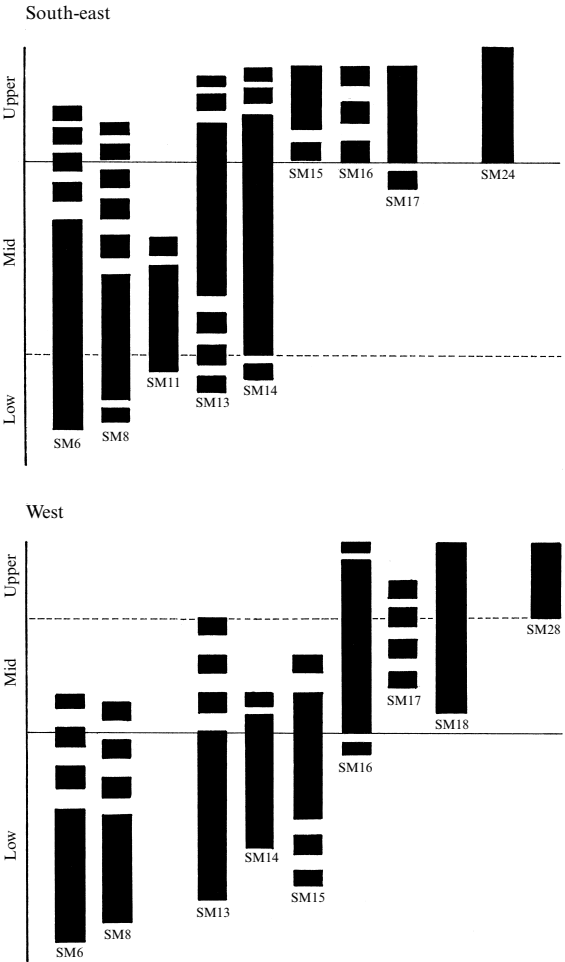
### Middle salt-marsh communities

Eight communities are distinguished from the middle salt-marsh zone (Figure 6). Three have a generally high frequency of *Festuca rubra*, *Juncus gerardii* and *Agrostis*

*stolonifera* with *Glaux maritima* and *Plantago maritima* and, more unevenly, *Armeria maritima* and *Triglochin maritima*. *Cochlearia officinalis*, *Plantago coronopus*, *Carex extensa* and *C. distans* occur patchily throughout

Figure 6. Generalised salt-marsh zonation in the south-east and west of Britain. The figure shows the relative extent of the major communities with an indication of the clarity of distinctions between low, mid and upper marsh.

SM6 *Spartinetum townsendii*  
SM8 *Salicornietum europaeae*  
SM11 *Asteretum tripolii*  
SM13 *Puccinellietum maritimae*  
SM14 *Halimionetum portulacoidis*  
SM15 *Juncus maritimus*-*Triglochin maritima* salt-marsh  
SM16 *Juncetum gerardi*  
SM17 *Artemisietum maritimae*  
SM18 *Juncus maritimus* salt-marsh  
SM24 *Atriplici-Elymetum pycnanthi*  
SM28 *Elymetum repentis*



and a variety of glycophytes, notably *Trifolium repens*, *Potentilla anserina*, *Holcus lanatus* and *Leontodon autumnalis*, attain prominence in some communities. Thero-Salicornion species such as *Puccinellia maritima*, *Halimione portulacoides* and *Limonium* cf. *vulgare* are infrequent. These communities correspond approximately to the Armerion alliance within the Glauco-Puccinellietalia.

The *Festuca rubra* salt-marsh (SM16, *Juncetum gerardi* Warming 1906) is, like the *Puccinellietum*, a large and varied vegetation type with a wide distribution, especially on the grazed marshes of the north and west of Britain. It includes swards which, on the one hand, grade to the *Puccinellietum* and, on the other, show diverse affinities with brackish and freshwater inundation communities of the Elymo-Rumicion *crispi*, Cynosurion pastures and Caricion *davallianae* mires. These reflect its considerable vertical range on salt-marshes, its widespread use for grazing and turf-cutting and the disturbance and freshwater flushing which it often experiences at higher levels.

*Juncetum gerardi* species form an understorey to a second community, the *Juncus maritimus* salt-marsh (SM18) which includes the bulk of those mid-marsh stands in which *J. maritimus* is dominant, often with abundant *Oenanthe lachenalii* and Elymo-Rumicion species such as *Elymus repens*, *Rumex crispus* and *Atriplex prostrata*. An *Artemisia maritima* salt-marsh (SM17, *Artemisietum maritimae* Hocquette 1927) has not traditionally been characterised in British accounts but it is a distinct vegetation type which shows affinities with both the Armerion communities (especially the *F. rubra*-dominated form of the *Juncetum gerardi*) and the Puccinellion (particularly the *Halimionetum*).

The six remaining mid-marsh communities are rather specialised vegetation types of either widespread but local occurrence or restricted geographical distribution. Two are dominated by colonial members of the Cyperaceae and are especially characteristic of damp depressions and brackish sites, especially to the north and west. The *Blysmus rufus* salt-marsh (SM19, *Bllysmetum rufi* (G. E. & G. Du Rietz 1925) Gillner 1960) and the *Eleocharis uniglumis* salt-marsh (SM20, *Eleocharitetum uniglumis* Nordhagen 1923) are sometimes accommodated within a distinct alliance, the Eleocharion uniglumis, and they represent a phytogeographical affinity with predominantly north European salt-marsh communities.

Two further communities are unique to Britain, and within the country confined to north Norfolk and Sussex, and are characterised by the occurrence of Mediterranean plants in highly distinctive salt-marsh/sand-dune/shingle transitions. The *Suaeda vera*-*Limonium binervosum* salt-marsh and the *Halimione portulacoides*-*Frankenia laevis* salt-marsh (SM22, perhaps equivalent

to the *Limonio vulgaris*-*Frankenietum laevis* Géhu & Géhu-Franck 1975) can be seen as the northernmost outpost of the vegetation of the Frankenio-Armerion, proposed as a sub-alliance of the Armerion.

Also, within the Glauco-Puccinellietalia is the *Spergularia marina*-*Puccinellia distans* salt-marsh (SM23, *Puccinellietum distantis* Feekes (1934) 1945), a community which is especially characteristic of the hypersaline conditions developing in drying pans and depressions on salt-marshes, in inland saline sites and, increasingly now, along the edges of inland roads which have received heavy applications of rock-salt in frosty weather. This kind of vegetation is usually placed in the alliance Puccinellio-Spergularion salinae Beefink 1965. Finally, among the mid-marsh communities, it is sensible to include ephemeral vegetation with *Sagina maritima*, *S. nodosa* and various local annuals which finds a place in turf-cuttings and other breaks in the salt-marsh swards of the *Puccinellietum* and *Juncetum gerardi* as an early stage in recolonisation. We have not characterised any separate communities here but referred the assemblages (SM27) more generally to the Saginion maritimae Westhoff, van Leeuwen & Adriani 1962, an alliance placed in its own class.

### Upper salt-marsh communities

Of the considerable variety of vegetation types which occur on salt-marshes towards the upper limit of tidal influence, three are described in this volume. They are characterised by the general prominence of *Elymus pycnanthus* and/or *E. repens*, patchy representation of Puccinellion and Armerion species and the scattered occurrence throughout of nitrophilous weeds and plants of fresh-water inundation communities. Predominantly perennial vegetation of this kind, characteristic of European drift-lines, has been variously placed in the alliance Elymion pycnanthi of the Elymetea pycnanthi or the Elymo-Rumicion crispi Nordhagen 1940 of the Molinio-Arrhenatheretea.

Two of the communities are grass-dominated. The *Elymus pycnanthus* salt-marsh (SM24, *Atriplici-Elymetum pycnanthi* Beefink & Westhoff 1962) is the vegetation type which commonly terminates the salt-marsh zonation in the south and east. To the north and west, it is replaced by the *Elymus repens* salt-marsh (SM28, *Elymetum repentis maritimum* Nordhagen 1940) which has a less conspicuous representation of salt-marsh species and which shows more obvious floristic affinities with the halophyte forms of Elymo-Rumicion vegetation. On drift-lines on the salt-marsh/sand-dune transi-

tion at scattered localities in the south-east, a third vegetation type, the *Suaeda vera* community (SM25, *Elymo pycnanthi*-*Suaedetum verae* (Arènes 1933) Géhu 1975), is characteristic.

### Other vegetation types on salt-marshes

A variety of vegetation types described fully in other sections of *British Plant Communities* occurs on salt-marshes where there is a combination of little tidal influence and low soil salinity with either some influence of fresh-water or types of treatment and/or disturbance characteristic of other habitats (Figure 9).

Three mesotrophic grasslands occur commonly on salt-marshes (see Rodwell 1992). Both the *Festuca rubra*-*Agrostis stolonifera*-*Potentilla anserina* inundation community (MG11) and the *Festuca arundinacea* coarse grassland (MG12, *Potentillo-Festucetum arundinaceae* Nordhagen 1940) have distinct halophyte sub-communities and are found at scattered localities, mainly on the west coast, the former sometimes extensively on the grazed open marsh, the latter more patchily on ungrazed sites and on ditch-banks where there is some brackish influence. The *Agrostis stolonifera*-*Alopecurus geniculatus* inundation grassland (MG13) is also widespread as small stands in areas where there is some brackish influence and poaching by stock.

Swamp vegetation may occur in estuaries and in salt-marsh ditches and pools where there is slow-moving or standing brackish water and is also occasionally encountered on the open surface of salt-marshes and around saline springs inland (Rodwell 1994a). Two such communities are largely confined to such situations: the *Scirpus maritimus* swamp (S21, *Scirpetum maritimi* (Br.-Bl. 1931) R.Tx. 1937), which is widespread and sometimes extensive and the *Scirpus lacustris* ssp. *tabernaemontani* swamp (S20, *Scirpetum tabernaemontani* Passarge 1964) which is more local. The *Phragmites australis* swamp (S4, *Phragmitetum australis* Gams (1927) Schmale 1939), the *Typha latifolia* swamp (S12, *Typhetum latifoliae* Soó 1927) and the *Phalaris arundinacea* tall-herb fen (S28, *Phalaridetum arundinaceae* Libbert 1931) are much more widely distributed in fresh-water habitats and salt-marsh stands are often only marginally halophyte in character.

Finally here, the *Iris pseudacorus*-*Filipendula ulmaria* tall-herb fen (M28, *Filipendulo-Iridetum pseudacori* Adam 1976) is a very conspicuous feature of the upper-marsh and some raised beaches on the west coast of Scotland where stands may be extensive and rich around freshwater flushes.

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# KEY TO SALT-MARSH COMMUNITIES

With something as complex and variable as vegetation, no key can pretend to offer an infallible short cut to diagnosis. The following should thus be seen as simply as a crude guide to identifying the types of vegetation found on salt-marshes and must always be used in conjunction with the data tables and community descriptions. It relies on floristic (and, to a lesser extent, physiognomic) features of the vegetation and demands a knowledge of the British vascular flora. It does not make primary use of any habitat features, though these may provide a valuable confirmation of a diagnosis.

Because the major distinctions between the vegetation types in the classification are based on inter-stand frequency, the key works best when sufficient samples of similar composition are available to construct a constancy table. It is the frequency values in this (and, in some cases, the ranges of abundance) which are then subject to interrogation with the key.

Samples should always be taken from homogeneous stands and be 2 × 2 m or 4 × 4 m according to the scale of the vegetation or, where stands are irregular, of identical size but different shape.

1 Open or closed vegetation of, or overwhelmingly dominated by, a single species 2

Vegetation with two or more co-dominants or, if with a single dominant, then some other species with cover values of Domin 4–7 3

2 Open or closed vegetation of, or overwhelming dominated by:

*Zostera marina*, *Z. angustifolia* or *Z. noltii* on sub- or eu-littoral flats, often with no other vascular plants but commonly with some fucoids and green algae

**SM1** *Zostera* communities

Zosterion Christiansen 1934

*Ruppia maritima*, sometimes with *Potamogeton pectinatus*, *Zannichellia palustris* and/or *Ranunculus baudotii* as submerged vegetation in brackish pools, in dried-up pans or, more rarely, on open flats

**SM2** *Ruppia maritima* salt-marsh

*Ruppium maritima* Hocquette 1927

*Suaeda maritima* in usually somewhat open vegetation and often in small stands

**SM9** *Suaeda maritima* salt-marsh

*Suaedetum maritima* (Conrad 1935) Pignatti 1953

*Aster tripolium* var. *discoideus*

**SM11** *Aster tripolium* var. *discoideus* salt-marsh

*Asteretum tripolii* Tansley 1939

Rayed *Aster tripolium*

**SM12** Rayed *Aster tripolium* stands

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Variation within *Aster tripolium* is complex and the phytosociological relationships of the forms are unclear.

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*Puccinellia maritima* in low, open or closed vegetation or occasionally in dense, tall swards but with no extensive understorey of turf fucoids

**SM13** *Puccinellia maritima* salt-marsh

*Puccinellietum maritimae* (Warming 1906) Christiansen 1927

*Puccinellia maritima* dominated sub-community

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In hot dry summers on the upper marsh, when the shoots of *Glaux maritima* may become shrivelled, some stands of the *Puccinellietum maritimae*, *Glaux maritima* sub-community may key out here.

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*Eleocharis parvula* in a very diminutive sward, sometimes obscured by algae or freshly-deposited silt

**SM3** *Eleocharis parvula* salt-marsh  
*Eleocharietum parvulae* (Preuss 1911/12) Gillner 1960

*Spartina maritima* in isolated clumps or as extensive stands

**SM4** *Spartina maritima* salt-marsh  
*Spartinetum maritimae* (Emb. & Regn. 1926) Corillion 1963

*Spartina alterniflora* in a dense cover with a little *S. anglica*, *Puccinellia maritima* and *Aster tripolium*

**SM5** *Spartina alterniflora* salt-marsh  
*Spartinetum alterniflorae* Corillion 1953

*Spartina anglica*, sometimes with *S. × townsendii*, often in very extensive stands

**SM6** *Spartina anglica* salt-marsh  
*Spartinetum townsendii* (Tansley 1939) Corillion 1953

*Arthrocnemum perenne* in dense pure stands or as open mosaic with *Halimione portulacoides*, *Puccinellia maritima* and *Suaeda maritima*

**SM7** *Arthrocnemum perenne* stands

Annual *Salicornia* spp. in usually somewhat open vegetation

**SM8** Annual *Salicornia* spp. salt-marsh  
*Salicornietum europaeae* Warming 1906

*Puccinellia maritima* or *Plantago maritima* with an extensive understorey of diminutive turf fucoids

**SM13** *Puccinellietum maritimae*  
*Puccinellia maritima*-turf fucoid sub-community

*Glaux maritima* in often small and fragmentary stands

**SM13** *Puccinellietum maritimae*  
*Glaux maritima* sub-community

*Halimione portulacoides* as an even-topped bushy canopy or discrete hemispherical bushes in species-poor vegetation without *Juncus maritimus*

**SM14** *Halimione portulacoides* salt-marsh  
*Halimionetum portulacoidis* (Kuhnholz-Lordat 1927) Des Abbayes & Corillion 1949  
*Halimione portulacoides*-dominated sub-community

*Halimione portulacoides* with some *Juncus maritimus* as scattered shoots or small dense patches

**SM14** *Halimionetum portulacoidis*  
*Juncus maritimus* sub-community

---

Small but discrete patches of these two sub-communities of the *Halimionetum* may occur in mosaics with the *Puccinellietum maritimae* and these should be distinguished from the intimate mixtures of *H. portulacoides* and *P. maritima* that characterise the *Puccinellia maritima* sub-community of the *Halimionetum*.

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*Juncus maritimus* as small dense patches within a ground of *Halimione portulacoides*

**SM14** *Halimionetum portulacoidis*  
*Juncus maritimus* sub-community

*Juncus maritimus* as tall dense patches with little or no *Halimione portulacoides*

**SM15** *Juncus maritimus*-*Triglochin maritima* salt-marsh

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*Juncus maritimus* may also be locally dominant in the *Juncus maritimus* salt-marsh but the consistent presence there of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* as an often thick understorey usually serves to separate this vegetation from the two above. *J. maritimus* may also be locally abundant in the *Atriplici-Elymetum pycnanthi* but there *Elymus pycnanthus* is consistently dominant.

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*Juncus gerardii* as generally small and often roughly circular patches of sometimes tall vegetation

**SM16** *Festuca rubra* salt-marsh  
*Juncetum gerardi* Warming 1906  
*Juncus gerardii*-dominated sub-community

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*Juncus gerardii* may also be locally abundant in other sub-communities of the *Juncetum gerardi*.

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*Festuca rubra* as a thick springy mattress of tall and dense vegetation

**SM16** *Juncetum gerardi*  
Sub-community with tall *Festuca rubra* dominant

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*Festuca rubra* may also be locally abundant in the shorter swards of other sub-communities of the *Juncetum gerardi*.

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*Blysmus rufus* in often small stands of sometimes open vegetation

**SM19** *Blysmus rufus* salt-marsh  
*Blysmetum rufi* (G. E. & G. Du Rietz 1925) Gillner 1960



*Eleocharis uniglumis* in often small stands of sometimes open vegetation

**SM20** *Eleocharis uniglumis* salt-marsh  
*Eleocharitetum uniglumis* Nordhagen 1923

*Suaeda vera* as an open bushy canopy with one or more of *Limonium binervosum*, *L. bellidifolium* or *Frankenlaevis* beneath

**SM21** *Suaeda vera*-*Limonium binervosum* salt-marsh

*Suaeda vera* as a more or less closed canopy in strand-line vegetation without the above species

**SM25** *Suaeda vera* salt-marsh  
*Elymo pycnanthi-Suaedetum verae* (Arènes 1933) Géhu 1975

*Spergularia marina* or *Puccinellia distans* in often small stands of usually somewhat open vegetation

**SM23** *Spergularia marina*-*Puccinellia distans* salt-marsh  
*Puccinellietum distantis* Feekes (1934) 1945

*Elymus pycnanthus* as stiff clumps, usually without any *Suaeda vera* or *Inula crithmoides*

**SM24** *Elymus pycnanthus* salt-marsh  
*Atriplici-Elymetum pycnanthi* Beeftink & Westhoff 1962

*Elymus repens* in a closed grassy sward

**SM28** *Elymus repens* salt-marsh  
*Elymetum repentis maritimum* Nordhagen 1940

*Inula crithmoides*, usually with some *Halimione portulacoides*

**SM26** *Inula crithmoides* stands

*Sagina maritima* or *Plantago coronopus* in often open or fragmentary vegetation in breaks within swards of other communities, especially the *Juncetum gerardi*

**SM27** Ephemeral *Sagina maritima* vegetation  
*Saginion maritimae* Westhoff, van Leeuwen & Adriani 1962

*Potentilla anserina* as small stands colonising breaks within swards of other mid- and upper-marsh vegetation

**SM16** *Juncetum gerardi* phase of sward regeneration in turf-cuttings

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Vegetation dominated by swamp species such as *Scirpus maritimus*, *S. lacustris* ssp. *tabernaemontani*, *Phragmites australis*, *Typha latifolia* and *Phalaris arundinacea* may be encountered on salt-marshes but these communities are included in Rodwell (1994a).

---

3 Low swards, sometimes rather open, dominated by various mixtures of annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* 4

Annual *Salicornia* spp. and *Suaeda maritima* not dominant or co-dominant 5

4 *Suaeda maritima* and annual *Salicornia* spp. co-dominant with less than 10% *Puccinellia maritima*

**SM9** *Suaedetum maritimae*

Annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* co-dominant in various proportions, often with a little *Aster tripolium*

**SM10** Transitional low-marsh vegetation

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Vegetation of this kind frequently occurs as mosaics between the *Salicornietum europaeae* and the *Puccinellietum maritimae*, *Spartinetum maritimae* and, especially in the south-east, the *Asteretum tripolii* and *Halimionetum portulacoidis*.

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5 *Aster tripolium* var. *discoideus* or rayed *Aster tripolium* dominant 6

*Aster tripolium* absent or present in small amounts 7

6 *Aster tripolium* var. *discoideus* dominant

**SM11** *Asteretum tripolii*

Rayed *Aster tripolium* dominant

**SM12** Rayed *Aster tripolium* stands

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Variation within *Aster tripolium* is complex and the phytosociological relationships of the different forms are unclear.

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7 *Arthrocnemum perenne* co-dominant with *Halimione portulacoides* and some *Puccinellia maritima*

**SM7** *Arthrocnemum perenne* stands

*Arthrocnemum perenne* absent or present in small amounts 8

8 *Puccinellia maritima* a major constituent of the vegetation 9

*Puccinellia maritima* absent or present in small amounts 16

9 Any of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* present in more than a trace and often co-dominant with *Puccinellia maritima*

- SM16** *Juncetum gerardi*  
*Puccinellia maritima* sub-community
- Above species usually comprising less than 10% of the sward 10
- 10 *Limonium binervosum* and/or *Frankenia laevis* present with *Halimione portulacoides* 11
- Neither *Limonium binervosum* nor *Frankenia laevis* present 12
- 11 *Suaeda vera* present as a conspicuous component
- SM21** *Suaeda vera*-*Limonium binervosum* salt-marsh
- Suaeda vera* absent
- SM22** *Halimione portulacoides*-*Frankenia laevis* salt-marsh  
*Limonia vulgaris*-*Frankenietum laevis* Géhu & Géhu-Franck 1975
- 12 *Puccinellia maritima* dominant or co-dominant with *Plantago maritima* and/or *Armeria maritima* with a conspicuous understorey of diminutive turf fucoids
- SM13** *Puccinellietum maritimae*  
*Puccinellia maritima*-turf fucoid sub-community
- Turf fucoids absent or with low cover 13
- 13 *Spartina maritima* present
- SM13** *Puccinellietum maritimae*  
*Puccinellia maritima*-*Spartina maritima* sub-community
- Spartina maritima* absent 14
- 14 *Halimione portulacoides* co-dominant with *Puccinellia maritima* in intimate mixtures in which shoots of the latter emerge through an open network of shoots of the former; *Festuca rubra* rare and never abundant
- SM14** *Halimionetum portulacoidis*  
*Puccinellia maritima* sub-community
- 
- Prostrate *Halimione portulacoides* is also sometimes abundant in the *Limonium vulgare*-*Armeria maritima* sub-community of the *Puccinellietum maritimae* but other dicotyledons are usually co-dominant there and *P. maritima* itself rarely comprises more than 10% of the swards. Intimate mixtures of *Halimione portulacoides* and *Puccinellia maritima* such as are included here should
- be distinguished from mosaics of discrete patches of the *Halimionetum portulacoidis* and the *Puccinellietum maritimae*.
- 
- Halimione portulacoides* infrequent and never co-dominant 15
- 15 *Puccinellia maritima* and *Glaux maritima* co-dominant in species-poor vegetation usually in small stands
- SM13** *Puccinellietum maritimae*  
*Glaux maritima* sub-community
- Puccinellia maritima* dominant in open vegetation with *Spergularia marina* and/or *Puccinellia distans*
- SM23** *Puccinellietum distantis*
- 16 Varied swards dominated by mixtures of dicotyledons including *Armeria maritima*, *Triglochin maritima* and *Plantago maritima* with usually less than 10% *Puccinellia maritima* and without *Frankenia laevis*, *Limonium binervosum*, *L. bellidifolium* and *Suaeda vera* 17
- Vegetation not dominated by mixtures of the listed dicotyledons or, if so, then some of *Frankenia laevis*, *Limonium binervosum*, *L. bellidifolium* and *Suaeda vera* also present 18
- 17 *Limonium vulgare* (or, locally, *L. humile*), *Halimione portulacoides* and annual *Salicornia* spp. present and sometimes abundant
- SM13** *Puccinellietum maritimae*  
*Limonium vulgare*-*Armeria maritima* sub-community
- Glaux maritima* and rayed *Aster tripolium* constant and sometimes abundant with no *Limonium vulgare* and little *Halimione portulacoides*
- SM13** *Puccinellietum maritimae*  
*Plantago maritima*-*Armeria maritima* sub-community
- 18 *Suaeda vera* and *Limonium binervosum* present and/or *Frankenia laevis* 19
- Not as above 21
- 19 *Frankenia laevis* present 20
- Frankenia laevis* absent
- SM21** *Suaeda vera*-*Limonium binervosum* salt-marsh  
Typical sub-community

20 *Suaeda vera* present

**SM21** *Suaeda vera*-*Limonium binervosum* salt-marsh  
*Frankenia laevis* sub-community

*Suaeda vera* absent

**SM22** *Limonia vulgaris*-*Frankenietum laevis*

21 *Artemisia maritima* prominent in usually small stands of somewhat variable vegetation ranging from rank grassy swards with much *Festuca rubra* to open bushy canopy of *A. maritima* over low *Halimione portulacoides*

**SM17** *Artemisietum maritimae*

*Artemisia maritima* absent or inconspicuous 22

22 Grassy swards in which *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* are generally important components in the absence of *Juncus maritimus* 23

*Juncus maritimus* an important component of the vegetation 25

23 *Trifolium repens*, *Leontodon autumnalis* and *Potentilla anserina* present and often abundant in various combinations, sometimes with *Carex distans* and/or *C. flacca* 24

Short swards of very variable composition but usually dominated by *Festuca rubra* and *Agrostis stolonifera* with some *Juncus gerardii*, *Glaux maritima*, *Triglochin maritima*, *Armeria maritima* and *Plantago maritima* and with the above species absent or at less than 10% cover

**SM16** *Juncetum gerardi*

*Festuca rubra*-*Glaux maritima* sub-community

On heavily-grazed marshes, especially in north-west England, swards lacking *Trifolium repens*, *Leontodon autumnalis* and *Potentilla anserina* may also have a very low cover of either *Festuca rubra* or *Agrostis stolonifera* or *Juncus gerardii*. These are best considered as derivatives of the *Festuca-Glaux* sub-community of the *Juncetum gerardi*.

24 *Carex flacca* constant and sometimes abundant

**SM16** *Juncetum gerardi*

*Carex flacca* sub-community

*Carex flacca* infrequent

**SM16** *Juncetum gerardi*

*Leontodon autumnalis* sub-community

On heavily-grazed marshes, especially in north-west England, swards lacking *Carex flacca* but also poor in *Leontodon autumnalis* and *Potentilla anserina* may be encountered. *Trifolium repens* remains a conspicuous component and such swards are best considered as derivatives of the *Leontodon autumnalis* sub-community of the *Juncetum gerardi*.

25 *Oenanthe lachenalii* constant and often abundant 26

*Oenanthe lachenalii* rare and never abundant but *Plantago maritima* and rayed *Aster tripolium* often conspicuous

**SM18** *Juncus maritimus* salt-marsh

*Plantago maritima* sub-community

26 *Festuca arundinacea* constant and often co-dominant with *Juncus maritimus*

**SM18** *Juncus maritimus* salt-marsh

*Festuca arundinacea* sub-community

*Festuca arundinacea* infrequent and never abundant

**SM18** *Juncus maritimus* salt-marsh

*Oenanthe lachenalii* sub-community

A variety of other vegetation types encountered on salt-marshes may fail to key out here. These are most likely to be certain kinds of driftline vegetation, of mires and of mesotrophic grasslands. The mesotrophic grasslands are likely to be the most troublesome to distinguish as they often grade into forms of the *Juncetum gerardi* which have been much altered by agricultural treatment or into the communities of brackish pools with an increase in soil water salinity.



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# COMMUNITY DESCRIPTIONS

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# SM1

## *Zostera* communities

### Zosterion Christiansen 1934

In Britain, three species of eel-grass, *Zostera marina*, *Z. angustifolia* and *Z. noltii*, form distinctive stands in the sub-littoral and eu-littoral zones of sand and mud flats. Very few samples of this vegetation were taken and the following account relies heavily on published and unpublished material relating in particular to The Solent (C. R. & J. M. Tubbs), the Thames estuary and Essex (Wyer & Waters 1975; Charman 1975, 1977*b*, 1979), north Norfolk (Ranwell & Downing 1959, Charman & Macey 1978), Lindisfarne (D. O'Connor), the Moray Firth (Rae 1979), and the west coast of Scotland (A. Currie). There are two difficulties in making use of existing information. First, *Z. angustifolia* is not consistently distinguished from narrow-leaved forms of *Z. marina*: this partly reflects the long-standing discussion on the taxonomic status of plants variously described as *Z. marina* var. *angustifolia*, *Z. hornemanniana* or *Z. angustifolia*. Second, eu-littoral stands have often been described simply as '*Zostera*' irrespective of whether they comprise *Z. angustifolia*, *Z. noltii* or both these species. This has been particularly true of accounts of the grazing of *Zostera* spp. by wildfowl and a separate note on this important aspect of the conservation value of the vegetation has therefore been appended.

#### *Zostera marina* stands

*Zosteretum marinae* Harmsen 1936

*Zostera marina* forms stands with a cover of trailing leaves up to 1 m long. Algae, especially *Enteromorpha* spp., are usually the sole associates. *Z. marina* is essentially a sub-littoral species, extending from 1–4 m below to just above low water of spring tides, although it also occurs in lagoons. The lower salinity limit for the species is about 35 g l<sup>-1</sup> (chloridity 24 g l<sup>-1</sup>) but the exact limits of its distribution may be controlled by light requirement below and susceptibility to dessication above. Around The Solent, plants are exposed for only 1½ hours even at low water of spring tides.

*Z. marina* shows considerable morphological variation with a decrease in leaf size and density upshore. Narrow-leaved plants from the lower eu-littoral have been described as *Z. marina* var. *angustifolia* or confused with *Z. angustifolia*. There also appears to be some variation in phenology in relation to the position of the plants on the shore. *Z. marina* shows considerable leaf loss in autumn and early winter but this may be much more apparent in eu-littoral plants than in those which are permanently submerged where a dense cover is maintained throughout the winter. Regrowth occurs in all plants in spring and early summer. Flowering seems to be most frequent in eu-littoral plants and in those sheltered from wave action with larger sub-littoral plants reproducing vegetatively.

In Britain, *Z. marina* always grows on a firm substrate, usually sand or sandy mud, though sometimes with an admixture of fine gravel.

Where their ranges overlap, as in The Solent, *Z. marina* passes upshore to *Z. noltii*; elsewhere *Z. marina* stands may be separated by a considerable expanse of bare substrate from salt-marsh vegetation proper. In The Solent, *Z. marina* may have a potential competitor in the sub-littoral brown alga *Sargassum muticum*, a native of Japan which has colonised some sites once occupied by *Z. marina*.

*Z. marina* was much reduced in the early 1930s by a wasting disease which seems to have been a combination of attack by a protozoan and an ascomycete fungus. Butcher (1934, 1941) catalogued the most substantial decrease on the East Anglian and north Kent coasts and around The Solent. In recent years, the species has certainly reappeared in abundance in The Solent but seems to have remained rare elsewhere in the south-east. Butcher (1934) did not examine changes on the Scottish coast but *Z. marina* is now abundant down the western coast of the mainland and the Outer Hebrides and also in the Moray Firth. The map shows the distribution of the species in Perring & Walters (1962) with modifications.

*Zosteretum marinae* has been widely reported from throughout Europe though its exact status following the 1930s disease and subsequent erosion of substrates is uncertain. In The Netherlands, Beeftink (1962) records the association as rare; in France it appears to have recovered somewhat (Géhu 1975).

### *Zostera angustifolia* stands

*Zostera angustifolia* forms stands with a cover of trailing leaves up to about 25 cm long. It may occur pure, though it is often mixed with the smaller *Z. noltii* and with a variety of algae among which species of *Ulva*, *Chaetomorpha* and *Enteromorpha* are often abundant. The table lists some samples of mixed *Zostera* vegetation from the Exe estuary, Devon. On the extensive estuarine flats of the Cromarty Firth, it occurs with *Ruppia maritima* and annual *Salicornia* spp.

*Z. angustifolia* can behave as a short-lived perennial. Around the Moray Firth, Rae (1979) noted that few plants lasted longer than two years and, throughout its British range, the species seems to suffer heavy leaf loss in autumn and early winter by a combination of natural shedding, storm damage and wildfowl grazing. Regrowth in spring can be largely by seedling germination (Ranwell & Downing 1959, Wyer & Waters 1975, Rae 1979) though good regeneration from existing rhizomes has also been reported.

*Z. angustifolia* is a plant of the lower and middle eu-littoral zone, extending to well above low water of neap tides and sometimes to high water of neap tides. Its optimal salinity is about 25–34 g l<sup>-1</sup> (chloridity 16–20 g l<sup>-1</sup>; Proctor 1980) and, as with *Z. marina*, its exact limits seem to be controlled by light requirement below and susceptibility to desiccation above. In The Solent, it is exposed for a maximum of about 6½ hours on the spring tides. It certainly grows best in sites which are never deeply submerged at high tide nor ever fully dry at low tide and is particularly characteristic of shallow depressions on tidal flats, often with some standing water at low tide. In such situations, it may form distinctive mosaics with *Z. noltii* which prefers the drier tops of low marsh ridges (Tutin, 1942, Wyer & Waters 1975, Rae 1979). It also occurs in the wet bottoms of deep marsh creeks (Chapman 1959).

*Z. angustifolia* is most characteristic of muds and muddy sands. These may be quite firm and contain some fine gravel but the species is typically associated with very sloppy mud on which even duck boards are an unsuccessful aid to sampling.

*Z. angustifolia* may pass upshore to stands of *Z. noltii* through mosaics of the two species; elsewhere it may give way to salt-marsh vegetation proper with an expanse of bare substrate between or through *Salicornietum europaeae*. In the Exe estuary, *Z. angustifolia* is replaced

upshore by *Spartinetum townsendii* (Proctor 1980).

The disease of the 1930s seems to have left *Z. angustifolia* largely untouched and, at present, the species is widespread along the south and east coasts of England and the east coast of Scotland (Perring & Walters 1962). It is all but absent from the west coast of Scotland. There are very extensive stands in the Cromarty Firth (Figure 7) and also along the Essex and north Kent coasts.

In Europe, the equivalent community *Zosteretum marinae stenophyllae* Harmsen 1936 has been recorded from The Netherlands (Beeftink 1962) and France (Géhu 1975).

### *Zostera noltii* stands

*Zosteretum noltii* Harmsen 1936

*Zostera noltii* forms stands with a cover of delicate trailing narrow leaves up to about 20 cm long. It may occur pure or with *Z. angustifolia* (see table) and occasional plants of lower salt-marsh species such as annual *Salicornia* spp. or *Spartina anglica*. *Ruppia maritima* occurs with *Z. noltii* on the estuarine flats of the Cromarty Firth (Rae 1979).

Like *Z. angustifolia*, *Z. noltii* experiences considerable leaf loss in autumn and early winter through natural shedding, storm damage and wildfowl grazing but plants towards the lower limit may remain winter-green (Wyer & Waters 1975, Rae 1979). Unlike *Z. angustifolia*, expansion in spring seems to occur more consistently by the regrowth of existing rhizomes (Wyer & Waters 1975, Rae 1979) as well as by the germination of seed, production of which may be prolific, especially at higher levels.

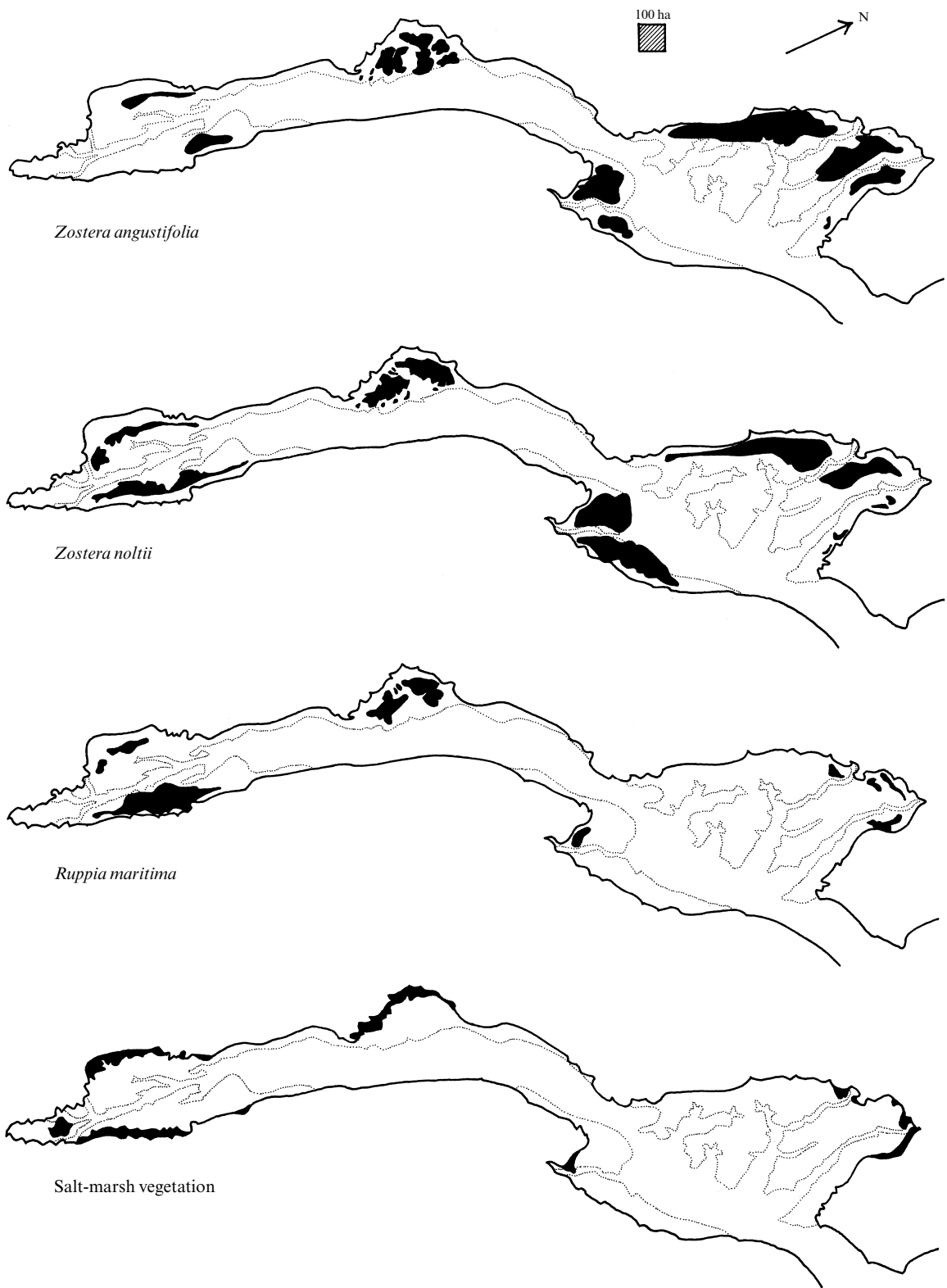
In general, *Z. noltii* is a species of the middle and upper eu-littoral zone and its lower salinity limit is about 15 g l<sup>-1</sup> (chloridity 9 g l<sup>-1</sup>; Mathiesen & Nielsen 1956). It occurs on mud/sand mixtures of a variety of consistencies from very soft to quite firm. It is most characteristic of situations where the substrate dries out somewhat on exposure and on flats with a gentle bar/hollow topography it forms distinctive mosaics with *Z. angustifolia*. It can also occur in shallow standing water.

Stands of *Z. noltii* pass downshore to *Z. angustifolia* and above may grade to communities of the lower salt-marsh, notably the *Salicornietum europaeae*. *Spartina anglica* is known to have invaded stands of *Z. noltii* at various sites (Chapman 1959, Goodman *et al.* 1959, Bird & Ranwell 1964, Hubbard & Stebbings 1968).

The British distribution of *Z. noltii* is similar to that of *Z. angustifolia* (Perring & Walters 1962) and there are particularly extensive stands in the Cromarty Firth (Rae 1979: Figure 7) and along the Essex and north Kent coasts (Wyer & Waters 1975).

In Europe the *Zosteretum noltii* is widespread in similar situations to those in Britain (e.g. Beeftink 1962, Géhu 1975).

Figure 7. Distribution of mud-flat and salt-marsh vegetation in the Cromarty Firth, Scotland.





*Zostera* and wildfowl grazing

*Zostera* spp. provide an important source of food for certain wildfowl, notably in Britain for overwintering brent goose (*Branta bernicla*) and wigeon (*Anas penelope*) and, to a lesser extent, of mute swan (*Cygnus olor*) and whooper swan (*Cygnus cygnus*).

The early wildfowling literature and some recent studies (e.g. Charman 1977a) consider *Z. marina* to have been the species most frequently eaten by brent in the past but it seems likely that, at the present time at least, *Z. angustifolia* and *Z. noltii* account for the bulk of the *Zostera* consumed. There is some suggestion (e.g. Ranwell & Downing 1959; Charman 1977a, 1979) that of these *Z. noltii* is the preferred species for brent. This may reflect its generally longer periods of exposure on flats but *Z. noltii* appears to reach its standing crop maximum later in the year than *Z. angustifolia*, around September/October (Wyer & Waters 1975, Rae 1979) just when brent are beginning to gather in their winter haunts. *Z. angustifolia* may be preferentially grazed by wigeon: its standing crop peak, in July/August, coincides with the gathering of that species.

A number of studies (Ranwell & Downing 1959; Charman 1975, 1977a, b, 1979; Charman & Macey 1978) have demonstrated a distinctive sequential exploitation of flat and salt-marsh food sources by brent. The accumulating birds begin feeding on *Zostera* in September/October and only when their numbers reach a peak and the *Zostera* is largely consumed do they move on, first to *Enteromorpha*, then to salt-marsh vegetation and sometimes to arable and pasture. This timing coincides to some extent with the maximum availability of nutritious food, though Charman (1979) has suggested that, among the various foods, only *Zostera* can provide an adequate daily energy requirement for brent.

*Zostera* stands therefore provide what seems to be an indispensable resource for some wintering wildfowl and vast numbers of birds exploit the larger beds. The 820 ha of *Zostera* along the coasts of south Suffolk, Essex and north Kent (Wyer & Waters 1975) receive about 30 000 dark-bellied brent (*Branta bernicla bernicla*) (Ogilvie 1978), the expanding stands of The Solent foreshore and harbours about 23 000 (figure for 1979/80), north Norfolk about 5000 and The Wash about 6000 (Ogilvie 1978), in total about half of the world population of this race. Smaller numbers of light-bellied brent (*Branta bernicla*

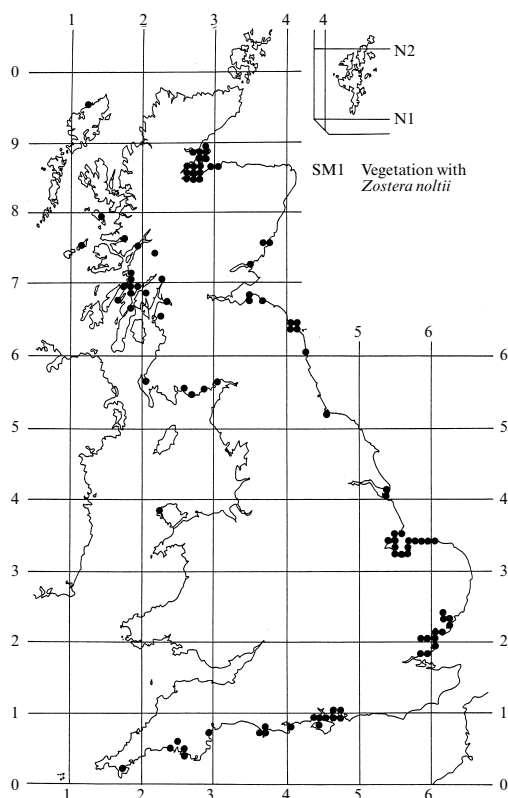
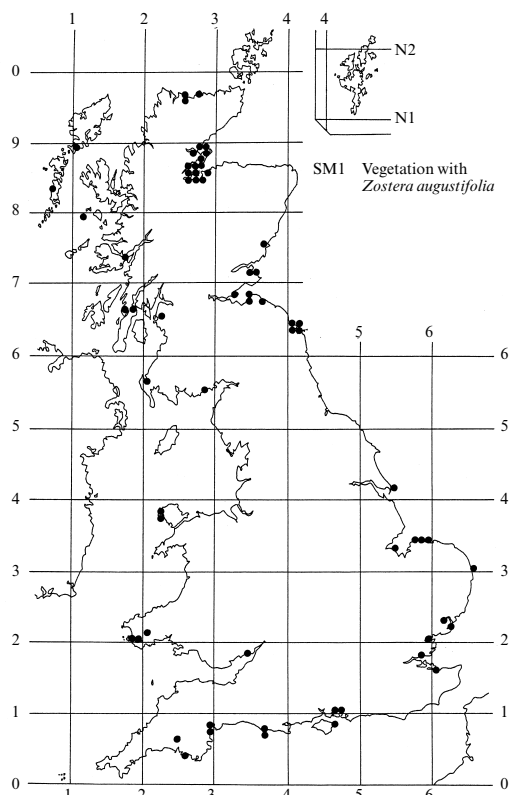
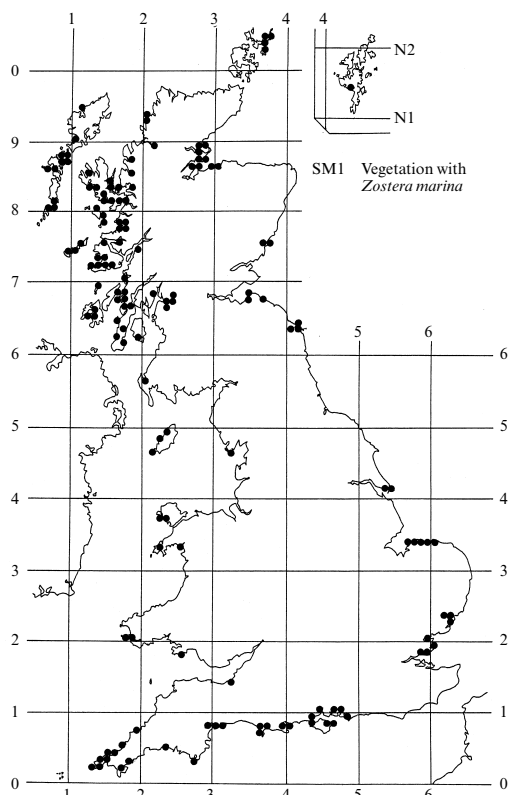
Floristic table SM1

<i>Zostera angustifolia</i>	V (2–8)
<i>Zostera noltii</i>	V (4–10)
<i>Fucus spiralis</i>	IV (1–4)
<i>Enteromorpha</i> cf. <i>E. marginata</i>	IV (1–7)
<i>Ulva lactuca</i>	III (1–4)
<i>Chaetomorpha linum</i>	II (1–6)
<i>Polysiphonia</i> cf. <i>P. insidiosa</i>	I (2)
<i>Ceramium rubrum</i>	I (1–2)
<i>Polyneura gmelinii</i>	I (1)
<i>Fucus vesiculosus</i>	I (1–2)
<i>Cladophora</i> sp.	I (4)
<i>Chondria dasyphylla</i>	I (1)
<i>Polysiphonia</i> cf. <i>P. nigrescens</i>	I (1)
<i>Enteromorpha intestinalis</i>	I (1–2)
<i>Ectocarpus</i> sp.	I (1)
<i>Chaetomorpha</i> cf. <i>C. tortuosa</i>	I (2)
<i>Porphyra umbilicalis</i>	I (2)
<i>Spartina anglica</i>	I (4)
Number of samples	15

Shells of the cockle (*Cerastoderma edule*) and common periwinkle (*Littorina littorea*) and casts of the lugworm (*Arenicola marina*) occasional to very abundant in the samples; spire shell (*Hydrobia ulvae*), mussel (*Mytilus edulis*) and shore crab (*Carcinus maenas*) recorded less frequently.

*hrota*), between 200 and 1100, winter at Lindisfarne NNR. What is probably the largest total area of *Z. noltii* and *Z. angustifolia* in Britain, the 1200 ha in the Cromarty Firth, is outside the winter range of the brent goose but the estuary is visited by enormous numbers of wigeon.

Although wildfowl sometimes uproot *Zostera* while feeding they seem mostly to eat the leaves and flowering shoots. Beds appear able to recover even from very heavy grazing and the resource to renew itself adequately from year to year by vegetative expansion and/or seed germination.



## SM2

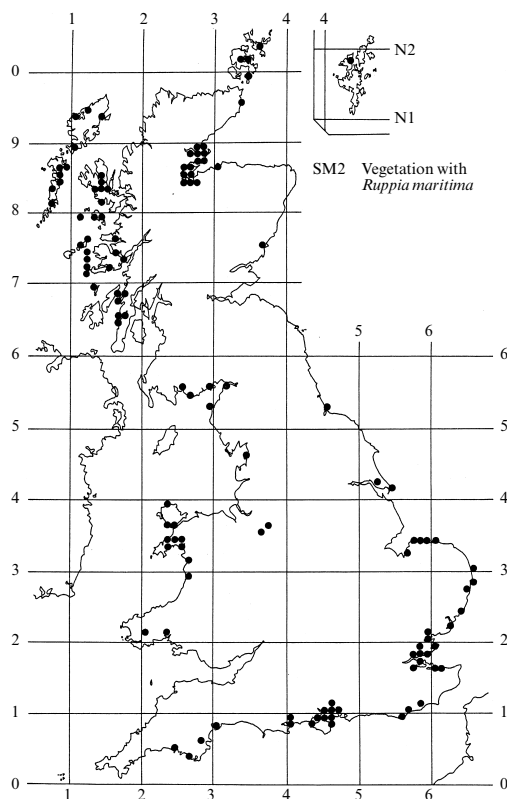
### *Ruppia maritima* salt-marsh community

### *Ruppia maritima* *Ruppia maritima* Hocquette 1927

*Ruppia maritima* is a monocotyledonous perennial which can occur as the dominant in a submerged aquatic community with *Zannichellia palustris*, *Potamogeton pectinatus*, *Ranunculus baudotii* and, within its rather restricted range, *Ruppia spiralis*. The community occurs locally in permanently-filled pans and creeks on coastal salt-marshes, at some inland saline sites (Lee 1977) and also in brackish counter-dykes behind sea walls (Rose & Géhu 1964, Jermyn 1974). In the tidal portion of the outlet stream of the Loch of Wester in Caithness there is a zonation from *R. maritima*-dominated vegetation through *Potamogeton pectinatus* to *Hippuris vulgaris* at the tidal limit.

*R. maritima* can also occur as a plant of estuarine flats and it is particularly abundant in this habitat in the Cromarty Firth (A. Currie, P. Steele, pers. comm.: Figure 7) where it forms a belt of varying width between the salt-marsh proper, sometimes overlapping with *Salicornietum europaeae*, and stands of *Zostera noltii*. Here *R. maritima* seems to behave as an annual (P. Steele, pers. comm.), disappearing very rapidly from September onwards. It is known to be a food source for widgeon (*Anas penelope*) but frost sensitivity may also play a part in its behaviour.

The *Ruppia maritima* has been described from The Netherlands (Beefink 1962) and from France (Géhu 1975) and in the latter it occurs on coastal flats.



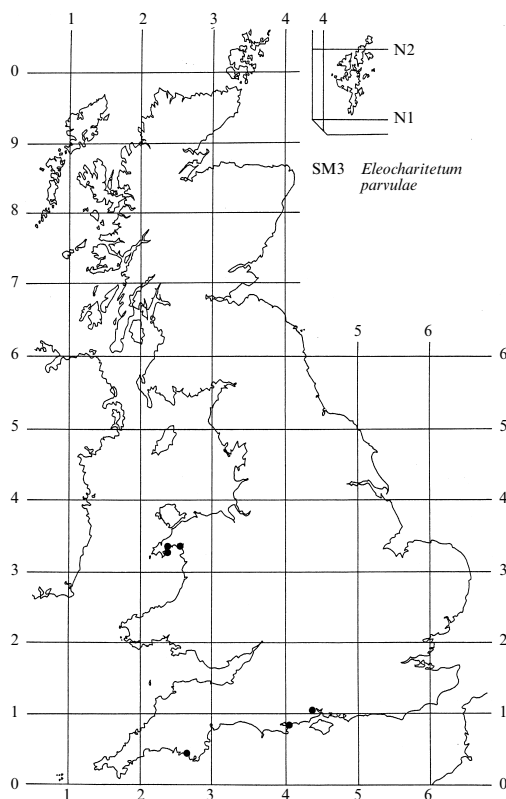
## SM3

### *Eleocharis parvula* salt-marsh community

### *Eleocharitetum parvulae* (Preuss 1911/12) Gillner 1960

*Eleocharis parvula* occurs as a short open sward which is 'physiognomically the least conspicuous of all sea-shore communities' (Tyler 1969*b*). The diminutive shoots, only 1–2 cm tall, are frequently matted with (mainly green) algae and obscured by freshly-deposited silt (cf. Praeger 1934). At Beaulieu in Hampshire, stands occur at the limit of tidal influence with some input of fresh-water from land drainage at low tide (Géhu 1973*a*) but in Ireland the species may extend further downshore (Praeger 1934; C. D. Pigott, pers. comm.).

*E. parvula* is a very rare species in Britain with records for Beaulieu, Poole Harbour in Dorset, Bigbury Bay in Devon and Tremadoc Bay in Gwynedd. It has a similarly disjunct distribution throughout much of Europe (Beef-tink 1972) but the *Eleocharitetum parvulae* has been recorded from the Biscay coast of France and Spain, from northern Portugal and the Mediterranean and Black Seas. The association is widespread in the Baltic where it frequently contains *Ruppia maritima* and *Zan-nichellia palustris* (Gillner 1960, Tyler 1969*a*). This led Gillner (1960) to place the association alongside the *Ruppium maritima*, a view which is now generally accepted.



## SM4

### *Spartina maritima* salt-marsh community *Spartinetum maritimae* (Emb. & Regn. 1926) Corillion 1953

*Spartina maritima* is a native species which seems to have reached a peak of abundance in the late nineteenth and early twentieth centuries when it grew in every harbour between Beaulieu in Hampshire to Chichester in Sussex and plentifully along the coasts of Kent, Essex and south Suffolk and around The Wash (Marchant & Goodman 1969*a*). It declined rapidly thereafter and now survives often as isolated clumps around The Solent and on the north Isle of Wight coast (Marchant & Goodman 1969*a*) though extensive stands remain in parts of Essex (Jermyn 1974, Boorman & Ranwell 1977). The population at Scolt Head Island in Norfolk (Deighton & Clapham 1925, Chapman 1934) is now extinct.

*S. maritima* grows as clumps of stiff shoots and at Wittering in Sussex it has some *Spartina anglica* and a little *Arthrocnemum perenne*, *Puccinellia maritima*, *Suaeda maritima* and *Salicornia* agg. (Géhu & Delzenne 1975). It is a pioneer community throughout its European range which runs south from The Netherlands to Portugal (Beefink & Géhu 1973). The cause of its demise in Britain is not fully understood. It may partly be due to competition with *S. anglica*: Some former *S. maritima* sites are now occupied by *S. anglica* and the former seems to survive best where the latter is least aggressive, on drier sites above mean high water of spring tides (Marchant & Goodman 1969*a*). However, *S. maritima* is at the northern limit of its range in Britain and small climatic fluctuations may have played a part in its reduction (Marchant 1967). Certainly, little viable seed is produced at the present time (Marchant & Goodman 1969*a*).

