The phytosociology of calcareous grasslands in the British Isles

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THE PHYTOSOCIOLOGY OF CALCAREOUS GRASSLANDS IN THE BRITISH ISLES

by

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being
a thesis
submitted for the degree of Doctor of Philosophy
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September 1968.

To the best of my knowledge, and apart from any text references to published works, the content of this thesis is entirely my own research, and has not been previously submitted for any degree or diploma.

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September 1968.

A B S T R A C T

The thesis attempts a broad overall survey and classification according to the Zurich-Montpellier system of plant sociology, of limestone grassland vegetation in the British Isles. The classification is based on some 535 grassland Aufnahmen and 75 Aufnahmen of contact communities. In all, some 13 grassland Associations are recognised, whilst the zonal and successional communities are classified in 16 Associations. The Associations are classified in the system of classification advocated by Lohmeyer *et al.* (1962), and the phytogeographical relationships of the related Association-groups or Alliances are considered in detail. The limestone grassland communities of the British Isles have been found to be representative of four Classes:-

(a) *Festuco-Brometea* - thermophilous dry grassland communities of the sub-mediterranean and sub-atlantic regions of Europe;

(b) *Elyno-Seslerietea* - dry sub-montane, sub-alpine grass heaths of the low alpine region of central Europe and Scandinavia;

(c) *Molinio-Arrhenatheretea* - mesophilous, grazed or mown hay meadows and pastures of the lowland zone of western Europe;

(d) *Violetea calaminariae* - open grassland communities

of heavy metal-rich strata and spoil banks.

The thesis is divided into 5 parts:-

Part 1 reviews the methods available for a vegetation survey and phytosociological technique in general; outlines the history and status of limestone grasslands; and summarises the methods used for previous description of British vegetation;

Part 2 presents the results of the grassland survey and relates the change in overall floristic composition and grassland type to climatic factors using the climate diagrams of Walter & Lieth (1967);

Part 3 considers the successional and zonal relationships of these grassland communities, whilst

Part 4 discusses the validity of the methods used for the survey and suggests some of the logical extensions of this work with reference to the conservation and management of an area limestone grassland on the Magnesian Limestone of Co. Durham.

Part 5 comprises 36 Association Tables and an Aufnahmen locality Appendix, and is to be found in the folio volume.

References

LOHMEYER, W. *et al*. (1962). Contribution a l'unification du systeme phytosociologique pour l'Europe moyenne et nord-occidentale. *Melhoramento*, 15, 137-151.

WALTER, H. & LEITH, H. (1967). <u>Klimadiagramm Weltatlas.</u>
Jena.

Foreword

The following references have been used for the nomenclature of species:-

Flowering plants and ferns - Dandy, J. E. (1958). List of British Vascular Plants. Br. Mus. Nat. Hist., London;

Mosses - Warburg, E. F. (1963). Census Catalogue of British Mosses (3rd ed.). Brit. Bryol. Soc. Publ., Ipswich;

Liverworts - Paton, J. A. (1965). Census Catalogue of British Hepatics (4th ed.). Brit. Bryol. Soc. Publ., Ipswich;

Lichens - James, P. W. (1967). A New Check-list of British Lichens. The Lichenologist, Vol. 3, 95-153.

Any deviations from these systems are noted in the text.

Part I of the thesis reviews some of the available phytosociological techniques and the history of their application to British vegetation, and considers many of the background problems associated with a survey of limestone grasslands.

Part 2 comprises the results of this survey. In order to make the details as explicit as possible, a set format is adhered to throughout this section. The Zurich-Montpellier system of classification as advocated by Lohmeyer et al. (1962) is used as the framework, and brief descriptions are given for each of the levels of classification, e.g. Class, Order and Alliance. Within each Alliance, the

Associations are described in the following manner:-

I. Synonymy - names given by previous authors to the grasslands in question.

2. Habitat details - (a) Geographical and altitudinal distribution;

(b) Climate - related as far as possible to the climate-types described by Walter & Lieth (1967);

(c) Topographical limitations;

(d) Soils.

3. Characteristics of the Association - details of the floristic composition and community structure of the Association and its constituent Sub-associations.

4. Zonation and Succession - the relationship of the Association to other plant communities, (see also Part 3, Chapter 5).

With the appropriate Association Table and the Limestone Grassland 'Matrix Diagram' (see Volume 2) at hand, the interpretation of the text is straightforward.

For each Alliance, the phytogeographical relationships of their constituent Associations are considered - (a) within the British Isles; (b) in western Europe.

This general approach is considered to be the most appropriate and most explicit method of presentation of the basic data for readily available reference purposes.

In Part 4, the value of a broad phytosociological survey is discussed and some of the logical extensions of this work are illustrated with reference to the conservation of areas of Magnesian Limestone grassland in Co. Durham.

-o-o-o-O-o-o-o-

In the text, all Latin species names and all other names in italics are underlined with a continuous line. The names of Alliances, Associations, Noda etc., are underlined with a broken line.

ACKNOWLEDGEMENTS

I wish to thank Dr. D. J. Bellamy for his constant enthusiasm during the three years research and his criticism of the manuscript; Professor R. Tüxen for his guidance and generosity during my stay at Todenmann, West Germany, and for permission to include unpublished data; Father J. J. Moore S.J. for explaining some of the finer points of the Z-M system of plant sociology; Dr. R. F. McKee, Messrs. P. Bridgewater, D. Welch and T. C. E. Wells, for making available unpublished data; Professors D. H. Valentine and D. Boulter on whose department the research was based; The Natural Environment Research Council for a Research Studentship for the three years of research; the Cement Marketing Board for an additional grant to provide transport for the research; Miss M. Berryman for her perseverance and efficiency in the typing of the thesis; Mr. A. Jamieson for his help in the reproduction of text figures; my parents for providing transport during the first field season and the initial opportunities for the project; and to my wife for her help with the preparation of the phytosociological tables and for her forbearance throughout.

CONTENTS

FIGURES AND TABLES

Figures 1-13, 15-20, and 23-34 are all included in the subsequent text. Figures 14, 21, and 22 are to be found in the folio volume along with Association Tables 1 to 36 and an Aufnahmen Locality Appendix.

"The increasing recognition of the genetic principle on the continent is a great gain on the one hand, and increased attention in England and America to the continental methods of analysing communities will also contribute in an important degree, to mutual understanding and eventual accord".

A. G. Tansley, 1922.
J. Ecol., 10, p. 245.

PART I.

Chapter 1.

A commentary on the present state of phytosociology in the British Isles.

'Plants are gregarious beings, because they are mostly fixed in the soil and propogate themselves largely in social masses, either from broadcast seeds (or spores), or vegetatively by means of rhizomes, runners, tubers, bulbs, or corms; sometimes by new shoots ('suckers') arising from the roots. In this way they produce vegetation, as plant growth in the mass is conveniently called, which is actually differentiated into distinguishable units or plant communities'.

The foregoing statement from Tansley (1939) summarises the basic concept that vegetation forms a series of communities capable of being classified. The actual process and progress of vegetation classification, however, has been, and continues to be the subject of much controversy. The initial divergence in method was based upon the desire for either an ecological approach relative to environmental gradients (Clements 1904, 1916; Moss 1910; Tansley 1911, 1920), or a floristic, sociological approach (Du Rietz et al. 1920; Nordhagen 1923; Braun-Blanquet 1928; Raunkiaer 1928). Within these two groups, other dichotomies have developed resulting in confusion, not only of method, but also of nomenclature. An admirable appraisal of such plant ecological and phytosociological methods and nomenclature has been undertaken by Westhoff

(1951), Becking (1957) and Whittaker (1962), and discussion is left with these references.

British workers followed the ecological principles of Tansley, who attempted to apply continental techniques - Tansley and Adamson (1926) - but was unable to form an opinion as to their usefulness. More recently, Poore (1955a, b) has reviewed the methodology of the Zurich-Montpellier School in a comprehensible and up-to-date account; and in English. Unfortunately for the science, Poore rejected some of the concepts of this school and proposed a further technique, similar to that of Nordhagen (1936, 1954) and Dahl (1956), but using different descriptive scales. His multidimensional approach, however, has been followed by McVean & Ratcliffe (1962), and their monograph 'Plant Communities of the Scottish Highlands' must rank amongst classic phytosociological literature.

The use of more objective methods in the establishment of vegetation units has been the desirable aim of many Anglo-American ecologists in the last decade, often so much so that preoccupation with technique has tended to obscure the ultimate purpose. Thus, with the development of statistical, quasi-objective, theoretical approaches to vegetation description, over 80% of the appropriate literature has been concerned with technique based on a minimum of field data. An adequate summary of much of this work is presented by Greig-Smith (1964) and Kershaw (1964).

These ideas appear to have originated from the individualistic hypothesis of Gleason (1926, 1939) and became commonly associated with the idea of continuity in vegetation and the continuum concept (McIntosh, 1967). From this in turn the concept of gradient analysis (Whittaker, 1952, 1956), which concentrates on the construction and study of gradients of species, communities or environment, was developed. Goodall (1954a) proposed the term ordination and defined it as "an arrangement of communities, species or environment in sequence which it is hoped will reveal maximum relationships among them and which will also reveal such classes as exist". Ordination techniques have been widely used in America by Curtis (1957, 1959), and in Britain by Greig-Smith and his fellow workers (Anderson 1963, Gittins 1965, Austin & Orloci 1966 and Orloci 1966).

The application of various multivariate analyses using a computer has been tried recently by Williams and Lambert (1959, 1960, 1961), Lambert & Williams (1962, 1966), and has introduced a new dimension into problems of vegetation analysis. These methods have been used to support the concept of both classification and ordination, and Williams & Lambert (1959, 1961) consider the former as the most effective. The use of multivariate techniques has been reviewed by Lambert & Dale (1964).

Finally, Yarranton (1967a,b,c) has proposed a principle components analysis of the distributional relationships of individual species and thus has provided a further interpretation of Gleason's original hypothesis.

There has been a growing awareness of the diverse nature of phytosociological techniques and several attempts have been made to standardise the subject. On the continent, Lohmeyer et al. (1961) have produced a synopsis of the hierarchical classification of the Zurich-Montpellier (ZM) School in an attempt to standardise nomenclature. In Britain, standardisation of method has been the most recent object. Gittins (1965) has considered stand ordination and normal association analysis and has concluded that they 'lead to substantially identical interpretations of the data'; Ivimey-Cook and Proctor (1966), using association analysis techniques have obtained much the same results as traditional phytosociological methods (Braun-Blanquet and Tüxen 1952), and consider association analysis to be a mechanised technique comparable to the recognition of 'Kennarten' by exponents of the ZM system; Bannister (1966) has successfully used subjective estimates of cover-abundance as the basis of an ordination.

The relative merits of ordination and classification and their individual contribution towards a demonstration of the nature of vegetation have been discussed at length by McIntosh (1967). He points out that for most schools of phytosociology, classification is an end in itself, the aim being a taxonomy of vegetation. He asks why we attempt to classify vegetation, and if a preference for classification is developed in childhood as Goodall (1954a) suggests, or if the biologist is so indoctrinated at a later date with the hierarchical classification of organisms that he finds it difficult to think in other ways (Webb, 1954)?

Whatever the answer, the classification of vegetation cannot continue to function solely as an academic exercise. There must be an ulterior motive. As Curtis (1959) says:- 'It is the task of phytosociology to describe the combinations of plants that do occur in each region of the world, to find how they came into being and how they maintain themselves, to relate them to the physical environment and to reach an understanding of the material and energy changes which occur within them'. With this statement in mind, it becomes apparent that the initial application of phytosociological techniques should be to provide a scientific basis for future conservation proposals.

This thesis is presented for this purpose and the problem considered along the following lines:-

(1) The application of the Zurich-Montpellier system of phytosociology to British vegetation in order to:-

(a) provide a common basis which will facilitate the overall floristic comparison of British vegetation with that of the rest of the continent of Europe, and in doing so, will answer some of the broader problems of plant geography in relation to climatic factors;

(b) provide a basic description of some British vegetation types, thus giving some insight into the variety of particular communities so that immediate action may be taken to conserve rare and local ones;

(c) provide a basis for ecological studies via -

(2) the application of ordination techniques to stands of vegetation, (a) within the units defined by (1) and their relation to environmental factors; (b) across the units defined by (1) and along the continuum of Zonation/succession:

(3) the determination of boundaries of units (not necessarily delimited by (1), but relative to (1)), and of boundary type using techniques of association analysis:

(4) the determination of structure, periodicity, and some

idea of the energy budget of the units so defined.

Clearly the collection of data for such a set of directives is the work of more than three years research, and only the first two of the above four categories are considered in detail in this thesis.

Chapter 2.

Limestone grasslands: their history and status.

The application of any system of phytosociology can follow two lines: (a) the description of all vegetation types within a geographical region, e.g. Ivimey-Cook & Proctor (1966); or (b) the description of a particular Class of vegetation (sensu Zurich-Montpellier School) or series of communities defined by a broad ecological factor, such as "ombrophilous mires" (Bellamy, 1967), or "grassland on calcareous soils". This latter approach is preferred, mainly because the description of all communities within a small geographical region often leads to erroneous creation of Associations etc., which, when compared to a broad overall view, may appear only as minor variations in a widespread Association.

With these basic premises in mind, problems relating to the development of grasslands on calcareous soils were selected. Undoubtedly, the work of Tansley & Adamson (1925, 1926), Hope-Simpson (1940, 1941a, b) and Perring (1958, 1959, 1960), had a major influence on the choice of topic, creating a desire to complement some of their work on chalk grasslands with a survey of grasslands overlying the older limestones. In his book, "Wild Flowers of Chalk and Limestone", Lousley (1950) remarks on the gradual spatial changes in the flora of various chalk and limestone districts throughout Britain, and it seemed that an

FIGURE 1. The Distribution of Limestone Grasslands in the British Isles: areas covered by the present survey.

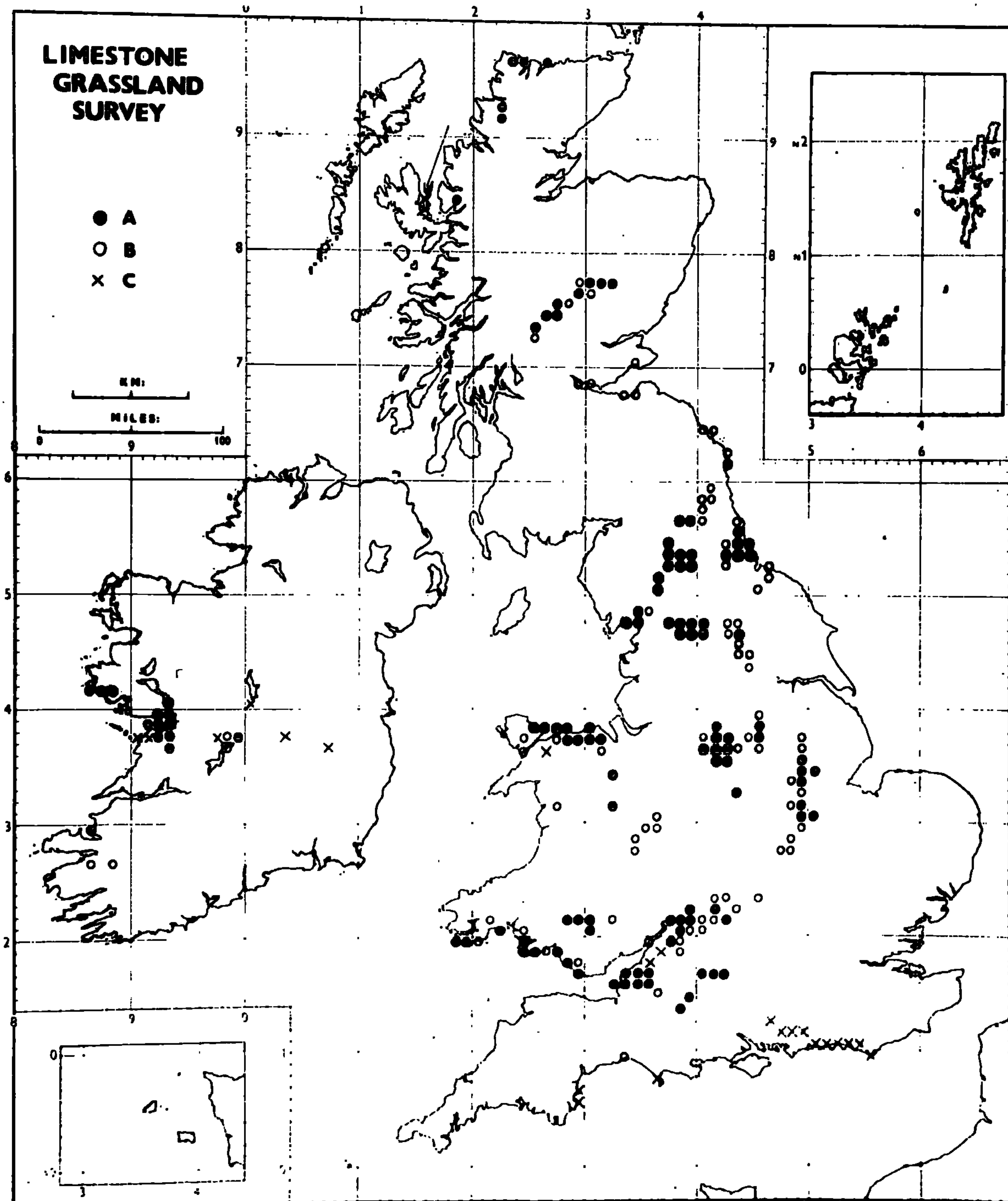
(Base map reproduced by permission of Dr. F. H. Perring for the B.S.B.I.)

Legend:

A. 10 km surveyed and some Aufnahmen included in the thesis.

B. 10 km with no areas suitable for sampling; or where no suitable sites were located.

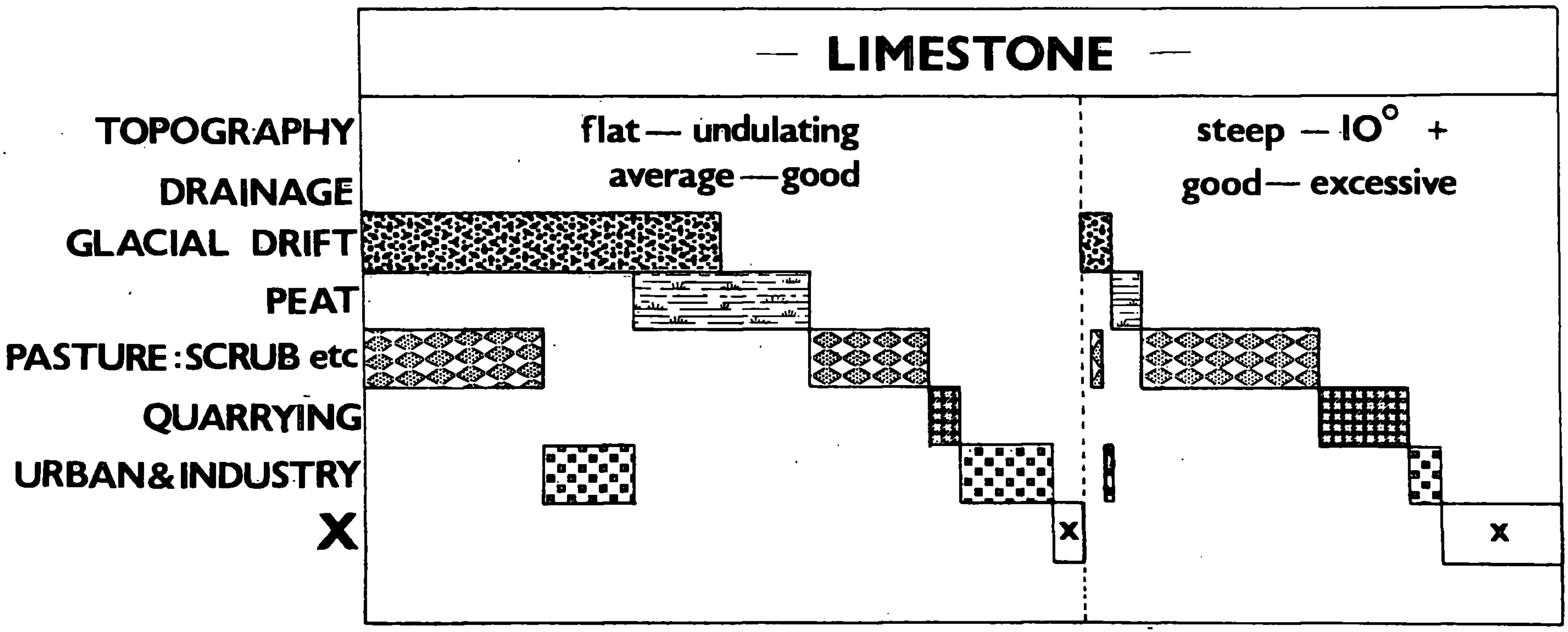
C. Data included from other sources.



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

FIGURE 2. Delimitation of the project: the relative proportions of agricultural and industrial practices in the limestone regions of the British Isles.

X Semi-natural limestone grasslands.



— LIMESTONE —
TOPOGRAPHY
DRAINAGE
GLACIAL DRIFT
PEAT
PASTURE : SCRUB etc
QUARRYING
URBAN & INDUSTRY
X
flat — undulating
average — good
steep — 10° +
good — excessive
x
x

amplification of some of his work using phytosociological techniques might elucidate some of the broad problems of phytogeography.

Figure 1 shows the regional distribution of limestone in the British Isles, and the areas visited and sampled, or considered unsuitable for sampling. Whilst geology represents the framework, and directly influences physical factors such as topography and drainage, it is by no means the sole criterion on which the study is based. Some idea of the factors involved in delimiting the project, and an estimation of the amount of semi-natural limestone grassland in Britain can be obtained from Figure 2. Only some 10-15% of the total surface area of limestone as seen on a geological map supports "natural or semi-natural grassland", and an apparently impossible and overwhelming task at first sight becomes a feasible proposition.

Historical evidence suggests that the creation and control of dry grassland areas seems likely to have been started by the Neolithic pastoralists and cultivators about 2000 B.C., and maintained and extended by the Bronze Age people. It has been postulated that initial colonisation took place on the ridges above scarp slopes, where the forest was less dense or absent. Tansley (1949) considers the origin of the grasslands to be somewhat puzzling, suggesting that these ridges were free from forest, and hence, that "the grassland is in origin, a natural plant community", since extended and exploited by Man.

The Iron Age and Belgic peoples appear to have shown the same soil preferences as their predecessors, though their cultures were generally restricted to the south and east of the British Isles. With the advent of the Romans, there seems to have been an all-round increase of pasture, but the Saxons, being valley cultivators, left the fields on the chalk and limestone plateaux derelict (Darby, 1936). Since then, the extension of grassland and the depletion of woodland have proceeded hand in hand at a steady rate, checked only by such national disasters as the Black Death of 1349, when depopulation resulted in the grasslands becoming extensive sheep ranges.

The Enclosure Acts of 1760-1820 meant that by the end of the 18th Century, the bulk of the open fields and commons had disappeared and consequently, the areas of natural and semi-natural vegetation decreased. Plateau regions were divided more or less regularly and eventually became "permanent pasture", whilst steep scarp slopes were left as irregular enclosures and became "rough grazings". The distinction between these two categories is important and as previously explained, depends largely on history and topography. In well-drained, calcareous localities, rough grazings are restricted to relatively steep slopes such as the chalk downs and the limestone dale sides. Permanent pasture is found on higher plateaux where the soil is too shallow, or the topography is too undulating for arable culture.

Management is a third important factor in the distinction of the two types. Permanent pasture is frequently subjected to controlled grazing and is often manured, limed and re-seeded, whereas rough grazings are only influenced by uncontrolled grazing. Thus, the latter are probably the most natural grassland communities, receiving little anthropogenic influence and maintained in a plagioclimax by grazing, (denoted as X in Figure 2).

Of the remaining limiting factors shown in Figure 2, those of "urban/industry" and "quarrying" are more or less self-explanatory. The limestones of the Central Lowlands of Scotland are almost completely covered by the extensive Glasgow-Edinburgh conurbation, with only a few relict localities remaining in the Ferry Hills of Fifeshire. Examples of the effects of quarrying are innumerable, but areas such as the Magnesian limestone of County Durham and the Peak District of Derbyshire with ready markets in the industrial areas close at hand are perhaps extreme cases. It is noteworthy that quarrying appears to be the main factor affecting the remaining semi-natural grasslands, mainly because the steep slopes where the latter occur often contain a maximum depth of readily accessible strata and a minimum of overburden, thus presenting ideal situations for modern quarrying techniques.

The final two factors, denoted "glacial drift" and "peat", are closely related, and their relation to many edaphic and climatic factors demands that they be considered under the comprehensive title of "soil complex". Jenny (1941) considers soil to be the product of the interaction of five pedogenic factors - parent material, climate, organisms, topography and time. In a given region, the influence of one factor is usually predominant and the variations in soil development can be mainly attributed to that factor. The two main factors relative to soil development over limestone in the British Isles are undoubtedly climate and parent material. In the Mendip Hills, Wales, Derbyshire, etc., leaching, promoted by high precipitation is the dominant pedogenic process, and a climosequence of soil development can usually be recognised. The actual character of the soil sequence is determined by the degree to which the regional influence of climate has overcome the local influence of parent material. Such climosequences are described by Balme (1953) and Bryan (1967) for the limestones of Derbyshire, where the parent material is normally freely-drained Carboniferous limestone.

Figure 3(a) shows the climosequence described by Bryan (1967) to illustrate that succession of development corresponds to a progressive increase in leaching. In general, soils on south facing slopes and at lower altitudes show less degradation than others on north and west facing slopes and above 1000 feet. On steep thermophilous slopes, where run-off is at a maximum, Rendzinas have developed. These are characterised by a poor horizon differentiation, excess carbonates derived from the parent material and the accumulation of dark brown organic matter. There is a humic A horizon, no B horizon and the C horizon is represented either by scree or bedrock. On gentler slopes with greater vertical water movement, a B horizon becomes perceptible and, due to increased weathering, more clay is seen in the profile. An increase in the depth of the humic A horizon gives the name Brown Rendzina to this latter stage in the sequence. Subsequent development of the Brown Rendzina to a Brown Calcareous soil is very gradual, and their distinction is based on the degree of development of the B horizon and the amount of total carbonates remaining in

FIGURE 3. Soils overlying Carboniferous Limestone in Derbyshire.

(a) Climosequence of soils; (based on Bryan 1967).

(b) Related soil types; (mainly from drift-covered areas).

Legend:

(a) A_o humic horizon.

(b) Friable loamy A (A_1).

(c) B horizon.

(d) Loamy sand A_2.

(e) Podsolisation.

(f) Brash/scree C horizon.

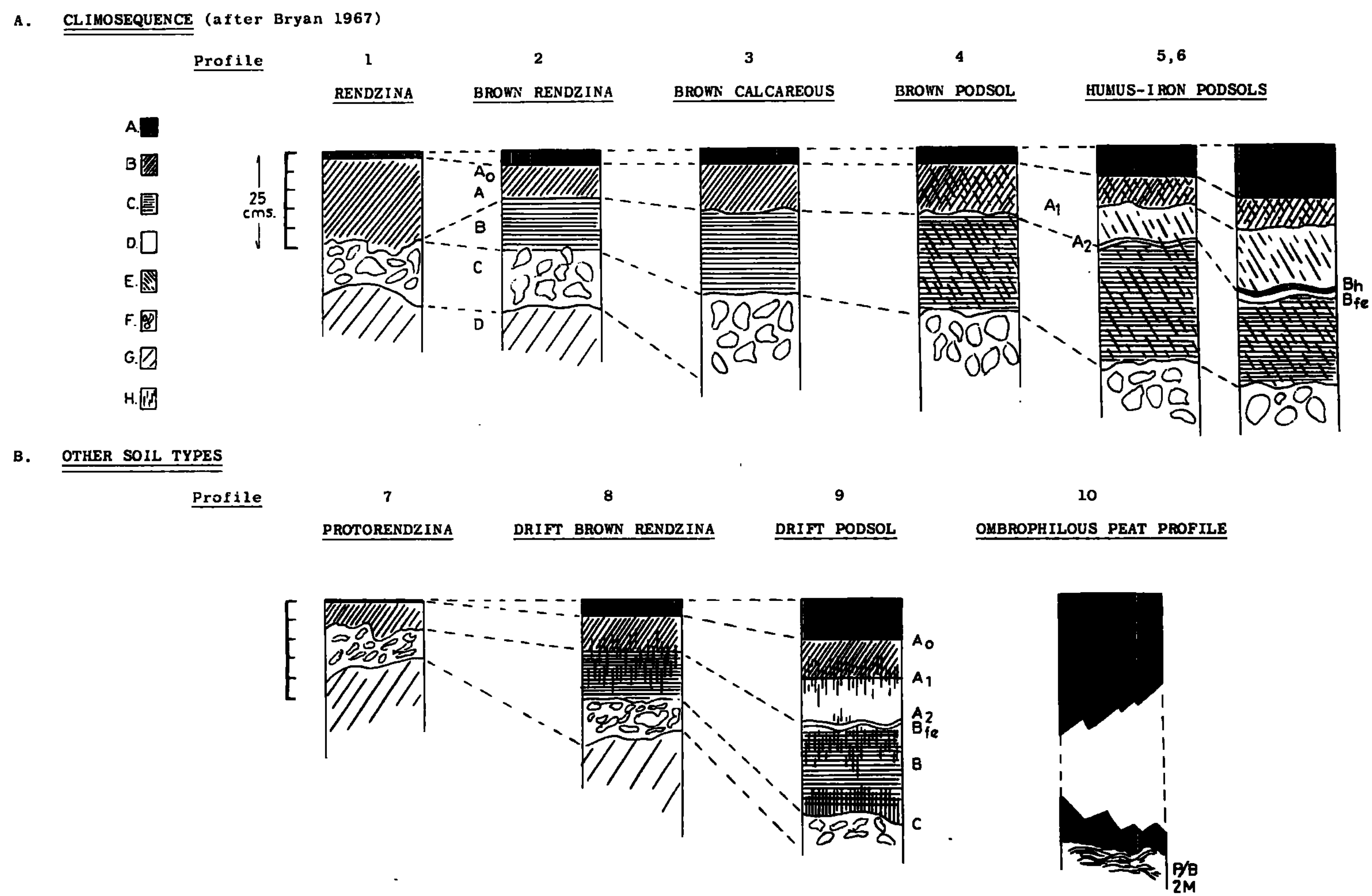
(g) Parent rock.

(h) Drift influence.

Bh. Humus band.

Bfe Iron band.

P/B Pine/Birch basal zone.


A. CLIMOSEQUENCE (after Bryan 1967)
Profile
1
RENDZINA
2
BROWN RENDZINA
3
BROWN CALCAREOUS
4
BROWN PODSOL
5,6
HUMUS-IRON PODSOLS
A.
B.
C.
D.
E.
F.
G.
H.
25 cms.
Ao
A
B
C
D
A1
A2
Bh
Bfe
B. OTHER SOIL TYPES
Profile
7
PROTORENDZINA
8
DRIFT BROWN RENDZINA
9
DRIFT PODSOL
10
OMBROPHILOUS PEAT PROFILE
Ao
A1
A2
Bfe
B
C
P/B
2M

SOIL-TYPE	NOMENCLATURE OF MOSS (1913)	ZURICH-MONTPELLIER NOMENCLATURE (Shimwell)
SCREE	Communities of screes, rakes, etc.	Arrhenatherum-Mercurialis Fragment. Dryopteridetum robertianae Kuhn 1937. Minuartio-Thlaspeetum.
PROTORENDZINA	Retrogressive Corylus Scrub	Geranion sanguinei Community.
RENDZINA	Climax Ash Woodland Progressive Scrub	Campanulo-Fraxinetum Shim. & Bell. 1967. Prunetalia communities.
BROWN RENDZINA BROWN CALCAREOUS	Limestone Grassland	Helictotricho-Caricetum flaccae. Filipendulo-Arrhenatheretum. Centaureo-Arrhenatheretum O'Sullivan 1965.
BROWN PODSOL	Neutral/Acidic Grasslands (Calcareous Heath)	(Festuco-Poetum). Nardo-Galietum saxatilis.
HUMUS-IRON PODSOL	Gorse Scrub	Agrosto-Ulicetum gallii.

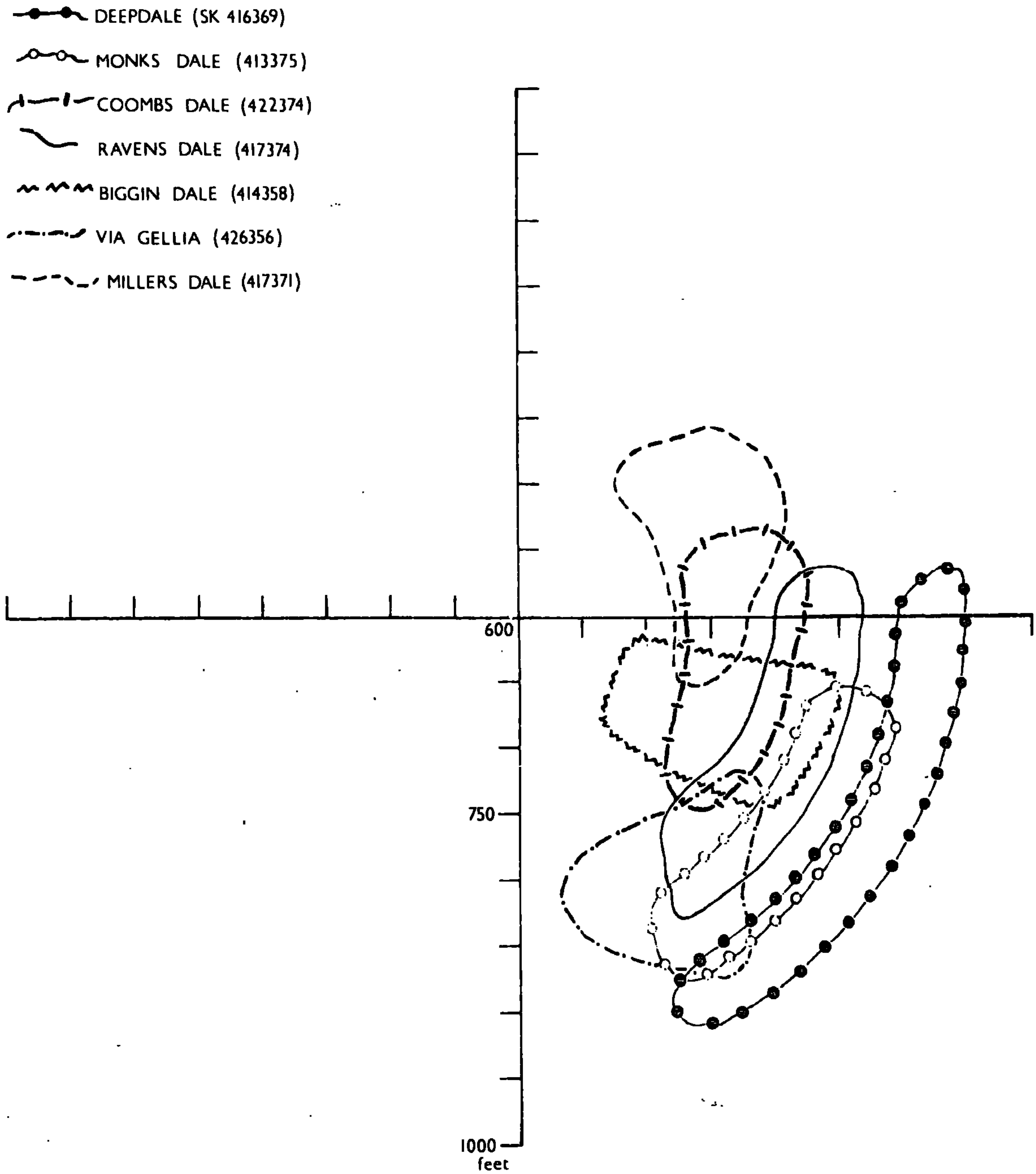
FIGURE 4. The Relationships between Soil type and Plant Communities on the Derbyshire Limestone.

the profile. Brown Podsolic soils are characterised by an eluvial A horizon showing bleaching and an illuvial B horizon, in which the presence of ferric oxide is marked by a red colouration. The end point of the climosequence is a Humus-Iron Podsol with up to 4 inches of black undifferentiated raw humus for the A horizon, a compacted iron pan, B(fe) as a barrier to roots, and a pH varying from 4.0 to 6.5 through the profile.

Accompanying these changes in soil type, there are frequently changes in the vegetation. Thus, the rendzinas and brown calcareous soils support calcareous grassland and scrub, whilst the development of a podsolic soil favours the development of _Calluna_ heath. Figure 4 summarises the main vegetation types using the nomenclature of Moss (1913) and that of the Zurich-Montpellier School of phytosociology (Lohmeyer _et al._, 1961).

At the other end of the sequence to the podsols are a group of soil types and plant communities which are more puzzling; i.e. the Retrogressive _Corylus_ Scrub of Moss (1931) or _Geranion sanguinei_ of Tüxen (1961), on shallow Protorendzinas (Figure 3(b), Profile 7). At first sight, it appears that these soils are eroded derivatives of rendzinas, having lost most of the humic A horizon by overgrazing. Their most significant feature, however, is that

FIGURE 5. Aspect and altitudinal limits of Retrogressive *Corylus* scrub in Derbyshire.



DEEPDALE (SK 416369)
MONKS DALE (413375)
COOMBS DALE (422374)
RAVENS DALE (417374)
BIGGIN DALE (414358)
VIA GELLIA (426356)
MILLERS DALE (417371)
600
750
1000
feet

they are all developed on steep slopes exposed in a north-westerly direction (Figure 5), where, according to Bryan (1967), they are more susceptible to the effects of climate as an important pedogenic factor. Considering this fact and the fact that most of the semi-natural Fraxinus woodlands in the Peak District are found on scree or protorendzina, it appears that, whilst the plant communities in question are a retrogressive "Saumgesellschaft" (Tüxen, 1937) of the woodlands, there is a positive pedogenic trend towards rendzina formation.

All the stages in the climosequence are seldom seen as a horizontal series in a specific area such as a dale side, although a transition from a rendzina to a brown calcareous soil is usually visible. Where there is an underlying deposit of glacial drift, more stages are visible in a similar small area and the vegetation often appears as a mosaic. In the south east of the limestone plateau of the Peak District there is often a layer of yellow or red sandy clay of Triassic origin, sealing off the limestone from the soil, with the result that the amount of free carbonates is less and the effect of leaching more rapid. This is seen most effectively in Long Dale, where the transition from rendzina to iron podsol is reflected in the rapid change from calcareous grassland to Ulex gallii-

Calluna heath, (Figure 3(b), Profiles 8 and 9). At Calling Low (Profile 10), the Triassic deposit lies in a limestone basin, drainage is impeded and a local "transition mire" (Kulczynski, 1949), with up to 1 metre of peat occurs.

These patterns of soil development are represented in all areas of limestone in the British Isles. The climo-sequences in Wales and western Ireland are accelerated towards heath and iron-podsol formation, due to the increased precipitation. Robinson (1949) and Ivimey-Cook (1957) describe the soils of the Welsh limestones as a series from rendzina to red/brown calcareous to incipient podsol, and the latter author notes the interference of blown calcareous sand in the profiles. Apart from the Mendip Hills of Somerset and the Derbyshire limestone, many of the other limestone areas are greatly affected by glacial drift; e.g. virtually all of the limestone of Northumberland is overlain by thick drift deposits, and localities of semi-natural grassland are rare occurrences amongst arable fields and moorland. Similarly, blanket peat is widely distributed over limestone at higher altitudes in the northern Pennines, from Craven to Cheviot, and in northern Scotland.

Whilst the sequence of variations described above occurs widely throughout Britain, several anomalies to the overall plan are to be found, the classic example being Upper Teesdale. Here the picture is complicated, not only by irregular patches of glacial drift and impeded drainage, but also the effects of an intrusive sill of dolerite known as the Whin Sill. The heat generated at the intrusion of the latter has metamorphosed the limestone to give a granular material known as "sugar limestone", because of its appearance and texture. In the vicinity of areas where the sugar limestone outcrops, the soils show little or no horizon differentiation, only a complex intermixture of roots, some organic matter and the coarse limestone grains. Fitzpatrick (1964) uses the term "Silicate Syrosem" (from Kübiena, 1953) for undifferentiated soils on sand dunes, and similarly, the term "Calcareous Syrosem" may be used for the soils in question, (Figure 6, Profile 1).

The large population of moles, which populate the grassland areas in the vegetation mosaic, has contributed to the erosion and has also reassorted virtually all of the soil profiles overlying the sugar limestone, so that the rendzinas and brown rendzinas have diffuse boundaries with humus widely dispersed through the profile, (Profile 2). Humus-iron podsols are widespread wherever the limestone is sealed from the soil by a drift deposit (Profile 3),

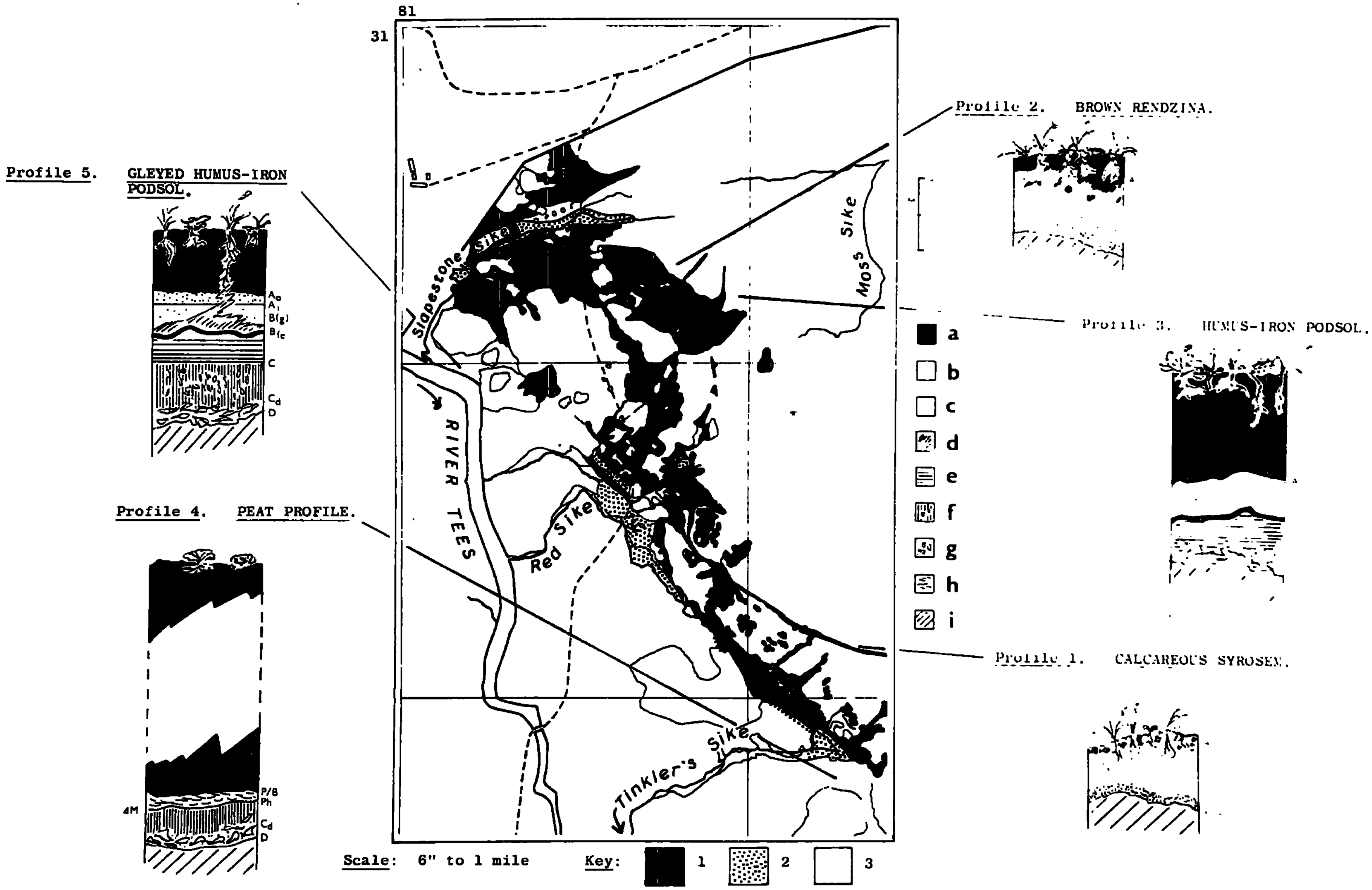
FIGURE 6. Grassland and Soil Complex, Widdybank Fell, Upper Teesdale.

(The grassland map is based on a provisional map of the area by Dr. M. E. Bradshaw, and reproduced with her permission).

Legend:

1. Limestone Grasslands.
2. Calcareous Flushes.
3. Other communities, e.g. Blanket Bog and Heath.

(a) Humus (Peat in Profile 4).
(b) Granular sugar limestone.
(c) Intermixed sugar limestone and loam.
(d) Gleying.
(e) Reduced B/C Horizon.
(f) Drift - clay and gravel.
(g) Limestone brash.
(h) Phragmites Peat; P/B - "Pine/Birch" peat.
(i) Limestone Bedrock.



81
31
Profile 5. GLEYED HUMUS-IRON PODSOL.
Ao
A1
B(g)
Bfe
C
Cd
D
Profile 4. PEAT PROFILE.
4M
P/B
Ph
Cd
D
Profile 2. BROWN RENDZINA.
Profile 3. HUMUS-IRON PODSOL.
Profile 1. CALCAREOUS SYROSEM.
Moss Sike
Slapestone Sike
RIVER TEES
Red Sike
Tinkler's Sike
a
b
c
d
e
f
g
h
i
Scale: 6" to 1 mile
Key: 1 2 3

and in shallow basins, where drainage is impeded, up to 4 metres of peat have developed over the calcareous drift, (Profile 4). Downslope from the limestone outcrops, the higher water-table causes varying amounts of gleying. These soils are recognisable by a grey to dark grey mixture of organic and mineral material, of both limestone and drift origin, in a layer (G_1) below a black humified A horizon. There is often marked yellow-orange mottling around the roots, (Profile 5). Whilst the calcareous syrosems, rendzinas and humus-iron podsols occur on both Cronkley and Widdybank Fells, the soils showing gleying are seen only on Widdybank Fell, in small areas where the Fell meets the flood-plain of the river, and extending a little way up the sikes.

The factors enumerated in this chapter are the main historical and environmental factors responsible for the present distribution and status of limestone grassland in the British Isles.

Chapter 3.

The history of the description of British vegetation and the application of the Zurich-Montpellier system of plant sociology.

Classification of British vegetation began in the twentieth century, with the "Botanical Surveys" of Scotland by Smith (1900a, b), of Yorkshire by Smith & Moss (1903) and Smith, Moss & Rankin (1903), and of the Dublin region by Pethybridge & Praeger (1905). This school of thought, by name the British Vegetation Committee, advocated the production of relatively detailed vegetation maps based on the broad survey units of geographical botanists, such as, "Cotton Grass Bog", "Heath or Heather Moor", "Grass Heath", etc. At a later date, the Committee presented resolutions to the International Botanical Congress of 1910 in Brussels, concerning the nomenclature of plant communities. Several units were proposed, following the definitions of Moss (1910):-

a plant formation - "the whole of the vegetation which occurs in a definite and essentially uniform habitat"; e.g. vegetation on calcareous soils or "*Calcarion*":

a plant association - "of lower rank than a formation and characterized by minor differences within the generally uniform habitat; e.g. calcareous grassland (*Festucetum ovinae*)":

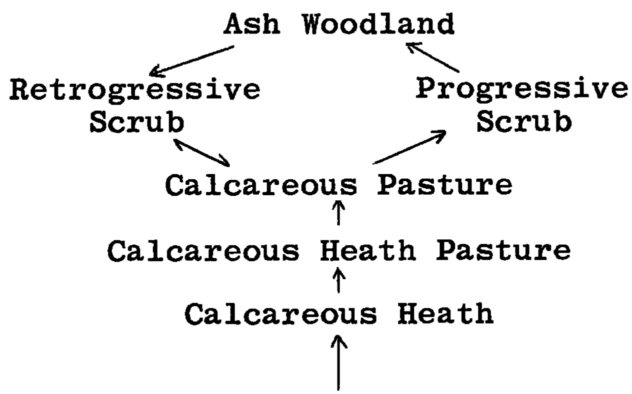
a plant society - "of lower rank than an association and marked by still less fundamental differences of habitat"; e.g. a clump of *Brachypodium pinnatum* within the "*Festucetum*

(a) THE PLANT FORMATION OF CALCAREOUS SOILS (CALCARION)
(from Moss 1913)

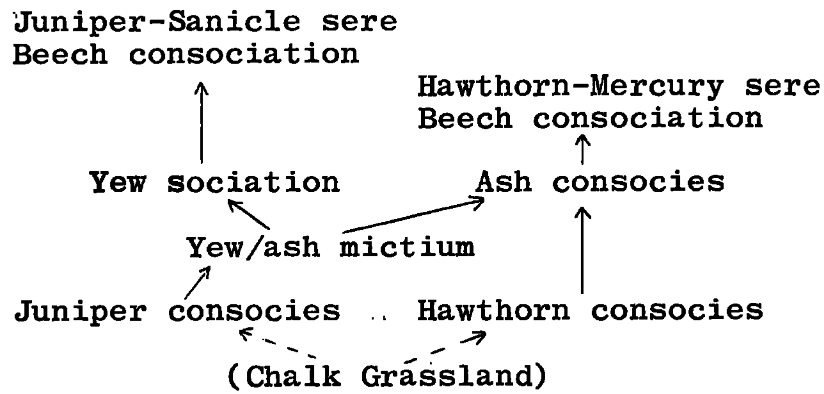
Group of Association	Chief Associations	Subordinate Associations
Woods	Ash wood (*Fraxinetum excelsioris*)	
Scrub		Progressive scrub Retrogressive scrub
Grassland	Calcareous grassland (*Festucetum ovinae*)	Calcareous heath grassland Calcareous heath Vegetation of swamps Vegetation of "rakes"
Vegetation of screes and rocks		Vegetation of screes Vegetation of rocks
Limestone swamps		

FIGURE 7. The Classification of British Vegetation; (a) Moss 1913.

(b) <u>SUCCESSION IN CALCARION (modified from Moss 1913)</u>



(c) <u>SERES OF WOODY VEGETATION ON CHALK SOILS</u> (from Tansley 1939, based on Watt 1934a, b)



<u>FIGURE 7.</u> The Classification of British Vegetation; (b) Moss 1913; (c) Tansley 1939.

ovinae", within the "Calcarion".

The suffix "-etum" of the association "Festucetum ovinae" was adopted from Schouw (1822) and the addition of the specific name "ovinae" followed the proposals of Cajander (1903). Moss (1910) proposed the suffix "-ion" for the formation. Using this terminology, Moss (1913) described the plant formation, "Calcarion" of the calcareous soils of the Peak District, (Figure 7a).

Influenced by Clements (1904) and his ideas on the development and structure of vegetation, Moss (1910), (1913) and Tansley (1911), concentrated their studies on the succession of associations within a formation, from initial "unstable associations", through intermediates to "stable associations", (Figure 7b). Further development along these lines by Clements (1916), (1923) and Tansley (1920) led to the organismal concept of vegetation; i.e. the idea that vegetation was an organism with structure, functions and a life history. At this time, all vegetation description in Britain was related to the "sere" nomenclature of Clements (1923), and complex successional sequences of communities of varying status were built up, notably by Watt (1934a, b); (see Figure 7c). This phase of vegetation description and survey was culminated by the production of Tansley's "The British Isles and their Vegetation" in 1939.

Up to 1955, the enthusiasm for vegetation description and its relation to succession was largely replaced by an experimental, ecological approach to vegetation, concerned mainly with the relationship of plant to habitat. Only the work of Hughes (1949), which postulated a classification of habitats as a framework for vegetation description, can be considered as a new approach to classification.

Poore (1955a, b, c), (1956) reviewed the techniques of the Zurich-Montpellier School of Plant Sociology - "the Braun-Blanquet System" (1955a) - and attempted to apply them to British vegetation. Tansley & Adamson (1926) had previously applied these techniques to the vegetation of the English Chalk, the results of which led to the conclusion of Tansley (1939) that he was unable to assess their usefulness. Poore (1956) reached a similar conclusion, but adopted a descriptive technique based on much the same theoretical and practical considerations of homogeneity, pattern, etc. He rejected the "index of sociability" and replaced the 1-5 "cover/abundance scale" with the 10-category scale of Domin (1933). He also rejected the Z-M method of grouping floristic lists into Associations and used a "process of successive approximation" to construct a Nodum, by definition "an abstract vegetation unit of any category" (1955b, c). Using this system, and adopting a hierarchical classification based on Dahl (1956) and Nordhagen (1943), McVean & Ratcliffe (1962) have produced a classification of the vegetation of the Scottish Highlands. Ivimey-Cook & Proctor (1966a) have used the same methods, but have related their noda to the accepted Z-M classification for Central Europe, (Lohmeyer, 1961).

Applications of the Z-M System (sensu stricto) to British vegetation are restricted to the work of Braun-Blanquet & Tüxen (1952), Moore (1964) and O'Sullivan (1965), all of which have proved that this method of vegetation analysis and classification may be easily applied.

Use and misuse of the various approaches listed above has resulted in a complex of nomenclature and a complex of problems associated with the interpretation and identification of the previous description of a particular community. Figure 8 comprises a "table of equivalents" of the types of British grasslands so far described, and their approximate Z-M equivalents.

Problems associated with the application of the Z-M System have been discussed by Poore (1956) and reassessed by Moore (1962). As Moore points out, many of Poore's conclusions are ambiguous and may be proposed either to uphold or negate the system of phytosociology in question. The over-estimation of the value of "Fidelity" to distinguish

ZURICH-MONTPELLIER	BRITISH (Tansley, etc.).
CLASS FESTUCO-BROMETEA (Brometalia erecti) MESOBROMION	Basic Grasslands - chalk, Inferior Ooolite and older limestones. Calcareous Grasslands (Moss). Brometum erecti (Salisbury 1920). Xerobrometum/Mesobrometum (Watt).
CLASS MOLINIO-ARRHENATHERETEA Molinietalia	Molinietum; Tussock-grass pasture (Salisbury). Siliceous grassland p.p. (Moss).
Arrhenatheretalia	Agrostis-Festuca complex (Tansley; King & Nicholson; etc.). Festuca-Agrostidetum (Watt). Arctic-Alpine grasslands. Meadow and pasture p.p. (Moss). Neutral grassland - Hay meadows and permanent pasture.
CLASS SEDO-SCLERANTHETEA (Festuco-Sedetalia) KOELERION ALBESCENTIS	Association of dune pasture plants (Moss). Stabilised dune pasture.
CLASS NARDO-CALLUNETEA (Nardetalia) NARDO-GALION SAXATILIS	Chalk Heath Nardetum Agrostis-Festuca
JUNCETEA MARITIMI	Maritime and Sub-maritime grasslands.
PLANTAGINETEA MAIORIS	Footpath communities.

FIGURE 8. The description of grassland communities in the British Isles: British terminology and the Zurich-Montpellier equivalents.

(British descriptions without authorship are those of Tansley 1939).

Associations is considered by Moore, and its relationship to "Constancy" and "Dominance" expounded. As Poore says, "the most satisfactory associations are those in which the dominant is also faithful", and this to a certain extent is true. But, reading Poore's ideas on the dominance of Schoenus in the Rosmarino-Lithospermetum Br.-Bl. 1935, it appears that underlying his reasoning is the idea of dominance in terms of the Tansley/Clements (loc. cit.) organismal concepts of vegetation, i.e. the affect of the dominant on the environment and other components of the community mainly via structural pressures, and not merely as the preponderance of a species over others in terms of cover. Indoctrination of many British workers with this idea of dominance and with other integral concepts of vegetation as an organism, e.g. succession as the process of growth and development of the organism, has led to a misunderstanding and misinterpretation of some of the basic premises of the Z-M System.

Apart from fidelity, the second major controversial point is the grouping of Associations into a hierarchy of Alliances, Orders and Classes. Webb (1954), Poore (1956) and Moore (1962) have discussed the relative merits and validity of this classification, and Poore points out that "Braun-Blanquet would be the first to admit that his system is not a natural classification". The exact nature is best illustrated by the following example.

Poore (loc. cit.) concludes that, "it is unnecessary to characterize the highest units by faithful species, for the grounds on which they were originally classified, physiognomy and habitat, are still quite adequate .....". This idea that initial classification is based on the above characters is to some extent true. However, the choice of primary limits for the study of a specific topic within any branch of learning is a built-in intuitive process characteristic of the human species. The more obvious limits for the description of vegetation are of necessity based on physiognomy and habitat. For example, the subject of this thesis is "Grasslands - (a physiognomic character) - on Calcareous Soils - (a habitat character), falling mainly into the Class Festuco-Brometea Br.-Bl. et R.Tx. 1943. But some grassland is "damp, tall herb" (physiognomic) and falls into the Class Molinion-Arrhenatheretea R.Tx. 1937, whilst a further type, resembling Festuco-Brometea but occurring at higher altitudes and latitudes (?) is placed in the Class Elyno-Seslerietea Br. Bl. 1948. This latter distinction is based upon the altitudinal and geographical distribution of the plants concerned, and hence, upon character species. Similarly, the distinction between the two component Orders of the Festuco-Brometea, Festucetalia vallesiacae Br.-Bl. et R.Tx. 1943 and Brometalia erecti Br.-Bl. 1936, is based upon groups of character species related to climatic factors and geographical distribution (see Chapter 4).

The statement of Poore quoted above is again based upon a different interpretation of the nature of the Z-M classification, due perhaps to past indoctrination with a particular school of thought. British workers have tended to interpret the system of classification as a "natural" one.

To quote Dobzhansky (1951), "the term 'natural classification' has meant one based on the common descent of organisms", or as Huxley (1940) had previously said, "Fundamentally, the problem of systematics, ..., is that of detecting evolution at work". The relationship of the taxonomy of living organisms to phylogeny is elucidated by Huxley (1959) in his theory of cladogenesis.

Parallel to these ideas on the classification of living organisms, Tansley's work on succession and evolution in plant communities led to his formulation of similar theories for the nature and classification of vegetation (Tansley, 1939).

But such theories cannot be applied to the Z-M System of classification. Braun-Blanquet (1932) states:- "In pursuance of the floristic principle of classification, orders of communities are primarily circumscribed by their component associations and alliances. Each order has its special characteristic species. The individual orders are also ecologically characterised".

From this statement, the point emerges that the Z-M classification is merely based on a series of groups of species of increasing ecological amplitude up the steps from association to alliance, and so on. This explains the use of faithful species to characterise the highest units of the classification and provides an alternative interpretation from that of Poore. Finally, the fact that, at higher grades of the classification the group of characteristic species represents a broad ecological situation often reflected by physiognomy, emphatically recommends the application of the Z-M system to problems in ecology (Poore, 1956a).

The over-emphasis of the use of fidelity and the mis-interpretation of the classification system seem to be the main stumbling blocks in the application of the Z-M techniques. The only other significant obstacle to the comparison of British vegetation with that of the continent of Europe is the lack of synonymy of plant nomenclature. Moreover, the continental phytosociologists recognise many forms and varieties of species which they consider to be valuable as indicators. As Braun-Blanquet (1932) says, ".... every species - indeed every race - has a definite, greater or lesser, indicator value".

But some taxa fall beyond the level of taxonomic validity. For example, as one of the character species for Gentiano-Koelerietum boreoatlanticum Knapp 1942, Bornkamm (1960) uses Festuca tenuissima. As he points out, this is more correctly referred to as Festuca ovina L. subsp. sulcata Hack., var. vallesiaca (Gaud) Link., subvar. tenuissima Hack. The Festuca ovina aggregate is one which needs detailed taxonomic revision. Huon (1968) has studied the complex in north-west France and has defined edaphic and climatic influences. But, the indicator value of these ecotypes is rather obscure, and the use of any taxon below the level of subspecies as a character species, seems to be unjustified.

Several examples occur where British taxonomists do not recognise species described for Britain by continental phytosociologists. Braun-Blanquet (1952) has described Antennaria hibernica for Ireland as a characteristic species of the association Antennarietum hibernicae Br.-Bl. & R.Tx. 1952. Yet it is not recognised in the British Flora. As Antennaria is predominantly an apomictic genus, and, in Ireland, A. dioica (L.) Gaertn. is at the southern limits of its distribution, it seems that Antennaria hibernica Br.-Bl. could be a true species.

Similarly, Koeleria albescens DC., characteristic of the alliance Koelerion albescentis R.Tx. 1937, though recognised in Britain, is a taxon whose status needs clarification.

The "splitting" of species into smaller units such as ecotypes and the use of these entities to validate sociological classification is one of the minor criticisms which can be levelled at the Z-M system of phytosociology. On the continent, the complex nomenclature of many species aggregates may be partly due to the search for ecological indicators by the phytosociologist. But on the other hand, some of the eco-sociological "splits", such as Antennaria hibernica Br.-Bl. may prove to be taxonomically sound.

PART II

Chapter 4.

A classification of the limestone grasslands of the British Isles.

Over a period of three years, most of the areas of limestone in the British Isles shown in Figure 1, were visited and some 535 grassland Aufnahmen were made. The areas chosen were mainly natural or semi-natural downlands, hill pastures and rough grazings. In general, permanently grazed meadows and hay meadows were not surveyed in detail, but several Aufnahmen were collected to complete the overall picture of limestone grasslands. A further 75 Aufnahmen were collected from communities such as calcareous heaths and scrub, in order to obtain a preliminary idea of the seral and zonal relationships of the grasslands under various environmental gradients.

The sampling procedure adopted was that of the Z-M school of phytosociology, and for each grassland type, a minimal area determination as described by Poore (1955) was carried out. It was found that for extensive downland or dale grasslands the minimal area required was 10 $metre^2$. In smaller areas of grassland 5 m^2 proved to be the minimal area, whilst in areas of mosaics, or where there was a rapid visible transition between communities, a 2 or 1 m^2 quadrat was needed to obtain a homogeneous stand. Minimal areas of 10 m^2 and 1 m^2 were never used in the same locality, since the existence of extensive stands needing a 10 m^2

quadrat adjacent to stands requiring 1 m^2 must indicate that the latter is merely a fragment.

The Aufnahmen thus obtained have been united into Associations and, together with data from various British workers have been classified according to the system of vegetation classification for central and north-west Europe advocated by Lohmeyer et al. (1962). These Associations have been related to one of the predominant measurable factors which influences plant geography, namely that of climate. For this purpose, the climate-type diagrams of Walter & Lieth (1967) have been used to illustrate the main climatic trends which are reflected by the floristic composition of the limestone grassland communities. (An explanation of these diagrams is given in the Appendix).

The following synopsis forms a basic classificatory framework for the calcareous grasslands of the British Isles, and the subsequent text is based upon this sequence:-

A. Class Festuco-Brometea
  Order Brometalia erecti
    Alliance Bromion
      Sub-Alliance Xerobromion
    Alliance Mesobromion erecti
      Sub-Alliance Eu-Mesobromion
      Sub-Alliance Seslerio-Mesobromion

B. Class Elyno-Seslerietea

Order Elyno-Dryadetalia Br.-Bl. 1948.

Alliance Kobresio-Dryadion (Nordh. 1936) emend McV. & Rat. 1962.

C. Class Molinio-Arrhenatheretea

Order Molinietalia

Alliance Molinion

Order Arrhenatheretalia

Alliance Arrhenatherion elatioris

Alliance Cynosurion

Alliance Ranunculo-Anthoxanthion (Gjaerevoll, 1956) emend.

D. Class Violetea calaminariae

Order Violetalia calaminariae

Alliance Thlaspeion calaminariae

(The citation of authors after the classification unit represents a deviation from the system of Lohmeyer et al. (1962)).

Other related communities which have close seral affinities with calcareous grasslands are dealt with in Chapter 5.

(A) Class FESTUCO-BROMETEA Br.-Bl. & R.Tx.1943

This Class of dry, anthropogenic, base-rich grasslands includes most of the grasslands on calcareous soils in central and western Europe. The eastern limits are obscure, but large areas of the steepe grassland of Poland can be referred to this Class. In Scandinavia, anthropogenic grasslands are more or less replaced by grass-heaths and extensive arctic-montane heathlands, and the damper, colder climate restricts Festuco-Brometea to such regions as Scania in southern Sweden and the Baltic islands of

Öland and Gotland (Braun-Blanquet, 1963).

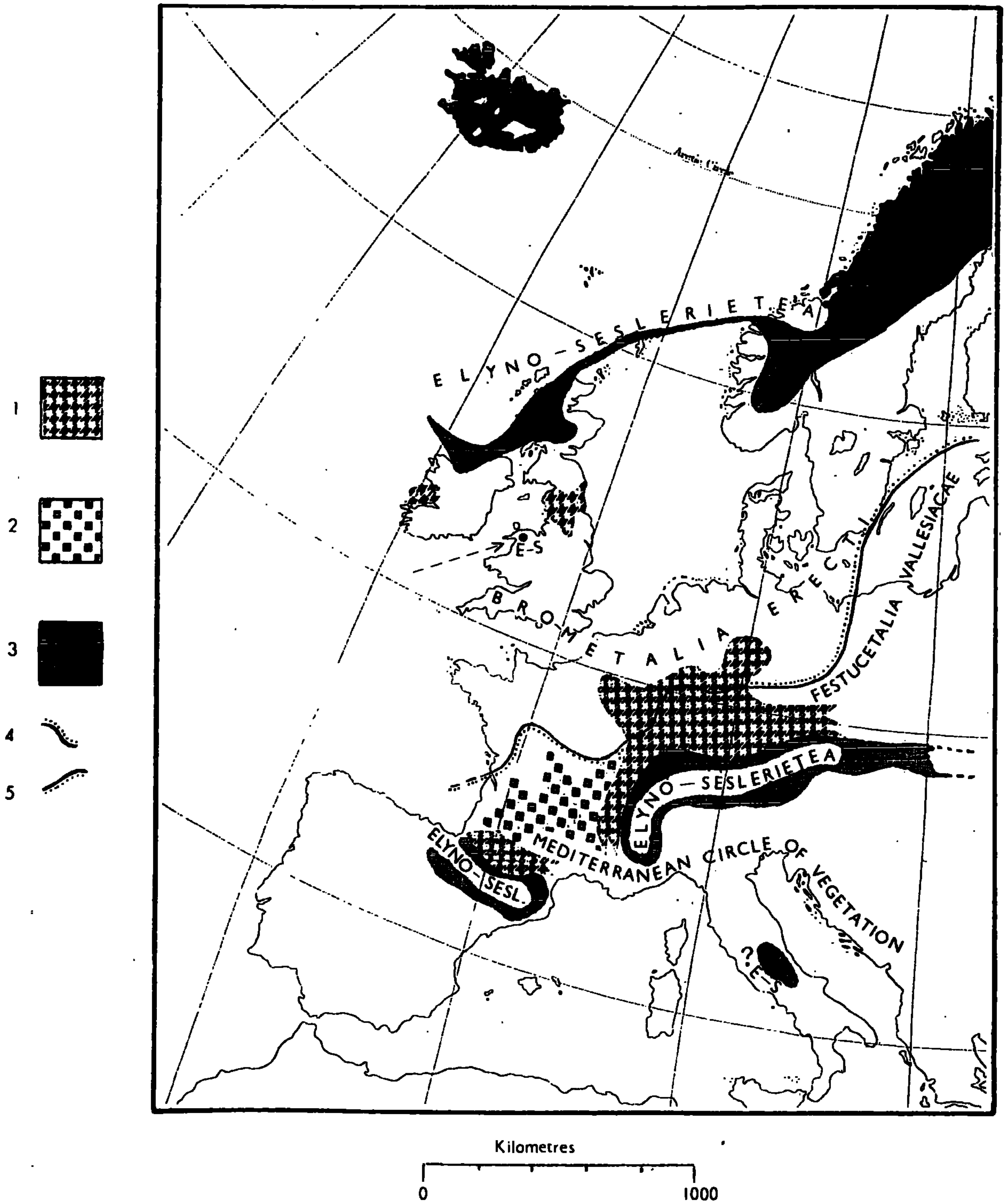
Grasslands representative of the Class are uncommon in Denmark, the North German Plain and Holland (occurring only in South Limburg province), due mainly to the lack of the appropriate calcareous strata and soils. South from the Weser Mountains in Germany and the Ardennes in Belgium to the Vosges and the pre-alpine region of north-central Europe, dry grassland communities are widely distributed and well described by Oberdorfer (1957) and Bornkamm (1960).

The Class is poorly represented in the Mediterranean region of Europe, being found only in the north of the region and on north facing slopes on mountains, (Braun-Blanquet, 1951). Similarly, Rivas-Martinez (1968) remarks on the rarity of the Class in the Cantabrian Mountains and the Spanish Pyrenees. In the Mediterranean region, Festuco-Brometea is commonly replaced by the Class Thero-Brachypodietea Br.-Bl. 1947, the characteristic, extremely dry "garrigue" which occupies vast areas of the region from Spain to Dalmatia. At higher altitudes, the Mediterranean-montane Class Ononido-Rosmarinetea Br.-Bl. 1947, replaces Festuco-Brometea, in all but a few localities. This Class contains many of the communities of the so-called "shrubby garrigue", where shrubby species of Helianthemum, Lavandula, Ononis and Rosmarinus assume co-dominance.

FIGURE 9. The distribution of the Class Elyno-Seslerietea and the component Orders of the Class Festuco-Brometea in western Europe.

Legend:

1. De-alpine, *Sesleria*-rich communities (e.g. *Seslerio-Mesobromion*, *Seslerio-Xerobromion*).
2. *Brometa* rich in Mediterranean species.
3. *Elyno-Seslerietea*.
4. *Brometalia*/Mediterranean *Brometa* boundary.
5. *Brometalia/Festucetalia vallesiacae* boundary.



1
2
3
4
5
Arctic Circle
ELYNO-SESLERIETEA
E-S
BROMETALIA ERECTI
FESTUCETALIA VALLESIACAE
ELYNO-SESLERIETEA
ELYNO-SESL.
MEDITERRANEAN CIRCLE OF VEGETATION
?E-S
Kilometres
0
1000

It is interesting to note that several of the character species cited for the latter Class by Braun-Blanquet (1951), are also considered to be characteristic species of the Class Festuco-Brometea in central and western Europe; e.g. Cirsium acaulon, Carex humilis, Asperula cynanchica, Helianthemum canum and Sesleria coerulea, (ssp. elegantissima Br.-Bl.). This overlap in groups of character species represents a transition zone between two broad climatic and phytogeographical regions whose actual boundaries need more detailed clarification.

In the British Isles, Festuco-Brometea is well represented in the south and east of England on the Chalk Downs from Kent and the Salisbury Plain to the Yorkshire Wolds, and along the Jurassic Limestone escarpment running from Dorset and Gloucestershire, through the Cotswold Hills to the Lincoln Edge. Less extensive areas of dry grassland are found on the older Carboniferous Limestone of the Derbyshire Dales, and along the north and south coasts of Wales. In the northern Pennines, and Lake District and the Magnesian Limestone escarpment in eastern County Durham, the Associations of Festuco-Brometea are affected by the infiltration of species characteristic of the Class Elyno-Seslerietea (see Figure 9). This is also the case in the Burren district of County Clare in western Ireland, an area which is extremely rich when compared to the rest of Ireland where non-calcareous glacial deposits cover most of the Carboniferous Limestone strata. There are, however, several localities in the Midlands where deposits of calcareous drift support a basic soil and a species-poor association of the *Festuco-Brometea*.

North of the Cheviot Hills, in the Southern Uplands and the Highlands of Scotland, the Class is virtually absent, mainly due to the lack of the appropriate base-rich soils and also the wetter climate. In a few areas where the soils receive some calcareous enrichment and where drainage is adequate, communities of the Class *Elyno-Seslerietea* occur.

There are two Orders of the Class *Festuco-Brometea* in central and western Europe:-

O. Festucetalia vallesiacae Br.-Bl.&R.Tx. 1943.

This Order is absent from the British Isles and comprises most of the dry steppe grasslands from regions with a typical eastern continental climate manifested by a wide annual range of temperature and a low annual rainfall. These grasslands are composed almost entirely of species with a continental distribution and are often dominated by species of *Stipa*, e.g. *S. capillata*. According to

Klika (1939) and Braun-Blanquet (1963), the Order occurs mainly to the east of the present border between East and West Germany, throughout Poland and Czechoslovakia, and on the Baltic islands of Öland and Gotland. There are also a few isolated localities in the pre-alpine region of southern Germany, e.g. the Association Erysimo-Stipetum Oberd. 1957 is reported in the Nahe valley and the province of Rheinhessen.

O. BROMETALIA ERECTI Br.-Bl. 1936.

This is the Order containing the majority of the anthropogenic, dry, base-rich, central and west European grasslands, referred to in continental literature as "sub-mediterranean and sub-atlantic", but extending through south and east England to the Atlantic coasts of Wales and Ireland. The distribution of the Order is much the same as that described for the Class Festuco-Brometea in western Europe, from the Mediterranean region and the Alps to south Scandinavia and northern England (Figure 9).

Characteristically, the grasslands within this Order are dominated by coarse grasses such as Bromus erectus, Brachypodium pinnatum, Festuca ovina, and often Helictotrichon pratense. A preponderance in numbers of hemicryptophytic herbs such as Plantago lanceolata, P. media, Asperula cynanchica, Ranunculus bulbosus, Leontodon taraxacoides, and others over chamaephytes such as Thymus drucei and other life-forms completes the familiar structure of the grassland communities.

Since the Order Brometalia erecti is the only Order of the Class Festuco-Brometea represented in the British Isles, the character species for Class and Order are the same. This is not the case on the continent. In addition to the Order Festucetalia vallesiacae, the Order Festuco-Sedetalia R.Tx. 1951 was originally included in the Festuco-Brometea, and older references to the Class character species make allowances for this fact. But since the inclusion of the latter Order in the Class Sedo-Scleranthetea Br.-Bl. 1955 emend.Oberd.mscr., character species such as Poa compressa, Arabis hirsuta, Cerastium arvense and Camptothecium lutescens have become invalid.

Moreover, the value of a character species varies from region to region, and those cited for Brometalia erecti for south Germany by Oberdorfer (1957) do not necessarily apply to a region such as the British Isles. The main drawback in the adoption of these character species is that species faithful to calcareous grassland in the central continent frequently occur on the calcareous dunes around the coast of Britain where the overall floristic composition of the community indicates another Order of a different Class. A good example here is Erigeron acer, listed by Oberdorfer as a character species of the Alliance Mesobromion Br.-Bl.&Moor 1938 emend.Oberd. 1948 in the Order Brometalia erecti. In Britain this species shows a high fidelity to the Alliance Koelerion albescentis R.Tx. 1937 within the Class Sedo-Scleranthetea.

The point emerges that until an overall view of a particular vegetation type or Class in a definite region has been obtained, no choice of character species for the communities in question can be considered to be useful. The broad survey of calcareous grasslands undertaken in this thesis has enabled a fairly meaningful selection of character species for several Classes and Orders to be completed. However, it is impossible in a primary survey to determine the actual indicator value of each species, and thus, the list of character species for any level of classification may be lessened or supplemented by more detailed investigation.

With these considerations in mind, the character species for the Class Festuco-Brometea and the Order Brometalia erecti in the British Isles are:-

Acinos arvensis (Lam.)Dandy

Anthyllis vulneraria L.

Blackstonia perfoliata (L.) Huds.

Brachypodium pinnatum (L.) Beauv.

Bromus erectus Huds.

Carlina vulgaris L.

Centaurea scabiosa L.

Cerastium pumilum Curt.

Filipendula vulgaris Moench

Scabiosa columbaria L.

Gentianella amarella (L.) Börner

Helianthemum canum (L.) Baumg.

H. chamaecistus Mill.

Helictotrichon pratense (L.) Pilg.

Hippocrepis comosa L.

Koeleria cristata (L.)Pers.

Potentilla tabernaemontani Aschers.

Poterium sanguisorba L.

Viola hirta ssp. calcarea (Bab.) E.F. Warb.

The distribution maps taken from Perring & Walters (1962) of any of these character species, give some idea of the distribution of the Order in the British Isles (Figure 10a,b). Bromus erectus shows a marked south-eastern, continental distribution and follows the areas of calcareous soils quite closely. This species occurs in calcareous pastures but also along disturbed and recolonised roadsides, unlike Helictotrichon pratense, which is more selective of areas of grassland. In northern England and Scotland the picture is slightly complicated in that records are mainly for the polyploid (n = 126) and the apparently distinct species H. alpinum (Sm.)Henrard, (Hedberg 1967).

FIGURE 10. (a) The distribution of *Bromus erectus* in the British Isles.

(b) The distribution of *Helictotrichon pratense* in the British Isles.

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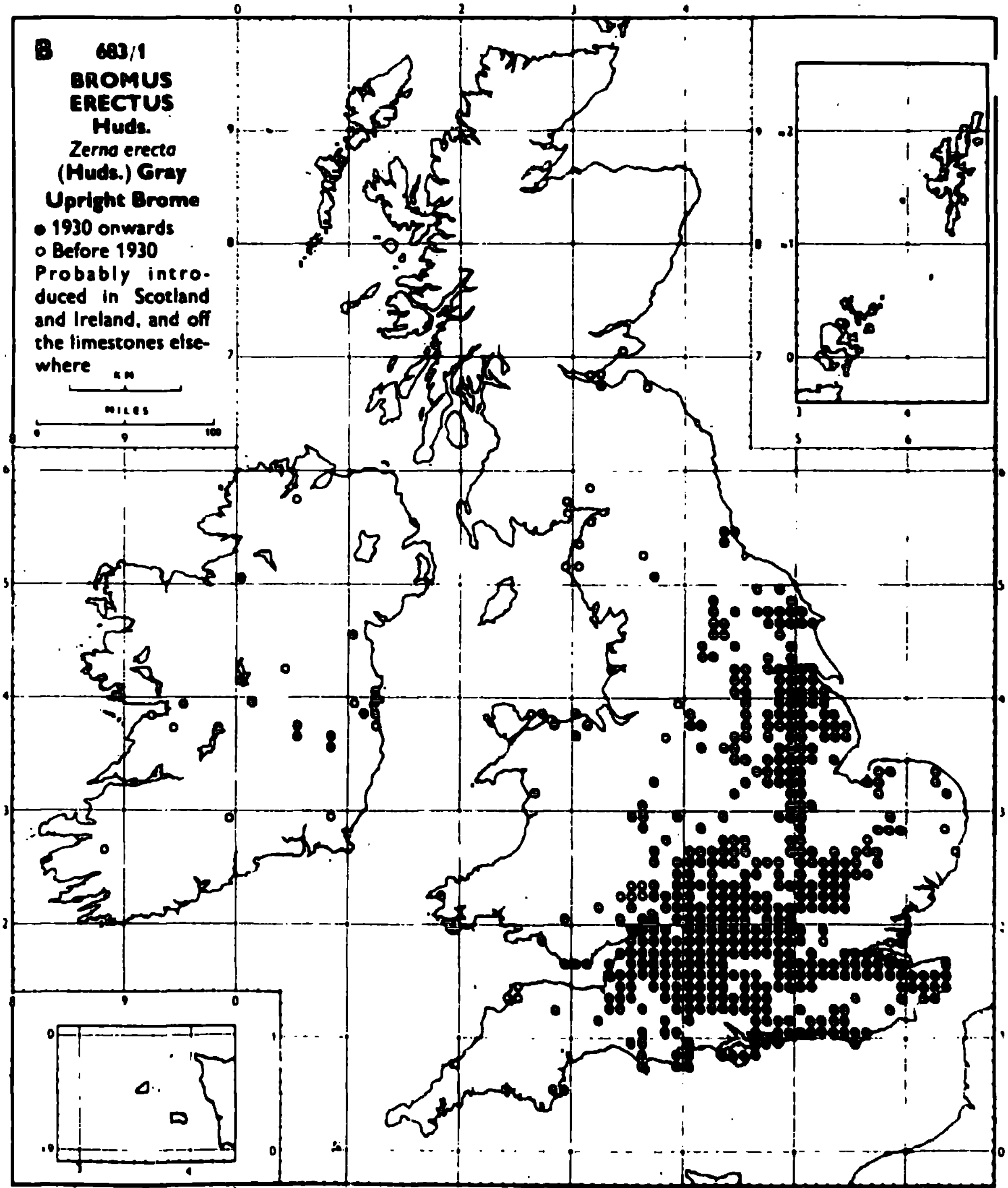
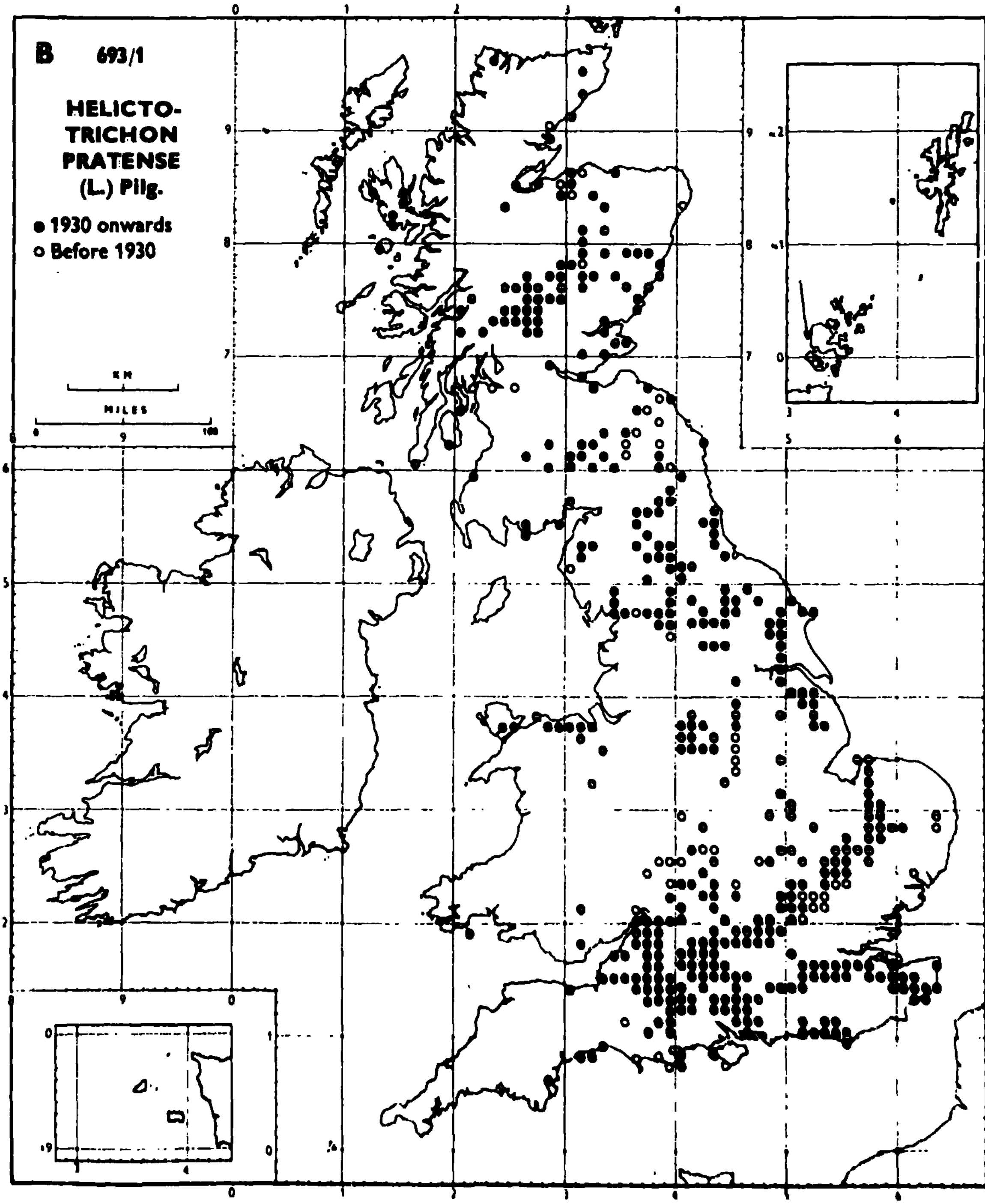

B 683/1
BROMUS ERECTUS Huds.
Zerna erecta (Huds.) Gray
Upright Brome
● 1930 onwards
○ Before 1930
Probably introduced in Scotland and Ireland, and off the limestones elsewhere
KM
MILES


B 693/1
HELICTOTRICHON PRATENSE (L.) Pilg.
● 1930 onwards
○ Before 1930
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MILES

All the other character species, with the exception of the rarer Cerastium pumilum, Helianthemum canum and Pulsatilla vulgaris have similar distribution patterns to these two examples.

Amongst the bryophytes and lichens there are few species which show a pronounced degree of fidelity to communities of the Festuco-Brometea. Oberdorfer (1957) lists four character species for southern Germany:- Pleurochaete squarrosa, Thuidium abietinum, Rhytidium rugosum and Camptothecium lutescens.

Of these the Mediterranean species Pleurochaete squarrosa is widely distributed on the chalk of southern England in dry open habitats on rocks and in grassland. Thuidium abietinum and Rhytidium rugosum are uncommon species locally abundant in rocky grasslands in the areas where they are found. In England they are usually found in communities referable to the Festuco-Brometea, but in the Highlands of Scotland, Rhytidium often occurs in base-rich communities of the Class Elyno-Seslerietea. Camptothecium lutescens is a thermophilous species often found in calcareous grasslands but also in sand-dune communities whose systematic position is transitional between Brometalia and the Alliance Koelerion albescentis. Also in this latter category are Ditrichum flexicaule and Entodon concinnus.

Several other bryophytes are marked calcicoles, but often extend their ecological range from grasslands to limestone rocks and walls and calcareous flushes and fens. Common examples of this group are:- Campylium chrysophyllum, Ctenidium molluscum, Encalypta vulgaris, E. streptocarpa, Fissidens cristatus, Hypnum cupressiforme var. lacunosum, Scapania aspera, Tortella tortuosa and Weissia spp. Two rarer examples are the oceanic western species Breutelia chrysocoma, which is often co-dominant in the grasslands of the Burren district of Ireland, but also in ombrophilous mires, and the thermophilous Mediterranean species Scorpiurium circinatum which occurs in coastal grasslands in southern England, Wales and Ireland.

Lichens are occasionally found in Brometalia communities, but with the exception of Certraria aculeata and Solorina saccata few show a marked calcicolous preference. Neither of these species is a good character species for the Order or Class.

The status of the constituent Alliances and Sub-alliances of the Order Brometalia erecti in the past, has been a controversial point. In Volume 5 of "Prodromus der Pflanzengesellschaften", Braun-Blanquet & Moor (1938) erect a single Alliance and three Sub-alliances, thus:-

All. Bromion erecti Br.-Bl.(1925)1936.

Sub-all. Xerobromion Br.-Bl. & Moor 1938.

Mesobromion Br.-Bl. & Moor 1938.

Violion calaminariae Schwickerath 1931.

Subsequent synecological investigations led to the exclusion of the Violion calaminariae from the Class Festuco-Brometea and the formation of the Class Violetea calaminariae R.Tx. 1961, in which were placed all the communities tolerant of high heavy-metal concentrations. The present classification within the Order Brometalia erecti follows Lohmeyer et al. (1962):-

All. Bromion Br.-Bl.1936.

Sub-all. Xerobromion Br.-Bl. & Moor 1938.

Seslerio-Xerobromion Oberd. 1957.

All. Mesobromion erecti Br.-Bl. & Moor 1938 emend.Oberd.1949.

Sub-all. Eu-Mesobromion Oberd.1957.

Seslerio-Mesobromion Oberd.1957.

This classification is readily comparable with that of Braun-Blanquet & Moor (1938), the main difference being the introduction by Oberdorfer (1957) of the two Sub-alliances Seslerio-Xerobromion and Seslerio-Mesobromion to represent the altitudinal transition communities between the Classes Festuco-Brometea and Elyno-Seslerietea.

(a) ALLIANCE BROMION Br.-Bl. 1936

This Alliance contains communities typical of steep, rocky grasslands around limestone and, less frequently, chalk cliffs. The climatic conditions of the regions which these pioneer grassland communities occur, are quite rigorous and are characterised by cold winters, often with extreme effects of frost, and then hot summers with periods of drought followed by the highest monthly average rainfall in July and August. Braun-Blanquet (1932) considers that the annual precipitation of 70-90 cms. appears to be one of the main limiting factors in the distribution of the Alliance in central Europe, though in habitats that are especially favourable - such as south-facing slopes on limestone - the 90 cms. isohyet is often overstepped. At higher altitudes in the pre-alpine region of central Europe, the 90 cms. limit is frequently surpassed by communities of the Sub-alliance Seslerio-Xerobromion, whose alpine components require a more mesophilous situation.

The soils on which Bromion communities occur are skeletal in nature, being mainly of the protorendzina type, but often reaching the developmental stage of a rendzina. The Alliance is widely distributed in central and southern Europe from the Harz Mountains in central Germany (Bornkamm 1960) and north-east France to Switzerland and north Italy to the northern limits of the Mediterranean region, (Braun-Blanquet & Moor 1938). In Britain, Bromion is restricted to two local areas of Somerset and Devon in south-west England. The Xerobrometum brittanicum Br.-Bl.&Moor 1938 derived from the work of Tansley & Adamson (1925) on the chalk grasslands of southern England, does not belong to this Alliance, but to the Mesobromion erecti (q.v.).

Areas of thermophilous, xeric grassland with an edaphic resemblance to continental Bromion localities are quite widespread in the British Isles, and theoretically, true Bromion communities could be well represented. However, the lack of continental species and the general floristic composition of these areas rarely reflect the Alliance in question. For example, the familiar over-grazed grasslands of Great Orme's Head, the Gower Peninsula, the Breckland, or the sugar limestone grasslands of Cronkley Fell in Teesdale, all have similar edaphic qualities to south-facing "felsig Trockenrasen" in the

Schwäbische Albrasse of southern Germany. But the historical and climatic effects in the British Isles enhance the performance of mesophilous species, and these drier grassland areas occur merely as xeric variants of Associations within the Mesobromion erecti Alliance. Hence, the communities with Helianthemum canum described by Proctor (1958) show marked affinities to continental Xerobrometa, edaphically and by the presence of several continental species of disjunct distribution, e.g. Helianthemum canum and Asperula cynanchica. But an overall comparison with British and continental Mesobromion communities, and the lack of continental character species of Xerobromion reveals a closer affinity to the mesophilous Alliance.

SUB-ALLIANCE XEROBROMION Br.-Bl.&Moor 1938.

Of the two Sub-alliances of the Bromion Alliance, only Xerobromion is represented in the British Isles. In general, representative stands are poor in character species and the proportion of mesophilous species demands that these British communities be placed on the boundaries of Xerobromion and Eu-Mesobromion. Character species for the Sub-alliance Xerobromion and the Alliance Bromion in the British Isles are:-

Helianthemum apenninum (L.) Mill. Trinia glauca (L.) Dumort.
Koeleria vallesiana (Honck.) Bertol.

The hybrid between H. apenninum and H. chamaecistus, H. x sulphureum Willd. is also valid as a character species, but is restricted to a single locality where the two parents come into contact. Carex humilis Leyss. and Scilla autumnalis L. are quite good differential species for the Alliance and Sub-alliance, but their fidelity is not absolute.

Oberdorfer (1957) recognises four Association-groups in the Xerobromion of southern Germany:-

(a) a group of Teucrium-rich pioneer communities;

(b) a base-poor dry grassland group;

(c) a typical group of "Collinen" or steep hill grasslands;

(d) a pre-alpine group.

Groups (a) and (c) are the more widespread groups in western Europe. In the first category, the common occurrence of the three Teucrium species, T. botrys, T. chamaedrys and T. montanum with other Bromion character species such as Globularia vulgaris and Linum tenuifolium gives the characteristic make-up of the continental Xerobromion communities. Although Teucrium botrys is sparsely distributed in the chalk grasslands of south England, the nearest communities to Britain which resemble this floristic composition are in northern France in the valleys of the rivers of Seine-Maritime, (de Blangermont & Liger, 1964; Rose, 1965). Across the English Channel from these localities, the only other possible geographical "link" species of these Xerobromion communities, Seseli libanotis and Bupleurum baldense occur together in a single locality - namely, the maritime Chalk grasslands of Sussex, between Cuckmere Haven and Beachy Head. Teucrium chamaedrys also occurs here, indicating that perhaps its status in this locality may be regarded as relict instead of introduced.

Group (c) of Oberdorfer (1957) shows a close relationship to the Xerobromion communities of the British Isles through the high constancy of Trinia glauca and Carex humilis and the occurrence of Koeleria vallesiana and Scilla autumnalis. These communities are found only on steep south and west-facing limestone slopes in Somerset and Devon. In Somerset, Brean Down is the centre of distribution and has stands most similar to continental Xerobrometa, whilst other Carboniferous Limestone hills such as Purn Hill and Crook Peak, support communities which represent the first stage of transition to Mesobromion. In Devon, on the local outcrops of Devonian Limestone, Xerobromion communities are found mainly in isolated pockets of south- and west-facing grassland near Brixham and Torquay.

ASSOCIATION POTERIO-KOELERIETUM VALLESIANAE Table 1.

Synonymy:- Natural pasture (pro parte) Moss 1907.

Carboniferous Limestone grassland (p.p.)
Hope-Simpson & Willis 1955.

Helianthemum apenninum localities (p.p.)
Proctor 1956.

Koeleria nodum Bridgewater 1967 mscr.

Habitat details

The Association *Poterio-Koelerietum vallesianae* occurs in a few sparse localities on the Carboniferous Limestone of the seaboard region of the Mendip Hills in Somerset. The most extensive stands are found on the headland known as Brean Down, a steep, rocky peninsula jutting out into the Bristol Channel. Other localities inland are at Uphill and Walborough Hill, Purn Hill in Bleadon parish, Hutton Coombe, Wavering Down and Crook Peak. This latter site some 10 kms. inland is the furthest inland and most easterly site for the Association. A locality at Worlbury Hill north of Weston-super-Mare appears to have been recently destroyed by quarrying operations. Middle Hope and Sand Point, a similar headland to Brean Down and 7 kms. to its north does not have communities representative of the Association.

The altitudinal range of the Association varies between

25 and 500 feet (8-160 m). On Brean Down where the more gentle slopes and the plateau areas between 250 and 300 feet (80-90 m) were divided up into allotments in the 19th century (Knight 1902), the communities are confined to the steeper slopes between 100 and 200 feet (30-60 m). The lowest stands in the area are at Walborough at a height of about 25 feet on the first limestone outcrops above the salt-marshes of the Axe Estuary. On Crook Peak and Wavering Down, the Association occurs up to the 500 foot contour. In these localities, there is a large percentage cover of bryophytes such as Camptothecium lutescens, Frullania tamarisci and Neckera crispa, probably due to the altitude and increased precipitation on west-facing slopes.

The rainfall at this climatic extreme of the Association is approximately 35" (840 mm), whilst on the coastal levels and Brean Down it falls to 32" (770 mm). Monthly rainfall averages show that less than one third of the total annual rainfall falls in the five months from February to June. Average monthly temperatures at Weston-super-Mare never fall below 41 °F (5.2 °C), and air-frosts rarely occur after the end of March. South-facing slopes warm up rapidly in spring and the extra shelter from the predominant north-easterly and westerly winds (Findlay, 1965) seems to be an important factor affecting the periodicity of the

FIGURE 11. Climate-types of coastal S. W. England.

(Diagrams modified from Walter and Lieth, 1967).

V(VI)2
F
G
TORQUAY (9m) 11.1° 889
25–35
LONG ASHTON (49m) 10.1° 920
30–35

communities. The regional climate data are summarized with the climate diagram for Long Ashton in Figure 11, which has been modified from Walter & Lieth (1967).

The topographical limitations of the Association are quite rigorous. Brean Down and Crook Peak are the only two localities where the Association forms extensive stands of grass sward and these, like the remaining sites are commonly interrupted by limestone outcrops. Steep, south-facing slopes with a range of 20 to 40° are the most favourable areas, though some stands on Crook Peak have a westerly aspect. On Brean Down, as the apparently important influence of the onshore west winds and increased precipitation gets stronger towards the point of the headland, the Association gradually becomes replaced by communities dominated by Helictotrichon pubescens, Holcus lanatus and Pteridium aquilinum.

The soils which support stands of this Association have been mapped by Findlay (1965) as Brown Earths, but as he points out these soils developed on hard limestone are transitional between Brown Calcareous soils and Brown Earths. Leaching is not as complete as in true acidic Brown Earths and figures of up to 15% total carbonates were recorded from the A horizon of a profile at Purn Hill. At this locality and in scattered patches on Crook Peak the shallow soils are definitely rendizniform in nature with a dark grey-brown due to a high humus content and a simple A/C profile, 7 cms. deep on average. A pH of 7.3 was recorded at Purn Hill, though Proctor (1956) records 6.4. Other data from Proctor for this locality are as follows:-

Ca 38 K 1.04 Na 0.82 Organic C 23.4

(Exchangeable Calcium, Potassium and Sodium measurements in m.e.%; Organic Carbon in %).

In other areas on Crook Peak and on Brean Down, the profiles resemble the transition to a Brown Earth of the Lulsgate Series a little more closely. In a sample profile from Brean Down a pH range of 6.8 to 7.2 and a figure of 8% total carbonates was recorded. The following profile is typical of the soils on Brean Down, but is slightly atypical of inland profiles of the Lulsgate Series in that it has a fairly liberal admixture of blown calcareous sand in the A horizon.

Grid. ref. ST 290588. Altitude. 150 ft. (48 m).

Slope. 25°S. Drainage. Good to excessive.

0-16 cm. Red-brown stony loam, limestone fragments near surface;

A/B friable structure due to intermixed calcareous blown sand; moderate organic matter; root-mat in top 5 cm. with numerous roots below.

16+ C   Large limestone fragments with smaller chips; bedrock.

The red-brown coloration is normally due to hydrated iron oxides liberated by weathering of the limestone, but may also be derived from the weathering of inherited Triassic fragments which originally overlay the Carboniferous Limestone strata.

Findlay (1965) has analytical data for the exchangeable bases in soils of this type, but not from within the range of the Association. The A horizon of a profile of the Lulsgate Series from Westbury (ST 504506) produced the following results:-

Ca 18.8   Mg 3.5   K 0.3   Na 0.6
(Measurements in m.e./100 gm.)

Characteristics of the Association

The Association is fairly well characterised by the presence of Koeleria vallesiana, Helianthemum apenninum and Trinia glauca, and the constancy of the characteristic Brometalia species Poterium sanguisorba and Carlina vulgaris. Other ubiquitous species which occur as constants with high cover values are Festuca ovina, Hieracium pilosella, Lotus corniculatus, Thymus drucei, Galium verum and Dactylis glomerata.

The life-form structure of the Association similar to that of continental Xerobrometa, (Figure 12, modified from

	(a)	(b)	(c)	(d)	(e)
Chamaephytes	42.5	18.6	10.6	6.1	11.1
Hemicryptophytes	25.0	49.3	76.3	53.4	45.2
Geophytes	2.5	8.7	7.8	2.8	1.6
Nanophanerophytes	-	-	-	3.0	1.6
Therophytes	37.5	8.7	5.3	15.7	22.6
Bryophytes	-	no data	-	12.7	11.1
Lichens	-	no data	-	6.1	6.8

(a) *Anthylli-Teucrietum*
(b) *Xerobrometum*
(c) *Mesobrometum*
} from Ellenberg (1963) from the south-west Jura region.

(d) *Poterio-Koelerietum vallesianae*

(e) *Helianthemum appeninum-Euphorbia portlandica Nodum*

FIGURE 12. Comparative Life-form Structures of Xerobromion Associations.

Ellenberg 1965), in that the percentages of hemicryptophytes are almost the same, though the amount of chamaephytes is much smaller. The figure for therophytes falls between those for Xerobrometum and the initial rocky grassland Association Anthylli-Teucrietum. Also, the paucity of geophytes, due mainly to the lack of orchids is marked when compared to either the Mesobrometum or Xerobrometum Association.

These life-form calculations are based on the percentage of the total number of species in all stands and tend to give a slightly erroneous picture. If the percentage number of occurrences of a particular life-form of the total number of occurrences of all species is calculated, the hemicryptophytes emerge with a score of 82%. Then the therophytes such as Bromus ferronii, Aira caryophyllea and Catapodium rigidum, which only occur sparsely, have a figure of 8%.

The Association has a marked periodicity peak associated with local climatic and topographical conditions which produce a relatively early flowering period in May and June for many of the herbs, e.g. Helianthemum apenninum and Hippocrepis comosa. Carex humilis begins to flower in late March and by May is often in fruit. In July the dominant plants appear to be Festuca ovina, Poterium sanguisorba and Koeleria vallesiana as these three species reach their flowering period.

Two distinct Sub-associations of the Poterio-Koelerietum vallesianae are recognisable.

(i) Sub-ass. CARICETOSUM HUMILIS is characterised by the gregariousness and dominance of Carex humilis, and the constant occurrence of Helianthemum apenninum. Mesobromion character species are absent and the differential species of the Alliance are uncommon. The sub-association is restricted to south-facing slopes on Brean Down and the maritime influence is reflected by the presence of Blackstonia perfoliata and Centaurium erythraea as species of high constancy. Weissia microstoma is quite common on rocky outcrops and is found in several of the more open areas of grassland, whilst the uncommon Mediterranean bryophyte Scorpiurium circinatum is recorded for two stands.

(ii) Sub-ass. TRINIETOSUM represents an "Ubergangesellschaft" or transition community between Xerobromion and Mesobromion similar to the Trinio-Caricetum humilis Volk 1937 in Oberdorfer (1957). Trinia glauca the Xerobromion character species is the main differential species and the diagnostic species of Mesobromion also act as good differentials. The infiltration of these latter species is best seen by the partial replacement of Helianthemum apenninum by H. chamaecistus. Helictotrichon pratense is an important constituent of the sward and Koeleria cristata begins to replace K. vallesiana. The number of Mesobromion character species increases towards the east, and at Crook Peak reaches a total of nine. Mesophilous differential species, especially Briza media and Carex flacca play a more important part in community structure. Of the eight Order character species, only Scabiosa columbaria shows a preference for this sub-association. The sub-association is found at the inland localities listed on page .

Zonation and Succession

The sub-association caricetosum humilis is only grazed by small numbers of rabbits, but they probably help to maintain the communities and prevent the invasion of shrubs like Ligustrum vulgare and the introduced Cotoneaster microphylla. Ligustrum and Rubus cf. ulmifolius form extensive thickets around the islands of grassland, and the presence of patches of Brachypodium sylvaticum and Teucrium scorodonia probably indicates a shrinkage of scrub rather than a progressive invasion.

In several localities the sub-association is in contact with a salt-spray splash zone characterised by dominant Festuca tenuifolia, Plantago coronopus and Crithmum maritimum. North-facing slopes of Brean Down were formerly used for allotments and have reverted to a Pteridium-Arrhenatherum-rich community of the Class Molinio-Arrhenatheretea, which gradually replaces Poterio-Koelerietum at the seaward end of the Down.

At Walborough the sub-association trinietosum gives way to an extremely species-rich, lightly grazed Mesobromion community dominated by Anthyllis vulneraria, Cirsium acaulon and Helictotrichon pratense. At Purn Hill and Uphill the communities are mainly delimited by man-made boundaries such as footpaths, hedges and heavily grazed, re-seeded pasture. On the western slopes of Crook Peak the sub-association is replaced, on the deeper acidic Brown Earths, by a scrubby community dominated by Ulex europaeus, and in other areas Calamagrostis epigeios. In other places Brachypodium pinnatum is the sole dominant, but Mesobromion species such as Cirsium acaulôn and Asperula cynanchica are also present.

HELIANTHEMUM APENNINUM-EUPHORBIA PORTLANDICA Nodum

Table 2.

Synonymy:- Helianthemum apenninum localities p.p. Proctor 1956.

The term Nodum is used here according to the definition of Poore (1955), because the component Aufnahmen on which the unit in question is based are selected for the presence of *H. apenninum*.

Habitat details

The Nodum is confined to south- and west-facing maritime limestone cliffs and grasslands in three main localities in South Devon - Daddy Hole and Anstey's Cove near Torquay, and Berry Head near Brixham. The climatic type is the same as that of the Mendip seaboard region and the coastal regions of South Wales (Figure II), being characterised by an extensive period of low rainfall from March to June, a high average annual sunshine total (1733 hours at Torquay) and a high average temperature of 43.2 °F (6.2 °C) for the coldest month. Total annual rainfall figures vary widely within this small area, and whereas Torquay has a figure of 840 mm, the more exposed Berry Head reaches 930 mm.

The Broken slopes and ledges of the limestone cliffs and the narrow band of cliff-top grassland are the only habitats where these communities flourish. The reddish calcareous soils are rendziniform in nature and are similar to those of Brean Down and the Gower Peninsula. Proctor (1956) cites the following analysis for Anstey's Cove:-

pH 7.4 Exch. Ca 32 K 1.6 Na 2.6 Organic C 12.3
(Measurements as before).

Characteristics of the Nodum

The dominant plants are *Festuca ovina*, *Helianthemum apenninum* and *Poterium sanguisorba*, and in more open places the bryophytes *Weissia* cf. *microstoma* and *Tortella nitida*. Other species of high constancy are *Dactylis glomerata*, *Thymus drucei* and *Plantago lanceolata*. *Koeleria cristata* and *Anthyllis vulneraria* are common *Mesobromion* species, whilst others such as *Helictotrichon pratense* and *Scabiosa columbaria* are rarer. *Trinia glauca* and *H. apenninum* are characteristic of the Nodum and *Scilla autumnalis* and *Euphorbia portlandica* are good regional differential species.

The life-form structure (Figure 12), with a high percentage of therophytes and a median 45% of hemicryptophytes compares favourably with all three xeric Associations, but not *Mesobrometum*. The periodicity of the Nodum is similar to that of *Poterio-Koelerietum*, having an early peak in May-June due to climate and exposition.

Zonation and Succession

In several places the Nodum gives way to fairly extensive patches of the introduced species *Senecio cineraria*, but at many sites soils are more leached and support a mixed calcicole-calcifuge community often dominated by Ulex spp. and Pteridium aquilinum. This Association, the Agrosto-Ulicetum (see Chapter 5), of the Class Nardo-Callunetea Prsg. 1949 and similar Associations, are common zones of contact with the grasslands in many limestone regions.

The Phytogeographical Relationships of the British Associations of Alliance Bromion

The Association Poterio-Koelerietum vallesianae and the Helianthemum apenninum-Euphorbia portlandica Nodum show a great deal of similarity, especially through the sub-ass. caricetosum humilis. Life-form, periodicity, climate, topographical limitations and soils, all confirm their affinities. The two units are similar in the constancy of the Brometalia species Poterium sanguisorba and Carlina vulgaris and other species such as Festuca ovina, Thymus drucei, Dactylis glomerata, Cladonia rangiformis and Weissia microstoma. The Association-group character species Helianthemum apenninum and Trinia glauca are present in both, but Koeleria vallesiana is replaced by K. cristata in the Devon Nodum. The Nodum also shows close relationships to the sub-ass. trinietosum, but the presence of many Mesobromion species tends to mask the similarities.

Probably the nearest locality in the British Isles where similar communities to these occur is the Avon Gorge, Bristol with its Carboniferous Limestone cliffs noted for their rarities. The following Aufnahme was made by Bridgewater (mscr.):-

3.3 Carex humilis

(+) Trinia glauca

Mesobromion & Brometalia species

2.3 Helianthemum chamaecistus
2.3 Poterium sanguisorba
\+ Scabiosa columbaria
\+ Hippocrepis comosa
\+ Cirsium acaulon
\+ Filipendula vulgaris
\+ Carlina vulgaris
(+) Koeleria cristata

Companions

2.2. Festuca ovina
1.2 Helictotrichon pubescens
1.1 Pimpinella saxifraga
1.2 Carex flacca
2.2 Briza media
1.3 Lotus corniculatus
1.2 Hieracium pilosella
\+ Rubia peregrina
\+ Centaurium erythraea
\+ Euphrasia nemorosa
\+ Teucrium scorodonia

Bryophytes & Lichens

1.3 Pseudoscleropodium purum
1.3 Weissia sp.
\+ Caldonia pyxidata

Also:- + Plantago lanceolata, Betonica officinalis, Linum catharticum, Thymus drucei, Hypochaeris radicata, Solidago virgaurea, Origanum vulgare, Viola hirta, and Ligustrum vulgare (seedling)

Locality:	Black Rock Gulley.	Grid ref.:	ST 562746
Altitude:	75 ft. (14 m.)	Aspect:	SW 25°.
Quadrat:	$5m^2$.	Cover, Herbs:	90%.

This list bares a closer resemblance to a Carex humilis variant of a Mesobrometum Association rather than Xerobrometum, and Table 3 modified from Pring (1961) confirms that Trina is a frequent member of a Mesobrometum community in which the rare Arabis stricta occurs.

However, the old records of Helianthemum apenninum from the Avon Gorge (Riddelsdell et al. 1948) and the presence of Trinia indicate that a community similar to those on Brean Down probably survived here, but was gradually affected by changes of climate and grazing to give a Mesobromion community. Further evidence for this argument is lent by the occurrence of the continental Festuco-Brometea Class character species Allium sphaerocephalon, which is found in several of the Xerobrometa of southern Germany including Koelerio vallesianae-Brometum (Table 4f).

Table 3 summarises the main phytogeographical affinities of the Association Poterio-Koelerietum and the Helianthemum-Euphorbia Nodum. There appears to be a definite Association-group characterised by the three species Koeleria vallesiana, Helianthemum apenninum and Trinia glauca. These species are all Mediterranean or sub-Mediterranean in distribution, but occur in isolated localities north and west of this region, some details of which are included in Table 4. Braun-Blanquet (1951) considers that these and other species such as Carex humilis and Helianthemum canum are character species of the Mediterranean Class Ononido-Rosmarinetalia, but outside this region and in combination with Mesobromion and

Brometalia character species they form a distinct Association-group.

From near the centre of distribution of these character species in the Auvergne Mts. of southern France, the Association Koeleria vallesiana-Helianthemum apenninum (Luquet) Br.-Bl.&Moor 1938 resembles the two xeric British units (Tab. 4 (a),(b),(c)). Besides the species included in the table many Mediterranean species occur in this Association, but incomplete constancy details prevent a closer comparison.

The remaining four lists represent the Xerobrometum "Ubergangesellschaft" or transition community to a Mesobromion community. The British Poterio-Koelerietum s.-a. trinietosum shows close affinities with the other three Associations (e,f,g), having many Mesobromion and Brometalia character species in common as well as the three companions of high constancy Festuca ovina, Thymus spp., and Hieracium pilosella. Of the group of continental Xerobromion and Mesobromion character species, only Crinitaria linosyris acts as a link with the British Association, whilst the dominance of Carex humilis in the last three Associations indicates a relationship with the sub-ass. caricetosum humilis.

The nearest extra-British sites for similar communities to this Association-group seem to be those reported by Pigott & Walters (1954) at Les Andelys in north-west France, where Crinitaria and Helianthemum apenninum occur on steep Chalk cliffs in the Seine valley. The geographically distant nature of these communities and of the Associations of Table 4, from the British group, e.g. Trinio-Caricetum humilis in the Main valley of the Franconian Jura in southern Germany, Koelerio vallesianae-Brometum in the German Alsace region, and Xerobrometum divionense from the Cote d'Or Mts. north of Dijon, France, presents a big phytogeographical problem.

Pigott & Walters (1954) consider that most of the species of disjunct distribution in Britain are relicts of the widespread Late-Glacial "steppe tundra" vegetation. Subsequent Post-glacial climatic changes in the Boreal and Atlantic periods resulted in the spread of birch/pine and deciduous forest and bog development. These phenomena restricted the species in question to relict habitats such as sea cliffs and shallow soils on steep chalk and limestone slopes. Most of the relict species are calcicoles and their restriction depended on the availability of calcareous substrata. Thus, the disjunct distribution of Trinia and Crinitaria in south-west England is exaggerated by the lack of limestone outcrops.

The harder Palaeozoic Limestones which weather more slowly than chalk, and which remained as steep cliffs have the greatest concentration of these species, e.g. Berry Head and the Avon Gorge. Hence, the chalk of southern England provides few suitable refuges, apart from the Cuckmere Haven area of Sussex, (see page). But here, the only species in common with the western relict group is *Bupleurum baldense* which also occurs at Berry Head. This tends to indicate two lines of retreat of existing vegetation at the advance of Atlantic conditions in the Post-Glacial period. These retreats are represented by two groups of species, one comprising *Carex humilis*, *Helianthemum apenninum*, *Trinia glauca* and *Koeleria vallesiana*, and the other *Teucrium chamaedrys*, *Seseli libanotis* and probably some of the rarer chalk downland orchids. The lack of a group of species of relict distribution common to both regions, and the absence of any Late-Glacial records of these species suggests that they were not so widespread in the "steppe tundra" period. These two points and the general nature of the vegetation of this particular period described by Godwin (1953) do not vindicate a Late-Glacial survival for these species, and per-Glacial survival cannot be ruled out.

Of the component species of the western group of relicts, only Carex humilis is not restricted to a few localities. This gregarious sedge occurs over extensive areas of chalk downlands in Wiltshire and Dorset, often occupying prehistoric earthworks and steep south-facing slopes. This species has as its centre of distribution the area of Salisbury Plain and it seems significant that the centre of distribution of the Neolithic and Bronze Age cultures was also in this region. Other species showing a similar distribution pattern are Orchis ustulata and Thesium humifusum, and to a lesser extent Gentianella anglica and Cirsium tuberosum.

As Pigott & Walters (1954) point out, the early settlement of the chalk resulted in forest clearance and the creation of disturbed semi-ruderal habitats into which species of low competitive ability could spread. This seems to have been the case with Carex humilis which, having been restricted to localities such as Brean Down, the Avon Gorge and the Wye Valley expanded into these areas of initial forest clearance. The rate of vegetative reproduction is slow and the percentage of viable seed set is low, so that the assumption must be made that the species spread when climatic conditions favoured its reproduction. The continuous occupation of Brean Down from the Upper Palaeolithic era has probably enhanced its chances of survival in this locality.

(b) ALLIANCE MESOBROMION ERECTI Br.-Bl.& Moor 1938 emend. Oberd.1949.

This Alliance contains most of the familiar chalk and limestone grasslands of the British Isles and also includes some communities of stabilised, calcareous dune systems. Whereas the Associations of the *Xerobromion* Alliance probably survived the forest maxima and are more or less primary communities, the *Mesobromion* Associations are considered to be secondary in nature, being formed on the steeper scarp slopes laid bare by early deforestation.

The German word "Halbtrockenrasen" or semi-dry grassland sums up the nature of these communities. When compared to *Xerobrometa* they are more mesophilous and contain many species which can tolerate a damper local climate and the pressures of grazing in a closed community. One of their main characteristics is the high percentage - often 75% - the relatively low proportion of chamaephytes and therophytes and a higher geophyte percentage than *Xerobrometa*.

The overall distribution pattern of the Alliance is similar to that described for the Order and the Class. Perhaps the most extensive areas of *Mesobromion* occur in southern England on the chalklands of the North and South

Downs, Salisbury Plain and the Chiltern Hills. In limestone regions Mesobromion communities are more localised, occasionally found on scarp slopes, but more frequently in smaller areas on golf courses, around old quarry workings and along roadsides.

Many of the character species listed for Brometalia erecti only occur sparsely in British Xerobromion communities and reach their maximum indicator value in Mesobromion, e.g. Bromus erectus, Brachypodium pinnatum, Helianthemum chamaecistus and Helictotrichon pratense. Other good Mesobromion character species are:-

Anacamptis pyramidalis (L.) Rich.

Asperula cynanchica L.

Campanula glomerata L.

Cirsium acaulon (L.) Scop.

Onobrychis viciifolia Scop.

Orobanche elatior Sutton

Picris hieracioides L.

Polygala calcarea F. W. Schultz

Pulsatilla vulgaris Mill.

Thymus pulegioides L.

Thalictrum minus L. - excluding ssp. arenarium (Butcher) Clapham

There are a number of character species which are less widely distributed:-

Aceras anthropophorum (L.) Ait.f.

Carex ericetorum Poll.

Dianthus gratianopolitanus Vill.

Euphrasia pseudokerneri Pugsl.

Galium pumilum Murr.

Gentianella anglica (Pugsl.) E.F.W.

G. germanica (Willd.)Börner

Herminium monorchis (L.) R.Br.

Himantoglossum hircinum (L.) Spreng.

Orchis ustulata L.

Phyteuma tenerum R.Schultz

Polygala austriaca Crantz

Salvia pratensis L.

Senecio integrifolius (L.) Clairv.

Thesium humifusum DC.

Veronica spicata L.

Of the species in these two groups, Asperula cynanchica and Cirsium acaulon are the most widespread and the best indicators of Mesobromion communities. Onobrychis viciifolia is a questionable inclusion since it frequently occurs as a weed of arable and ruderal habitats. Although it is found in closed chalk and limestone grassland, it may merely be a relic of ancient cultivation. Orobanche elatior is quite widely distributed within the range of its host Centaurea scabiosa, but is rather rare and seldom occurs in colonies of more than ten plants per locality. The second group of species are all good Mesobromion character species with a much wider distribution in continental Europe than in the British Isles. Their rarity does not diminish their indicator value, although none of them play a major role in the typical community structure.

A further group of species serve to differentiate the Alliance Mesobromion from Xerobromion. These are usually species indicative of various grazing pressures, and their

Alliance	Sub-Alliance	Associations
ALLIANCE MESOBROMION ERECTI Br.-Bl.&Moor 1938 emend. Oberd. 1949	Sub-All. Eu-Mesobromion Oberd.1957	1. CIRSIO-BROMETUM
		2. HELICTOTRICHO-CARICETUM FLACCAE
		3. HELIANTHEMO-KOELERIETUM
		4. CARICETUM MONTANAE
		5. ANTENNARIETUM HIBERNICAE Br.-Bl. & Tx. 1952
		6. CAMPTOTHECIO-ASPERULETUM CYNANCHICAE Br.-Bl. & Tx. 1952
	Sub-All. Seslerio-Mesobromion Oberd. 1957	7. SESLERIO-HELICTOTRICHETUM
		8. SESLERIO-CARICETUM PULICARIAE
		9. ASPERULO-SESLERIETUM (Br.-Bl. & Tx. 1952) emend.
		(Sesleria-Carex ornithopoda community)
		(Breutelia-Sesleria pavement community)
		(Empetrum-Epipactis Nodum Iv.-Ck. & Proct. 1966)

FIGURE 13. Syntaxonomy of the Alliance Mesobromion erecti in the British Isles.

performance appears to be enhanced by the addition of raw humus to the habitat. In this group are:- Agrimonia eupatoria, Betonica officinalis, Briza media, Carex caryophyllea, C. flacca, Centaurea nigra, Leontodon hispidus, Medicago lupulina, Pimpinella saxifraga, Plantago lanceolata, P. media, Ranunculus bulbosus, Succisa pratensis and others.

A more or less continuous grazing regime is indicated by the presence of Molinio-Arrhenatheretea character species such as Holcus lanatus, Poa pratensis s.s., Cynosurus cristatus and Arrhenatherum elatius, but when these assume dominance there is usually a noticeable reduction of Mesobromion character species.

The Associations described in the ensuing text are summarised in Figure 13, and the broader environmental and ecological details are presented in Figure 14 (back pocket) to enable a rapid comparison of the habitat details of all the grassland Associations described.

SUB-ALLIANCE EU-MESOBROMION Oberd.1957

This Sub-alliance has been created to include almost all of the lowland Mesobromion Associations which are free from the influence of de-alpine species (Meusel 1939), such as Sesleria caerulea. Most of the grasslands of the Chalk, the Jurassic Limestones and the Carboniferous Limestones of

Derbyshire and Wales fall into this category. There is an almost continuous variation in floristic composition and the subsequent Associations are delimited mainly on the bases of phytogeography and community structure.

ASSOCIATION CIRSIO-BROMETUM Table 5.

Synonymy:- (for limestone areas only).

Inferior Oolite grasslands, Tansley (1939).

Oolitic limestone (unaltered) grassland, Hepburn (1942), (1955).

Habitat details

The Association Cirsio-Brometum is described mainly from the Jurassic Limestone escarpment of central England, from the Cotswold Hills, along the escarpment through Northampton and Rutland to the Lincoln Edge. Other stands of this Association are included from the maritime Jurassic Limestones of Dorset, the Carboniferous series of Somerset and Gloucestershire and the Magnesian Limestones of Derbyshire and Yorkshire as far north as Ripon.

The altitudinal range of the Association is from 50 to 1000 feet (16-320 metres). The majority of localities in the southern Cotswolds are around the 600 feet (190 m.) contour, but north of Stroud, the altitudes extend to 900 feet (280 m.) on Leckhampton Hill (SO 948185) and 1000 feet on

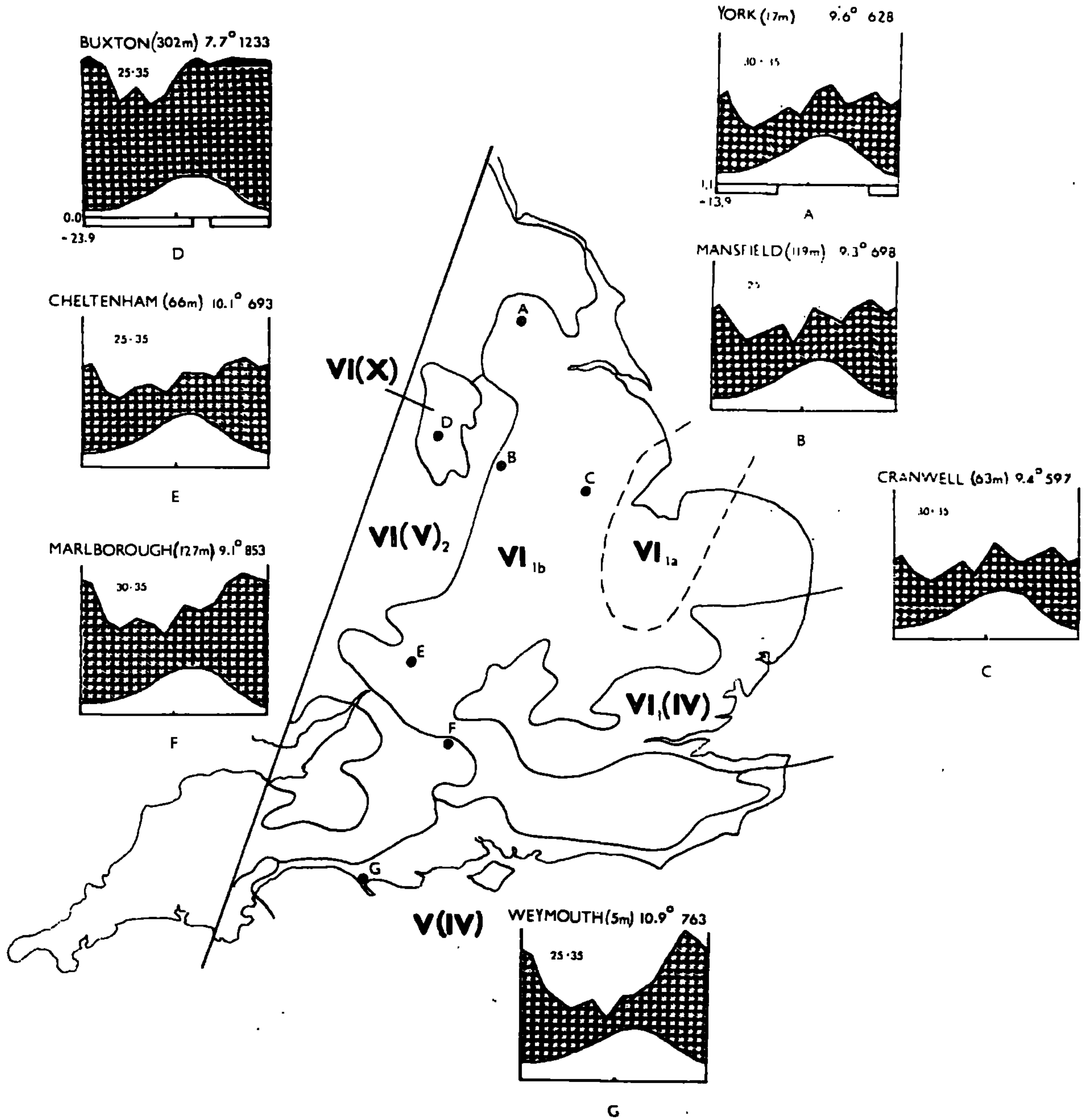
Cleve Cloud (SO 984260). The Northamptonshire and Lincolnshire localities range between 150 and 300 feet (45-90 m.), whilst most of the stands from the Magnesian Limestone are found at about 300 ft. Other localities in Dorset and the Mendip Hills vary between 50 and 200 feet (60 m.).

The majority of the stands of the Association overlying the limestones from the Cotswolds to south Yorkshire fall within the climate-type VI_{ib} of Walter & Lieth (1967). This type is characterised by an average mean annual temperature of 49 °F (9.4 °C) and a mean annual rainfall varying between 25 and 32 inches (600-768 mm). The highest mean monthly rainfall figures are either in the months of July or August. Ground frosts are usually absent between June and September, and air frosts are restricted to the period from October to April. It is notable that the northern and western boundaries of this climate-type are more or less equivalent to the limits of the distribution of Bromus erectus and Brachypodium pinnatum (Perring & Walters, 1962), the co-dominants of the Association, (cf. Figures 10(a) and 15).

The topographical and geological limitations of the Association are quite strict. The Jurassic Limestones occur in two main series, the Lias and the Oolites. The

FIGURE 15. Climate-types within the distribution range of the Association Cirsio-Brometum.

(Diagrams modified from Walter and Lieth, 1967).



BUXTON (302m) 7.7° 1233
25·35
0.0
-23.9
D
CHELTENHAM (66m) 10.1° 693
25·35
E
MARLBOROUGH (127m) 9.1° 853
30·35
F
YORK (17m) 9.6° 628
30·35
1.1
-13.9
A
MANSFIELD (119m) 9.3° 698
B
CRANWELL (63m) 9.4° 597
30·35
C
WEYMOUTH (5m) 10.9° 763
25·35
G
VI(X)
VI(V)$_2$
VI$_{1b}$
VI$_{1a}$
VI$_1$(IV)
V(IV)

former is mainly a clay formation, but does include some alternating shales and limestones which have a calcicole flora. However, all of the stands of the Cirsio-Brometum described from the Cotswolds, Northamptonshire and Lincolnshire are developed over the Inferior Oolite, the older formation of the Oolite series. The Association is found commonly on the steep, north- and west-facing scarp slopes formed by this limestone, and less commonly, in the predominantly agricultural areas of the Great Oolite series. The Cotswold region has the most extensive stands of Cirsio-Brometum. In the region around Stamford in Northamptonshire and Lincolnshire, where there are fewer scarp slopes and the country is more undulating, localities tend to be restricted to old quarry workings and roadsides. Similar topographical limitations apply to the occurrence of the Association in other limestone areas and are especially rigorous in the Magnesian Limestone regions. Here the friable nature of the rock gives rise to good deep soils, and the intensive agriculture restricts Cirsio-Brometum to a few semi-natural localities around quarries.

The soils associated with the Oolites are yellowish-brown calcareous soils and, on the steeper slopes are usually rendziniform in nature. Avery (1955) records that most of the soils of the Cotswolds belong to the Sherbourne series, a group named for the town in Dorset where they are also extensive over the Oolite. Deeper soils have similar profiles to the following type examined at Stinchcombe Hill in Gloucestershire:-

<u>Grid Ref</u>. ST 742982 <u>Altitude</u>. 650 ft. (205 m) <u>Slope</u>. 10°S

<u>Drainage</u>. Good to excessive.

0-7 cm. A	Dark-brown, humus-rich, containing angular fragments of friable yellow limestone; pH 7.0.
7.24 B	Brown clayey horizon with numerous limestone
24 C	Light yellowish-brown limestone brash.

The depth of the profile varies considerably, and less than ten metres away from the profile described above, on the steep (30°) north facing slopes, the brashy limestone C horizon can be found at a depth of only 9 cms.

The soils of the Aufnahmen from the Stamford region are also naturally brashy throughout the profile, but this phenomenon is probably exaggerated by the fact that most are developed over ancient quarry spoil-heaps. In Lincolnshire there added complications of drift and many profiles have a sandy A horizon similar to this example from near Wilsford:-

<u>Grid Ref</u>. TF 010430 <u>Altitude</u>. 100 ft. (30 m) <u>Slope</u>. 5°SW.

<u>Drainage</u>. Excessive.

0-4 cm. (A_o)	Compact root mat with intermixed coarse sand grains.
4-10	Yellow-brown fine sand/humus layer; no limestone fragments;
A	many roots; pH 7.1.
10-14 C	Brashy yellow limestone fragments with some dark brown humus accumulations and coarse sand. Bedrock.

Extensive areas of the Magnesian Limestone are also covered by glacial drift and their rich soils enhance arable farming. Soils which support Cirsio-Brometum communities however, are generally free from drift and are extremely local in distribution. Typically, they are shallow rendzinas and brown calcareous soils of the Aberford series, Holiday (1959). They resemble the Sherborne series in that they are developed from a friable yellowish-brown limestone and tend to have a brown loamy A horizon. The Magnesian Limestone apparently contains more iron oxides than the Oolites, and this A horizon is frequently more reddish-brown than those of the Sherborne series. Profile depth varies mainly between 12 and 30 cms. and the pH of the A horizon is usually in the range 6.8 to 7.2.

Characteristics of the Association

Cirsio-Brometum is characterised by the constancy of Brachypodium pinnatum, Bromus erectus, Cirsium acaulon and Asperula cynanchica, and the co-dominance of the first two of these species. The *Brometalia* character species *Helianthemum chamaecistus*, *Helictotrichon pratense*, *Poterium sanguisorba* and *Scabiosa columbaria* also show high constancy and are fairly characteristic of the Association. The abundance of mesophilous indicator species like *Briza media*, *Plantago lanceolata*, *Carex caryophyllea*, *C. flacca*, *Pimpinella saxifraga*, *Leontodon hispidus* and *Trifolium pratense* and other species of high constancy, such as *Lotus corniculatus*, *Thymus drucei*, *Festuca ovina*, *Hieracium pilosella* and *Leontodon taraxacoides* plays an important part in community structure.

Bryophytes are quite common in most of the stands from the Cotswold region, and two species, *Pseudoscleropodium purum* and *Camptothecium lutescens*, are found throughout the Association. A number of species such as *Neckera crispa*, *Frullania tamarisci* and *Scapania aspera*, appear to be indicative of wetter conditions on north- and west-facing slopes at higher altitudes in the Cotswolds. *Rhytidiadelphus triquetrus* and *Hylocomium splendens* attain a relatively high cover in several stands and probably represent a variant of damper disturbed habitats.

An investigation of the life-form structure reveals an overwhelming preponderance of hemicryptophytes. Several chamaephytes and geophytes, e.g. *Helianthemum chamaecistus* and *Anacamptis pyramidalis* and a few therophytes complete the picture. The characteristic structure, due mainly to the co-dominance of the coarse grasses *Bromus erectus* and *Brachypodium pinnatum* and the abundance of the unpalatable *Cirsium acaulon*, reflects a very lightly grazed or ungrazed grassland. In fact, only the localities described from the Cotswolds are extensive enough to allow grazing.

Three Sub-associations are recognisable:-

(i) Sub-ass. TYPICUM is the most widespread and is usually found in areas which are apparently undistributed such as the scarp slopes of the Cotswolds. The sub-association is rich in *Mesobromion* and *Brometalia* character species and *Galium pumilum* is restricted to this group.

A variant of this sub-association is recognisable in the Magnesian Limestone localities of Derbyshire and Yorkshire, by the presence of *Carex ericetorum*, the increase in constancy of *Koeleria cristata* and the presence of fewer *Mesobromion* species. *Sieglingia decumbens*, a mesophilous differential species also occurs more frequently in this variant.

(ii) Sub-ass. ASTRAGALETOSUM. The distribution patterns of *Pulsatilla vulgaris* and the inland distribution of *Astragalus danicus* are strikingly similar (cf. Perring & Walters 1962), and these two species are good differentials for a distinct sub-association in disturbed localities. Other differential species are Serratula tinctoria, Genista tinctoria and Aceras anthropophorum. Anthyllis vulneraria, Koeleria cristata and Campanula glomerata are of higher constancy in this sub-association than in s.-a. typicum, and seem to prefer the more open habitats and the reduction of the dominance Bromus and Brachypodium.

The sub-association is strongest in the disused quarries at Barnack, Collyweston and Bloody Oaks in the Stamford region, along roadsides in Lincolnshire and also occurs in the Cotswolds. The distribution patterns of Pulsatilla and Astragalus hints that the sub-association may be more widespread in this latter region than the examples in Table 5 indicate. Wells (1968) concludes that Pulsatilla shows a distribution associated with Roman activities, and the more or less simultaneous occurrence of Genista tinctoria and Serratula tinctoria - two important dye plants - with Pulsatilla in these Aufnahmen tends to suggest such a solution. In fact, several of the stands with Astragalus, Genista and Serratula, but without Pulsatilla are located along the broad road verges of Ermine Street in Lincolnshire.

(iii) Sub-ass. BRACHYPODIETOSUM is found in all the regions listed for the Association. It is characterised by an increase in cover and dominance of Brachypodium pinnatum at the expense of Bromus erectus. In addition, many of the Mesobromion character species show a marked decrease in cover and vitality, whilst Arrhenatherum elatius, Helictotrichon pratense, Trisetum flavescens, Holcus lanatus, and to a lesser degree Cynosurus cristatus, act as differential species. The sub-association is developed mainly on wetter north- and west-facing slopes and appears to require a more recently disturbed habitat than the other sub-associations. The Aufnahmen from regions of higher rainfall such as the maritime region of Dorset, north-facing slopes of Brean Down and Crook Peak in Somerset and in Cressbrook Dale, Derbyshire, all belong to this sub-association.

Zonation and Succession

Cirsio-Brometum is often closely associated with woodland border scrub communities dominated either by Crataegus monogyna, Clematis vitalba or Rubus ulmifolius. The first species mentioned is the most common invader of grasslands and seems to require no peculiar features of climate for its establishment. Clematis vitalba only encroaches on the grassland on thermophilous south-facing slopes in the Cotswolds, and the damper maritime stands of the Association are often limited by dense growth of Rubus ulmifolius. These three community types belong to the Order Prunetalia R.Tx.1952 of the Class Querco-Fagetea Br.-Bl.&Vlieger 1937.

Inland localities of the sub-association brachypodietosum are usually associated with the seral development of Ulex-scrub communities or a zonation to Arrhenatherion communities of hay meadows.

The remaining Associations of the Eu-Mesobromion form a complex Association-group which are poorer in Mesobromion character species than the Cirsio-Brometum. Williams & Varley (1967) proposed an Association-group named Thymo-Festucetum ovinae for a group of Festuca-Agrostis pastures in north Yorkshire, the Gower Peninsula, Derbyshire, and the Southern Uplands of Scotland. This group was classified tentatively in the Alliance Cynosurion of the Class Molinio-Arrhenatheretea, but it appears to be heterogenous containing pastures from the Sub-alliances Eu-Mesobromion and Seslerio-Mesobromion and the Alliance Agrosto-Festucion. The question of its classificatory status was probably due to its heterogenous nature which is obscured by the dominance of Agrostis and Festuca species, and the author's use of continental character species whose indicator value is not thoroughly worked out by an overall survey of British grasslands.

Although some of the data in this thesis is included in the *Thymo-Festucetum* by Williams and Varley, the present Association-group is more limited in terms of geography, topography and floristic composition. This group forms a peripheral zone of communities around the fringe of the distribution of *Bromus erectus* and *Brachypodium pinnatum* where *Festuca ovina* and *Helictotrichon pratense* are often the dominant grasses and where continental *Mesobromion* character species are rare. The following Associations have been described:-

Helictotricho-Caricetum flaccae - described from the coastal Magnesian Limestones of Co. Durham, the Derbyshire limestones, the maritime Liassic Limestones of south Wales, one inland locality in north Wales and in several localities in the Mendip Hills.

Helianthemo-Koelerietum - restricted to the maritime Carboniferous Limestones of north Wales, the Pembrokeshire coast and the Gower Peninsula.

Caricetum montanae - a local Association in two localities on the Carboniferous Limestones of south Wales.

Antennarietum hibernicae Br.-Bl.&Tx. 1952 - described from calcareous eskers and moraines by Braun-Blanquet & Tüxen (1952) in Co. Offaly and Co. Laoighise and probably more widespread. Further stands were located on calcareous drift in Co. Clare and on Carboniferous Limestone in Kerry.

Camptothecio-Asperuletum Br.Bl.&Tx.1952 - an Association of calcareous dunes in contact with Koelerion albescentis communities described by Braun-Blanquet & Tüxen in western Ireland. Also recorded in Pembrokeshire.

ASSOCIATION HELICTOTRICHO-CARICETUM FLACCAE Table 6.

Synonymy:- Calcareous grassland Association (Festucetum ovinae) Moss 1913, and subsequent authors.
Festucetum, Festuca-Agrostidetum Balme 1954 (p.p.).
Thymo-Festucetum (A) Williams & Varley 1967.
Helictotricho-Festucetum Shimwell & Bellamy 1967.

Habitat details

The most extensive stands of this Association are located on the steep slopes of the Derbyshire Dales overlying Carboniferous Limestone. Other fairly extensive areas are seen on the inland limestone of the Mendip Hills in the Cheddar Gorge, Burrington Coombe and Goblin Coombe, and on the maritime Liassic Limestones of Glamorgan between Southerndown and St. Donats. Only one locality was found in north Wales at Pantasaph, near Holywell and other Aufnahmen, collected on the draft covered Magnesian Limestone of the eastern Durham are also included in the Association.

The Altitudinal range varies between 600 and 1000 feet (190-320 m.) in Derbyshire, 50 and 550 feet (16-180 m.) in the Mendips, up to 800 feet (260 m.) in north Wales and around 100 feet (30 m.) in the other coastal localities.

The range of the climate types of the Association is illustrated in Figures 15 and 16, and it can be seen that there is a fairly wide tolerance. The south Wales and Mendip localities fall into the type V(VI)2 previously described for the _Poterio-Koelerietum vallesianae_. However, the rainfall is higher in south Wales (cf. Swansea diagram with Long Ashton in Fig. 11), and at higher altitudes in the coombes and gorges of the Mendips. In these latter areas there is a pronounced humid microclimate in the narrow, steep-sided gorges which tends to restrict the communities to the drier top slopes.

The dales of Derbyshire exhibit a similar phenomenon. Such areas as Monk's, Lathkill and Tideswell Dales are extremely steep and the period of full incident sunlight on the dale sides is often limited to two hours per day on either side of the dale (Garrett 1956). Other dales such as Monsal Dale and Long Dale are more open and support more typical thermophilous _Mesobromion_ communities. The overall climate-type in these areas is in many ways a transition type between that of the Midlands and the northern Pennine regions. The mean annual rainfall figures vary between 900 and 1270 mm with a mean minimum and maximum in April and December respectively. Temperatures are low throughout the year with monthly means varying from 36.1 °F (2 °C) in January to 57.7 °F (14 °C) in July at Buxton. Temperature inversions are common in the dales and cause severe frosts, while the plateau areas remain immune. Garrett (1956) has shown that these inversions last for about 12 hours in late spring and summer, but often persist throughout the day and night in winter.

Smaller temperature inversions also occur along the Durham Coast and this region has a different climate-type to the remainder of the east Durham plateau. This climatic difference seems to be of some significance, for the floristic composition of these stands indicate a closer relationship to the *Cirsio-Brometum* than to the *Sesleria*-dominated stands on inland Magnesian Limestone. On the other hand, several exceptions to this rule suggest that this pattern may be a phenomenon associated with past vegetation history.

Many of the stands of the *Helictotricho-Caricetum flaccae* seem to be located in wetter, more humid regions. The coastal sites in south Wales have a south and south-westerly exposition and those of the Durham coast face east and north. In the humid coombes and dales of the Mendips and Derbyshire the stands are mainly located on south- and east-facing slopes, and often towards the top of the slopes where insolation and evaporation are greater.

The range of soils is wider than in any of the Associations described. In Derbyshire, communities are found on soils of the first three stages of the climosequence from Rendzina to Brown Calcareous described by Bryan (1967), (Figure 3a, Chapter 2), and on soils affected by Triassic drift deposits, (Fig. 3b, Profile 8). In the Mendips the soils are rendziniform Brown Earths of the Lulsgate series described by Findlay (1965). The soils of the Lias in Glamorgan tend to be deeper Rendzinas due to the friable nature of the parent material and also to the intermixed blown sand which often reduces the surface pH to around 6.6. The coastal area of Co. Durham south of Castle Eden Dene was not mapped by McKee (1965), but the soils here appear to be closely related to his Mainsforth series which occur north of the dene mouth. The parent materials of these soils are calcareous glacial sands and gravels and profiles are seldom less than 70 cms. deep. The following profile was recorded south of Castle Eden Dene:-

Grid ref. NZ 457406 Altitude. 100 ft., (30 m) Aspect E 20°

Drainage Fair to free

0-24 cm A	Dark grey-brown clay loam with pebbles of various sizes; plastic, semi-granular, compact structure; pH 6.6

24-36 B Red-brown clay loam with many large size stones of sandstone, Magnesian Limestone, coal, etc.; few roots and humus between stones

36+ Similar to B and with a diffuse boundary; limestone boulders dominant

Characteristics of the Association

The name Helictotricho-Caricetum flaccae was chosen primarily to avoid confusion with the Thymo-Festucetum Williams & Varley (1967), and also for the co-dominance of Helictotrichon pratense and Carex flacca. This dominance is often shared with the Mesobromion and Brometalia character species Poterium sanguisorba and Helianthemum chamaecistus, and other constant species such as Festuca ovina, Thymus drucei, Leontodon hispidus and Lotus corniculatus. Other Alliance and Order character species found in the Association are Koeleria cristata, Scabiosa columbaria, Carlina vulgaris, Anthyllis vulneraria, Gentianella amarella and Viola hirta ssp. calcarea, and of low constancy Blackstonia perfoliata, Cirsium acaulon, Centaurea scabiosa, Filipendula vulgaris, Acinos arvensis, Thalictrum minus, Picris hieracioides, Bromus erectus and Hippocrepis comosa. The familiar mesophilous indicator species Briza media, Plantago lanceolata and Carex caryophyllea also show high constancy.

In many ways this Association represents a zone of communities poor in Order and Alliance character species around the northern and western limits of the Cirsio-Brometum. Cirsium acaulon occurs in some of the Mendip Aufnahmen and in two localities in Derbyshire, but it rarely forms an important constituent of the sward. Bromus erectus is infrequent and never attains co-dominance except in one Aufnahmen from Pantasaph in north Wales, where it is dominant over a small area on a quarry spoil-bank. The absence of Brachypodium pinnatum and Asperula cynanchica is also an important characteristic.

There are several regional differences in the Association, the most notable being the frequency of Galium sterneri in the lists from Derbyshire. This species is a fairly good differential species for the Sub-alliance Seslerio-Mesobromion when supported by other differentials such as Sesleria caerulea and Dryas octopetala. Other species in this group are Epipactis atrorubens and Rhytidium rugosum, and their presence in some of the Derbyshire localities forms a link with this Sub-alliance in northern England. The closely related southern species Galium pumilum was recorded in one stand in the Cheddar Gorge.

Other regional differences are seen in the presence of Blackstonia perfoliata, the partial replacement of Leontodon taraxacoides by L. hispidus in northern localities, and the increase in the abundance of Pimpinella saxifraga, Agrostis tenuis, Polygala vulgaris and several bryophytes in Derbyshire.

There are two poorly defined Sub-associations in the Association Helictotricho-Caricetum flaccae:-

Sub-ass. TYPICUM is a Sub-association which has the edaphic qualities of a typical thermophilous Mesobromion Association and is relatively free from the influence of grazing. Molinio-Arrhenatheretea are absent and the co-dominants are usually Helictotrichon pratense, Helianthemum chamaecistus, Carex flacca and Poterium sanguisorba.

Sub-ass. of Holcus lanatus and Trifolium repens represents a group of transition communities between Mesobromion and Molinio-Arrhenatheretea. It has already been mentioned that in Derbyshire and the Cheddar Gorge, the stands of the Association occur halfway up the dale sides away from the maximum temperature inversions. Here the slopes are less steep and there are considerable grazing pressures which are probably manifested by the frequency of the following Molinio-Arrhenatheretea and Arrhenatheretalia character species:-

Holcus lanatus, Trifolium repens, Trisetum flavescens, Arrhenatherum elatius, Festuca rubra, Cynosurus cristatus, Phleum bertolonii and Helictotrichon pubescens. The performance of these species appear to be encouraged by pasturing, continuous grazing and manuring. In several places Arrhenatherum or Helictotrichon pubescens assume dominance, and a transition to a community of the Arrhenatherion Alliance is suggested. In other areas the dominance of Cynosurus cristatus suggests a closer relationship to the Alliance Cynosurion.

This Sub-association and the typical Sub-association have a common variant of Brachypodium sylvaticum. In some places this grass apparently occupies the ecological niche of B. pinnatum, and its occasional coincidence with Teucrium scorodonia and Mercurialis perennis probably indicates the degeneration of scrub to grassland.

Zonation and Succession

One aspect of the zonation of this Association has already been mentioned with the reference to the transition to an Arrhenatheretalia community via the Sub-association of Holcus lanatus and Trifolium repens. In addition, a rapid lateral transition to heath due to the affects of leaching is quite common at the tops of the dales in Derbyshire and the coombes in Somerset. Various Associations of the Class Nardo-Callunetea are represented in these localities (Chapter 5), and ecological interpretations of these phenomena have been attempted by Balme (1953) and Grime (1963b).

Developing seral stages are relatively uncommon in close pröximity to the Association. In Derbyshire the grasslands are sometimes replaced by a Crataegus dominated Prunetalia community. In others a mosaic of Retrogressive Corylus Scrub forms a broad boundary between the grasslands and ash woodlands. These communities are closely related to the Alliance Geranion sanguinei of the Class Trifolio-Geranietea and are best developed in this region of the British Isles.

The Durham stands of the Helictotricho-Caricetum flaccae form part of a succession which proceeds to a low Salix nigricans-Salix repens scrub referable to the Alliance Salicion arenariae R.Tx.1952 of the Order Prunetalia. These communities are also quite restricted in the British Isles and probably only occur in a few more localities in eastern Scotland.

ASSOCIATION HELIANTHEMO-KOELERIETUM Table 7.

Synonymy:- Thymo-Festucetum (C) Williams & Varley 1967
Limestone grassland Gittins 1965a.

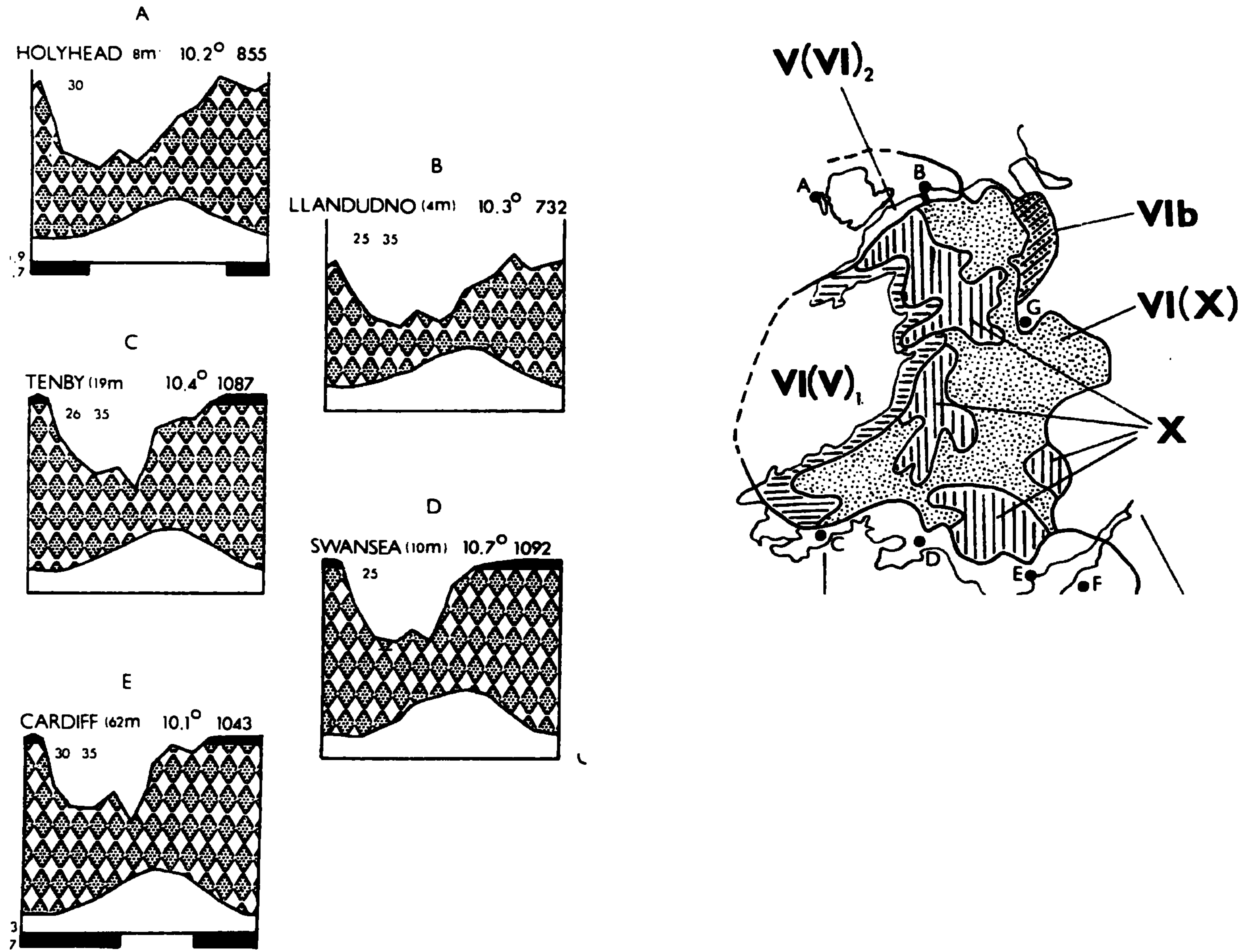
Habitat details

The Association Helianthemo-Koelerietum is found mainly in localities overlying Carboniferous Limestone in north and south Wales. In the latter region, the Association is confined to coastal grasslands of the Gower Peninsula in Glamorgan and St. Govan's Peninsula in Pembrokeshire. In north Wales, stands are described from Bwrdd Arthur in Anglesey, Great Orme's Head and the inland limestone hills at Pydew, Llysfaen, Cefn yr Ogof and in several localities from Prestatyn to the village of Cwm in the foothills of the Clwydian Range. Here the stands occur up to 850 feet (280 m.), at Cefn yr Ogof 650 feet (210 m.), while the remaining localities in both regions are found mainly between 250 and 350 feet (80-110 m.) on steep sea cliffs.

All the stands of the Association fall into the climate-type V(VI)2 of Walter & Lieth, characterised by rainfall minima and maxima in May and January or October respectively, and temperature maxima in July or August. The climate of both regions is distinctly maritime, the humidity being high and the minimum winter temperatures a few degrees higher and maximum summer temperatures a few degrees lower than those of inland regions of England and Wales, (cf. Llandudno and Welshpool, Fig. 16). The mean annual temperature ranges between 10.1 °C at Cardiff and 10.7 °C at Swansea in south Wales, and remains around the 10.2 °C figure in north Wales. The lowest mean annual

FIGURE 16. Climate-types of the coastal region of north and south Wales.

(Diagrams modified from Walter and Lieth, 1967).


A
HOLYHEAD 8m 10.2° 855
30
.9
.7
B
LLANDUDNO (4m) 10.3° 732
25 35
C
TENBY (19m 10.4° 1087
26 35
D
SWANSEA (10m) 10.7° 1092
25
E
CARDIFF (62m 10.1° 1043
30 35
3
7
V(VI)2
VIb
VI(X)
VI(V)1
X
A
B
C
D
E
F
G

rainfall of the climate-type is recorded on the stretch of coast from the mouth of the River Clwyd to Llandudno (732 mm). West towards Anglesey and inland across the Denbigh uplands, the rainfall increases to an average mean of 850 mm. The mean annual rainfall throughout the south Wales coastal fringe is much higher than similar localities in north Wales and figures of 1043 mm at Cardiff to 1092 mm at Swansea, give some idea of the range. All details of frosts are not recorded in the diagrams in Figure 15, but the periods recorded at Holyhead and Cardiff are quite prolonged and severe. Ball (1960) records the average shortest frost-free period for Llandudno as 205 days, a figure which compares favourably with that of Cardiff.

The topographical limitations of the Association are very stringent. In most regions the stands are restricted to small areas of rough grassland around rocky outcrops. In the Gower and Pembrokeshire the Association is found along a narrow strip of grassland between the south- and west-facing cliffs and enclosed land. Other localities are found on the ungrazed, steep cliff ledges. In north Wales the stands are more extensive and are often fairly heavily grazed by sheep, e.g. Great Orme's Head. In inland areas such as Cefn yr Ogof and the steep slopes of Moel Hiraddog behind Dyserth, the stands are the most extensive of the Association and are heavily grazed. As before, their exposition is mainly south and west.

The soils in the regions where the Association occurs are comparatively well known. The limestone regions of both north and south Wales are characterised by the presence of Red-brown Calcareous soils of the Gower series, first described by Robinson *et al.* (1930), and later by Roberts (1958) and Ball (1960). These are well-drained soils developed *in situ* over the parent limestone which has a dominant influence throughout the profile. There is little horizon differentiation and the profiles are seldom more than 25 cms. deep. The following profile was recorded near Llysfaen, north Wales:-

Grid Ref. SH 896766 Altitude. 500 ft. (160 m.) Aspect. SW 20°

Drainage. Good to excessive.

0-15 cm A	Dark red-brown sandy loam, with many limestone fragments; moist with much organic matter; diffuse boundary; pH 7.2.
15-20 (B) C	Dark brown sandy loam with large detached pieces of limestone. Bedded limestone rock.

This pattern is reflected in most of the profiles of the Gower series, (cf. Roberts 1958, Ball 1960 and Crampton 1966). The origin of these soils has been discussed by Crampton (1966). There is evidence of two phases of glaciation and an interglacial phase in south Wales, and soils normally associated with a Mediterranean climate developed locally on the outcrops of Carboniferous Limestone in the Vale of Glamorgan. These soils have been likened to *terra fusca*, defined by Kubiena (1953) as a soil characteristic of temperate regions. Since these soils are considered to be interglacial, a similar conclusion on the origin of some of the components of the associated vegetation is suggested.

In north Wales, Rendzinas occur in local patches and are recognisable by their grey-black colouration and shallow nature. They are classified in the Nant series (Ball 1960) and the Marian series in Anglesey (Roberts 1958). On flat or undulating areas over limestone Brown Earths of high base status are developed, but these are rarely coincidental with stands of the *Helianthemo-Koelerietum*. In the extensive limestone uplands of Halkyn Mountain these soils are greatly affected by Triassic drift and acidiphilous heath is quite common.

Characteristics of the Association

The name *Helianthemo-Koelerietum* was chosen for the presence of the two *Helianthemum* species, *H. canum* and *H. chamaecistus* and the abundance of *Koeleria cristata*. Other *Mesobromion* and *Brometalia* character species showing constancies of IV or V are Poterium sanguisorba, Anthyllis vulneraria and Carlina vulgaris, whilst companion species of high constancy are Festuca ovina, Thymus drucei, Euphrasia nemorosa, Lotus corniculatus, Carex flacca, C. caryophyllea, Plantago lanceolata and Hieracium pilosella. The relative frequency of Cerastium atrovirens and Aira caryophyllea indicates the maritime nature of the Association and also reflects the typical open community structure.

Three Sub-associations are recognised:-

Sub-ass. TYPICUM - a group of Aufnahmen poor in differential species, but with a similar average species number to other Sub-associations; described from Bwrdd Arthur in Anglesey and in some localities on Great Orme's Head. The grasslands studied by Gittins (1965) using ordination and association analysis techniques fall mainly into this group.

Sub-ass. Helictotrichon pratense is characterised by the prominent part that Helictotrichon pratense plays in the composition of the sward and the occurrence of two other differential species, Gentianella amarella and Potentilla tabernaemontani. Helianthemum canum is most frequent in this Sub-association. A distinct variant of Sieglingia decumbens and Filipendula vulgaris occurs mainly on the damper inland limestone hills from Llysfaen to Dyserth.

Veronica spicata occurs in several of the Aufnahmen from this variant. *Aira caryophyllea* and other therophytes are rarer here than in other groups, and an increase in the abundance of *Agrostis tenuis*, *Ctenidium molluscum* and *Pseudoscleropodium purum* suggests a more humid microclimate.

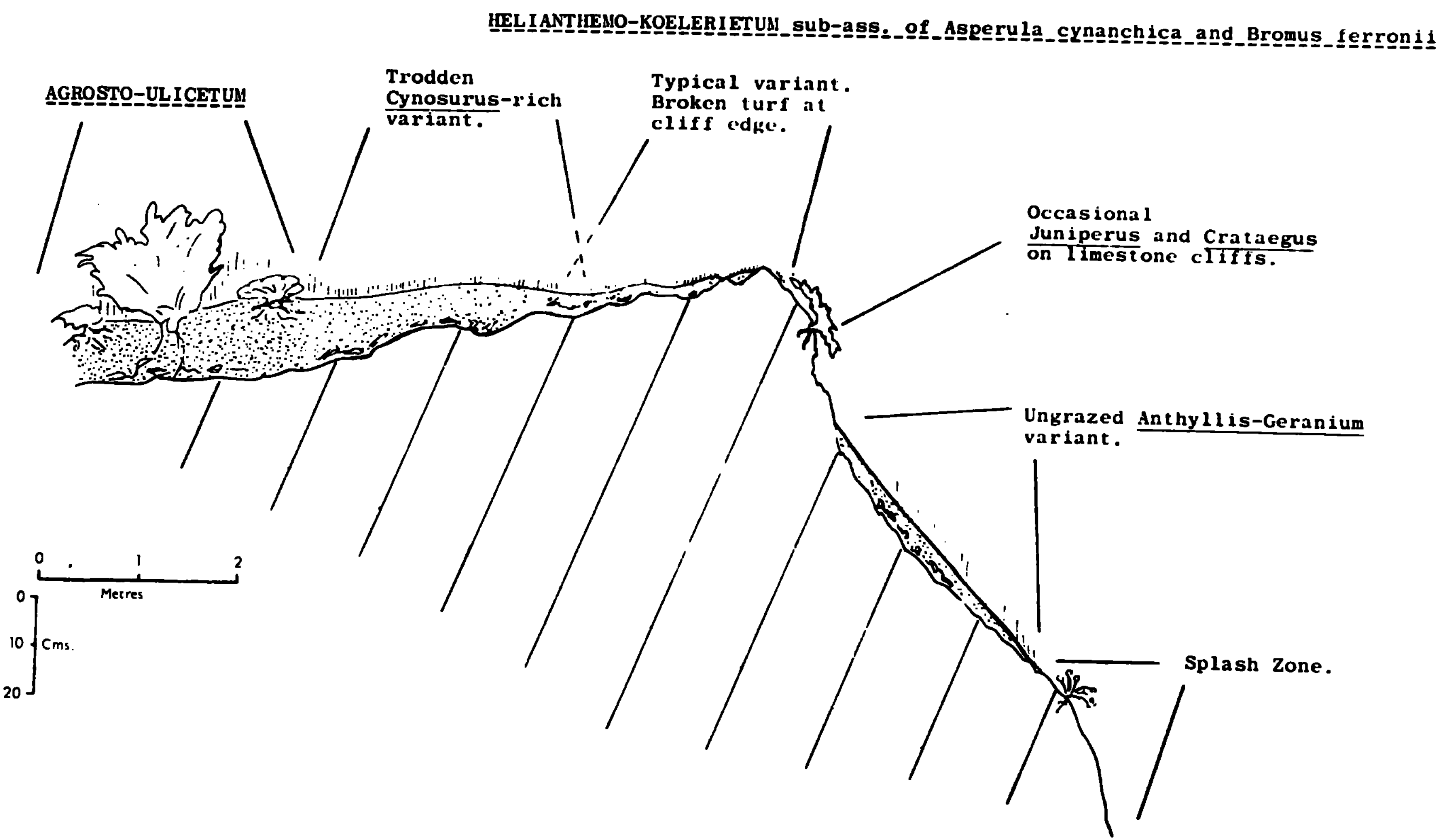
Sub-ass. of Asperula cynanchica and Bromus ferronii has numerous differential species but is characterised especially by *Asperula* and the small therophyte *Bromus ferronii*. In addition, *Trifolium scabrum*, *Euphorbia portlandica*, *Scilla verna* and *Centaurium minus* are differentials for this Sub-association. Other species of high constancy here and not in other Sub-associations are *Cerastium atrovirens*, *Ranunculus bulbosus*, *Festuca rubra*, *Anthoxanthum odoratum*, *Trifolium dubium*, *Leontodon hispidus* and others. This Sub-association is fairly heavily grazed and indication of this is seen in the abundance of *Cynosurus cristatus*, *Dactylis glomerata* and *Poa pratensis*. Regional differences between north and south Wales are manifested by the low frequency or absence of such species as *Pimpinella saxifraga*, *Agrostis tenuis* and *Campanula rotundifolia* in this Sub-association. The Sub-association is widely distributed along the south coast of the Gower Peninsula from Pwlldu Head to Shire Combe, along the cliffs of Port Eynon Bay and from Overton Cliff to Rhossilli. A single locality was described at Gilman Point, near Pendine, Carmarthen, and Aufnahmen were collected from several localities in Pembrokeshire, from Stackpole Quay to Stackpole Head, St. Govan's Head and Elegug Stacks.

Three variants of this Sub-association are recognisable and their pattern of occurrence is illustrated in the cliff section at Fox Hole, Gower, in Figure 17. The typical variant is characteristically a small zone some one or two metres broad at the cliff edge. In this open community, Asperula cynanchica, Helianthemum canum, Aira caryophyllea, Cerastium atrovirens and Bromus ferronii have their maximum expression. A second variant, where Cynosurus cristatus, Festuca rubra and Agrostis tenuis play a more important part, and where Asperula and Helianthemum canum are reduced in vitality is characteristic of the trampled areas on deeper soils. A third ungrazed variant on the steeper slopes is recognisable by the abundance of Anthyllis vulneraria, and the increase of Centaurea scabiosa and Geranium sanguineum. This variant is more distinct from the other two and was seen only in the Gower Peninsula.

Zonation and Succession

The three variants of the Sub-association of Asperula and Bromus form the main pattern of zonation. One stage further gives rise to a Ulex gallii-Erica cinerea heath of the Agrosto-Ulicetum Association. Similar communities occur

FIGURE 17. Zonation of the communities of the Association Helianthemo-Koelerietum at Fox Hole, Gower, South Wales.


HELIANTHEMO-KOELERIETUM sub-ass. of Asperula cynanchica and Bromus ferronii
AGROSTO-ULICETUM
Trodden Cynosurus-rich variant.
Typical variant. Broken turf at cliff edge.
Occasional Juniperus and Crataegus on limestone cliffs.
Ungrazed Anthyllis-Geranium variant.
Splash Zone.
0 1 2
Metres
0 10 20
Cms.

on Great Orme's Head on deeper, more leached soils. In north Wales, Cotoneaster microphylla is a frequent bird-sown introduction and the grasslands often give way to patches of scrub where this species plays a prominent role.

In the Gower and Pembrokeshire the salt-spray splash zone comes into contact with the Helianthemo-Koelerietum. Communities from this zone are characterised by the dominance of Festuca rubra and/or F. tenuifolia with other maritime species such as Armeria maritima, Plantago coronopus and Carex distans indicating the Alliance Armerion maritimae of the Class Juncetea maritimi Br.-Bl.1931.

Two unusual zonal communities on limestone were recorded. One on Stackpole Head, Pembroke, was a seagull roosting colony, where the layer of guano over the mineral soil enhanced the growth of nitrophilous weed species such as Atriplex spp. and Hyoscyamus niger. The second community was on a thermophilous rocky grassland at Llysafaen in north Wales and was dominated by Sedum album and many therophytes such as Arenaria serpyllifolia, Veronica arvensis and Poa annua.

ASSOCIATION CARICETUM MONTANAE. Table 8.

Synonymy:- Limestone grassland, group B Ivimey-Cook 1957.

Habitat details

The Association is restricted to two regions of

Carboniferous Limestone in south Wales. The more extensive stands are in Glamorgan along the valley known as Pant St. Brides between Ewenny and Ogmore Downs. A second locality was discovered in the valley of the River Taf north-west of Merthyr Tydfil, in Brecknockshire. In the former localities, the Association is found between 100 and 200 feet (33-66 m.) on fairly steep west- and east-facing slopes. In Brecknockshire the communities are found on extremely steep south-west facing, unstable scree slopes at about 1000 feet (320 m.).

The soils in this latter locality are Protorendzinas developed directly over scree and have a maximum depth of 10 cms. Drainage is excessive and the pH is 7.6. In Pant St. Brides the communities occur on Rendzinas which contain quite a high proportion of blown sand and have a pH varying between 7.0 and 7.4 (Ivimey-Cook 1957). These soils are closely related to the terra fusca described by Crampton (1966), but their relationships are obscured by the blown sand.

The region of the Ewenny and Ogmore Downs fall within the same climate-type as described for the previous Association - $V(VI)_2$, (Figure 16), but the Brecknock locality is classified in the montane type X by Walter and Lieth. This type is characterised by mean annual minimum temperatures of about 32°F (0°C) and mean summer maxima of 53°F (11.6°C) and a mean annual rainfall well above 1200 mm.

Characteristics of the Association

The Association is characterised by the dominance of Carex montana with Poterium sanguisorba, Helianthemum chamaecistus and Festuca ovina. The familiar companion species of Mesobromion communities, Thymus drucei, Hieracium pilosella, Lotus corniculatus and Carex flacca, are also constant. The stands from the two different regions show marked differences in structure and floristic composition, and two Sub-associations have been created:-

Sub-ass. TYPICUM is characterised by the high constancy of the Alliance and Order character species Cirsium acaulon, Asperula cynanchica, Koeleria cristata, Viola hirta ssp. calcarea and Polygala calcarea. Companion species of high constancy which act as differential species for the Sub-association are Agrostis tenuis, Sieglingia decumbens, Anthoxanthum odoratum, Carex pulicaris, Tortella tortuosa and Cladonia rangiformis. This Sub-association is found only in Pant St. Brides, Glamorgan.

Sub-ass. of Galium sterneri and Melica uniflora. This provisional category has Galium sterneri, Melica uniflora and Valerianella locusta as differential species. Scabiosa columbaria, Arrhenatherum elatius and Myosotis arvensis also show a preference for this Sub-association.

The Association Caricetum montanae is peculiar to these regions of south Wales and appears to be a retrogressive step from a scrubby woodland community. Support to this theory is lent by the presence of the predominantly woodland species Brachypodium sylvaticum and Melica uniflora. Moreover, in most of its other localities in Britain, Carex montana is found in an open Corylus-Crataegus scrub similar to the following aufnahme from Magnesian Limestone cliffs at Markland Grips, Derbyshire:-

3.2	Corylus avellana	(+)	Taxus baccata
+	Sorbus aucuparia	+	Taxus seedlings
2.1	Crataegus monogyna	+	Fraxinus excelsior (seedling)
2.3	Carex montana	+.2	Melica uniflora
3.3.	Brachypodium sylvaticum	+	Urtica dioica
1.2	Mercurialis perennis	+	Sanicula europaea
1.1	Poterium sanguisorba	+.2	Glechoma hederacea
1.2	Clinopodium vulgare	+	Primula veris
+	Carex flacca	+	Helictotrichon pubescens
+	Hypericum pulchrum	+	Centaurea nigra
+	Campanula rotundifolia	+	Cirsium palustre
1.2	Pseudoscleropodium purum	+	Isothecium pyosuroides
1.2	Mnium hornum	+.2	Eurynchium praelongum

Armitage (1914) lists Carex montana as a component of the herb layer in deep shade areas of a rich oak-beech Association ("Querco-fagetum") on the limestones of the Wye Gorge at Symonds Yat, where the species composition is similar to that of the above list.

Zonation and Succession

The Sub-ass. *typicum* passes rapidly to the *Agrosto-Ulicetum* Association of the Class *Nardo-Callunetea*, a transition which is associated with the change from Rendzinas to Incipient Podsols. At the tops of the slopes where the effects of leaching are more pronounced, Ulex gallii, Erica cinerea, Agrostis setacea and Molinia caerulea form a marked zone of heathland. The interface between the *Caricetum montanae* and the *Agrosto-Ulicetum* is frequently a mosaic area with a floristic composition characteristic of both Associations. The following Im^2 quadrat illustrates the composition of this mosaic transition zone:-

Agrosto-Ulicetum species		*Caricetum montanae* species	
2.2	Ulex gallii	2.2	Carex montana
1.2	Molinia caerulea	1.1	Poterium sanguisorba
1.2	Erica tetralix	1.1	Viola hirta ssp. calcarea
1.2	E. cinerea	+.2	Helianthemum chamaecistus
+.2	Calluna vulgaris	+	Asperula cynanchica
2.3	Agrostis canina	+	Carex pulicaris
1.2	A. setacea		

Companion species

3.3	Sieglingia decumbens	+	Campanula rotundifolia
2.2	Festuca rubra	+	Agrostis tenuis
2.1	Pteridium aquilinum	+	Prunella vulgaris
1.2	Potentilla erecta	+	Betonica officinalis
1.1	Viola riviniana	+	Cirsium palustre
1.2	Anthoxanthum odoratum	+	Taraxacum sect./vulgaria
1.1	Brachypodium sylvaticum	+	Plantago lanceolata
1.1	Hypericum pulchrum	+	Leontodon hispidus
2.3	Rhytidiadelphus triquetrus	+	Cephalozia bicuspidata
+.2	Pseudoscleropodium purum	+	Pohlia nutans
+	Pleurozium schreberi	+	Lophocolea bidentata

The above Aufnahme is equivalent to the "Group Z, Limestone Heath" delimited by Ivimey-Cook (1957) using positive interspecific correlations to describe the whole grassland/heath complex. An investigation into the occurrence of calcicole species such as Asperula and Helianthemum in calcifuge habitats by the above author led to the conclusion that the different rooting depths of calcicoles and calcifuges was a major influential factor. For example, calcifuges such as Calluna rooted in the top, humus-rich soil layers, whilst most of the calcicole rooting systems extended down to the less acid B horizon.

The Sub-association of Galium and Melica is closely related to an open limestone scree Association dominated by patches of Thelypteris robertiana, Brachypodium sylvaticum and Melica uniflora comparable to the continental Association Dryopteridetum robertianae (Kuhn)Tüxen 1937 of the Class Thlaspeetea rotundifolii Br.-Bl.1947.

ASSOCIATION ANTENNARIETUM HIBERNICAE Br.-Bl.&R.Tx.1952 Table 9.

This Association excludes the Sub-ass. of Sesleria caerulea Br.-Bl.&Tx.1952. No synonyms are recorded. The Antennaria dioica-Hieracium pilosella Nodum of Proctor & Ivimey-Cook (1966) is not the same community.

Habitat details

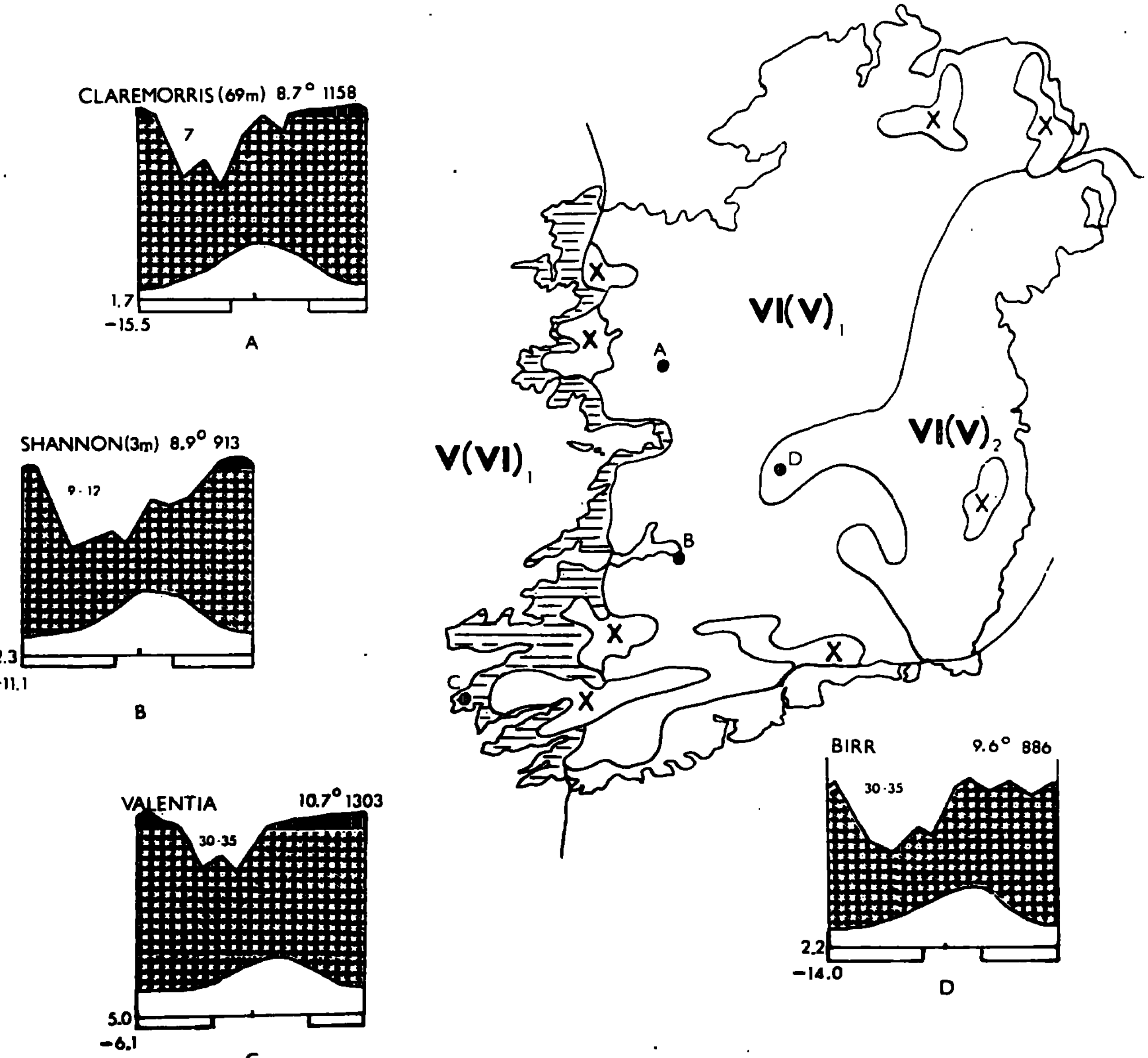
The communities of the Association described by Braun-Blanquet and Tüxen (1952), were mainly from calcareous eskers and moraines in Co. Offaly and Laoighise. These substrates really fall beyond the limits of this thesis, and though poorly represented here, the Association is probably much more widespread in central Ireland. However, several calcareous moraines were studied in the Ballyeighter Loughs valley in the Burren district of Co. Clare in an attempt to determine the status of the Association. One other locality for Antennarietum hibernicae was described on Carboniferous Limestone at Fenit Point, near Tralee in Co. Kerry.

The Association is essentially lowland and is found between the 100 and 250 feet contours (33-80 m.). In the areas around the Ballyeighter Loughs, the communities are found on the low mineral soil "islands" just above the damper areas of valley alluvium. The soils in these areas are moderately deep Brown Earths with a humus-rich A horizon and some gleying in the drift affected B horizon, probably due to a fluctuating water table. The localities at Fenit Point are over leached rendziniform Brown Earths of pH 6.8, and with varying influence of blown sand.

There are few detailed records of climate for the region of western Ireland. Proctor & Ivimey-Cook (1966)

FIGURE 18. Climate-types of Ireland.

(Diagrams modified from Walter and Lieth, 1967).


CLAREMORRIS (69m) 8.7° 1158
7
1.7
−15.5
A
SHANNON(3m) 8.9° 913
9 · 12
2.3
−11.1
B
VALENTIA 10.7° 1303
30·35
5.0
−6.1
C
BIRR 9.6° 886
30·35
2.2
−14.0
D
VI(V)1
VI(V)2
V(VI)1
A
B
C
D
X

quote the observations of Miss E. M. Shaw. The general impression obtained from her results is that the lowlands to the east of the Burren have a markedly lower mean annual rainfall than the upland areas to the west, e.g. Shannon 929 mm, Gort 1128 mm, Corofin 1300 mm, compared to the figures of 1650 mm for Ballyvaughan. The highest mean temperature for the hottest month (August) at Shannon is recorded as 60.25 °F (15.7 °C) and the coldest mean temperature for January 41.0 °F (5.0 °C). All these localities and those in Co. Offaly, but not the ones at Fenit are sheltered from the Atlantic winds and have a notably different climate-type to the western coast. Figure 18 summarises the climatic differences and a comparison of the diagram for Valentia with that of Birr clearly illustrates the drier climate; e.g. rainfall figures of over 1200 mm with a mean monthly maximum in December, compared to figures of below 960 mm with August maxima. There are also longer periods of frost at Birr and mean winter temperatures are some 2-3 °C lower here than at Valentia.

Characteristics of the Association

This Association is equivalent to the Sub-association polygaletosum dubiae Br.-Bl.&Tx.1952. Their Sub-ass. of Sesleria caerulea described from Portumna in Co. Galway is included with their Association Asperulo-Dryadetum in the

Asperulo-Seslerietum comb. nov. The composite Table 9 includes a constancy table for the 7 Aufnahmen of the Sub-ass. polygaletosum dubiae from Braun-Blanquet & Tüxen (1952), 5 of the author's own Aufnahmen and two lists from Ivimey-Cook & Proctor (1966), (Table XXVIII, page 288, lists 498 and 504.)

The Association Antennarietum hibernicae is characterised by the constancy and abundance of the species of unknown status Antennaria hibernica (x), the frequency of Polygala oxyptera (dubia) and by the replacement in many stands of Festuca ovina by F. rubra. Antennaria is found in most of the Burren grassland Associations, but usually in combination with Dryas octopetala and Sesleria caerulea. These two species are absent in this Association and the frequency of Mesobromion character species such as Koeleria cristata, Carlina vulgaris, Gentianella amarella and Anthyllis vulneraria is reduced. Companion species of high constancy are Briza media, Carex flacca, C. caryophyllea, Plantago lanceolata, Succisa pratensis, Galium verum, Lotus corniculatus, Thymus drucei and Pseudoscleropodium purum.

From the Table it can be seen that Polygala oxyptera occurs frequently throughout the lists but is replaced by

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(x) Until sound taxonomic evidence necessitates the use of the specific name Antennaria hibernica, plants identified according to the characters listed by Braun-Blanquet (1950) are listed as A. dioica.

P. vulgaris s.s. in Ivimey-Cook & Proctor's lists and the author's lists from Fenit. The status of a *Sub-ass. of Polygala dubia* is placed in doubt by this fact, but the differences between the lists of Braun-Blanquet & Tüxen and those from western Ireland indicate two distinct Sub-associations:-

Sub-ass. TYPICUM to replace *s.-a. polygaletosum dubiae* comprises the Aufnahmen of Braun-Blanquet & Tüxen (1952, Table 39, p.320) and is differentiated by the constancy of *Pimpinella saxifraga*, *Centaurea nigra* and *Anacamptis pyramidalis*.

Sub-ass. ASPERULETOSUM is described from western Ireland in a fringe zone around the Burren limestone, and occurs mainly on dunes and calcareous drift. This Sub-association is differentiated by the presence of *Asperula cynanchica*, *Gentiana verna*, *Bellis perennis*, *Plantago maritima* and several bryophytes reflecting the damper climate, e.g. *Scapania aspera*, *Thuidium delicatulum* and *Hylocomium splendens*. In several localities there appears to be a wetter variant of this Sub-association where *Breutelia chrysocoma* and *Rhytidiadelphus triquetrus* assume co-dominance.

Zonation and Succession

The main trend of succession is the one noted by Braun-Blanquet & Tüxen (1952) from the open, therophyte-rich

Aira praecox-Sedum anglicum Association to Antennarietum typicum and thence to the Centaureo-Cynosuretum of the Order Arrhenatheretalia. The development towards this latter Association seems to depend mainly on the different grazing pressures these grasslands are subjected to. The next recognisable step from the Antennarietum is the Centaureo-Cynosuretum sub-ass. of Thymus drucei Br.-Bl.&Tx.1952, or more correctly, Centaureo-Cynosuretum sub-ass. of Galium verum, subvar. of Thymus drucei O'Sullivan 1965.

In the Ballyeighter Loughs region the stands of Antennarietum asperuletosum often give way to a zone of damper grassland similar to the Schoenus nigricans-Cirsium dissectum Ass. Br.-Bl.&Tx.1952.

ASSOCIATION CAMPTOTHECIO-ASPERULETUM CYNANCHICAE Br.-Bl.&Tx.1952. Table 10. (Excluding Sub-ass. of Sesleria caerulea Br.-Bl.&Tx.1952)

Synonymy:- Galium verum-Asperula cynanchica Nodum Ivimey-Cook & Proctor 1966.

Habitat details

Braun-Blanquet & Tüxen (1952) described the Camptothecio-Asperuletum from the dunes at Ballyvaughan in the Burren, Co. Clare and at Roundstone, Co. Galway. These areas were visited by the author at an early stage of his research in order to obtain some idea of the techniques of the Z-M system of phytosociology and its interpretation of vegetation types. Thus, most of the lists in Table 10 are from these two localities. A more detailed survey of the Burren by Ivimey-Cook & Proctor (1966) has shown that communities of this Association are widespread on the Fanore dunes and also at Lehinch.

Similar communities have been noted in south Wales on the dune systems of Stackpole Warren and Brownslade Burrows in Pembroke and Pennard Burrows in the Gower. It seems probable that there may be other localities at Kenfig Burrows, near Porthcawl, Glamorgan, and at Laugharne Burrows, Carmarthen, but no details are available.

The Association often occupies large areas of the stable, landward side of dune systems and is frequently heavily grazed. All the areas noted fall within Walter & Lieth's climate-type $V(VI)_2$ described previously (Figure 18). The high rainfall in many of these regions, especially the west of Ireland (1650 mm at Ballyvaughan), appears to favour humus accumulation in the top 5 cms. of the profile, so that shallow-rooted herbs such as Asperula and Trifolium repens and several bryophytes can compete favourably with the deeper-rooted plants of more open dunes.

Characteristics of the Association

Only in western Ireland and south Wales does Asperula cynanchica form an important constituent of compact dune swards and because of this fact, it is reasonable to assume that the status of the Association is valid. However, a more detailed investigation of dune grasslands throughout Britain is desirable to determine whether this grassland type is merely a minor variant in a complex Association-group. The relationships with the Alliance Mesobromion are fairly clear, i.e. via the presence of Asperula, Koeleria cristata, Carlina vulgaris, Anthyllis vulneraria, Anacamptis pyramidalis and Gentianella amarella. The dominants are frequently Festuca rubra, Camptothecium lutescens and Lotus corniculatus, although the former is sometimes replaced by F. ovina. Ranunculus bulbosus, Agrostis stolonifera and Entodon concinnus serve to differentiate the Association from other Mesobromion Associations, and the presence of the rare Mediterranean orchid, Neotinea intacta, is quite characteristic of this group. The recent discovery of this orchid on dunes in the Isle of Man (Allen 1968), probably indicates another locality for a community referable to the Camptothecio-Asperuletum.

As suggested by Ivimey-Cook & Proctor (1966) the Sub-ass. of Sesleria caerulea Br.-Bl.&Tx.1952 is omitted and included in the Asperulo-Seslerietum comb. nov. With this omission, two distinct Sub-associations are recognised:-

Sub-ass. of Carex arenaria Br.-Bl. & Tx.1952 was described by these authors from both localities in western Ireland, and Table 10a contains two of their Aufnahmen and 4 of the author's. This Sub-association is extremely heavily grazed and this factor seems to indicate that less humus accumulation occurs and species like Carex arenaria, Tortula ruraliformis and Sedum acre, are found in a more or less closed grassland.

The same pattern can be seen in south Wales, but here the maintenance of open conditions by grazing is reflected by the presence Vulpia bromoides and Trifolium scabrum.

Sub-ass. of Rhytitidelphus squarrosus Br.-Bl.&Tx.1952 was described from older dunes with a large amount of humus in the top 5 cms. of the profile and where the influence of the underlying drift is greater. This Sub-association was not seen in south Wales. The Galium verum-Asperula cynanchica Nodum Iv.-Ck.&Proct.1966 falls into this Sub-association and is included as a constancy table in Table 10.

Zonation and Succession

The main zonation of the Association is that illustrated by Braun-Blanquet & Tüxen (p.327) on the dunes at Ballyvaughan. The Sub-ass. of Carex arenaria is located on the crests of the dunes over the maximum depth of sand and where erosion is greatest. Downslope, on the areas of shallower sand over drift this community is replaced by the Sub-ass. of Rhytidiadelphus squarrosus. In the dry hollows between dunes where there are only 2-3 cms. of sand over drift, Braun-Blanquet & Tüxen recorded the Sub-ass. of Sesleria. In addition to the floristic composition of this latter Sub-association, the edaphic conditions recommend its exclusion from the Camptothecio-Asperuletum.

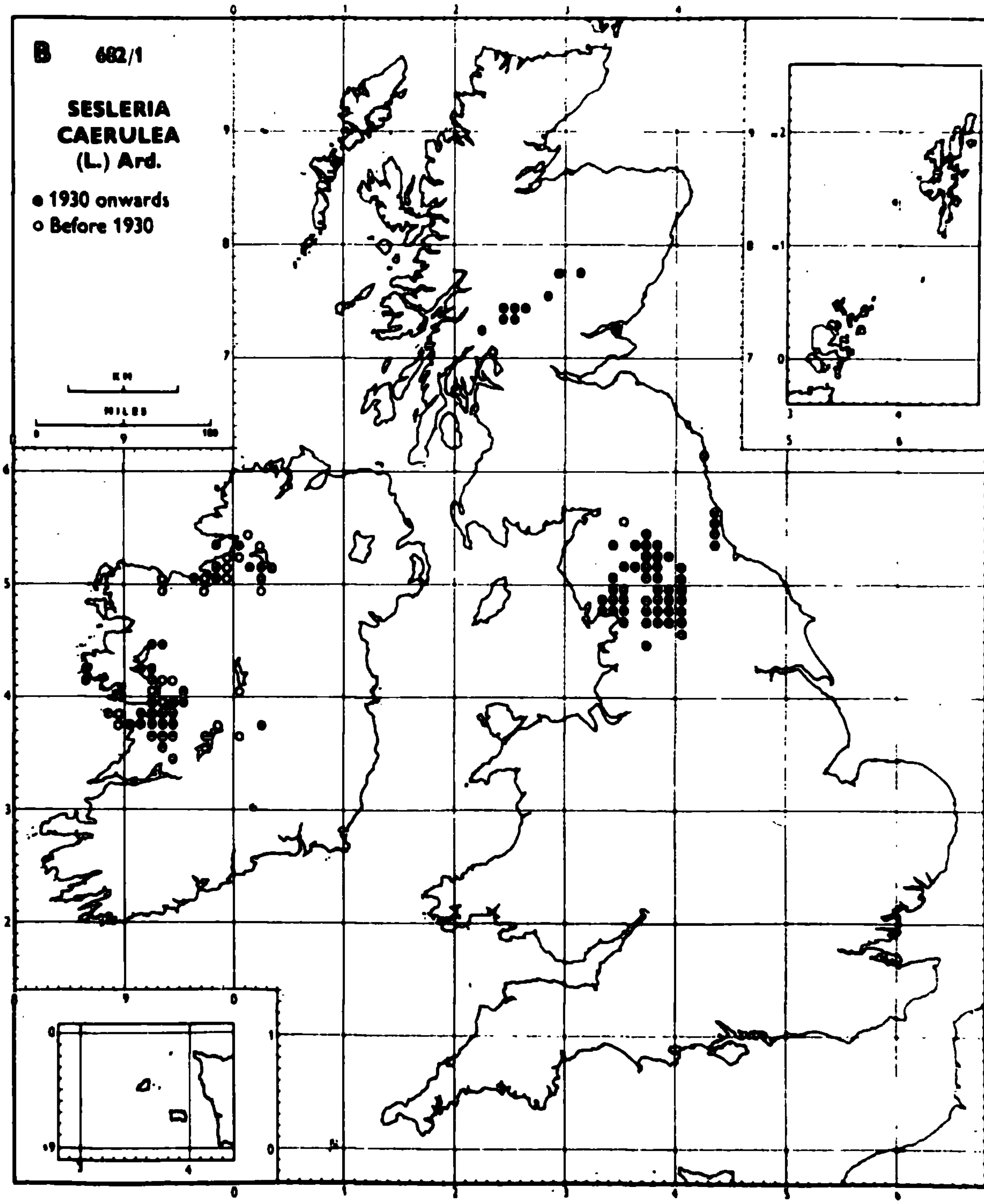
On the seaward side of the dunes in both western Ireland the south Wales, this Association is replaced by the Viola curtisii-Syntrichia ruralis Ass.Br.-Bl.&Tx.1952 (Ditrichum flexicaule-Thymus drucei Nodum Iv.-Ck.&Proct. 1960) of the Alliance Koelerion albescentis.

SUB-ALLIANCE SESLERIO-MESOBROMION Oberd.1957.

As it has been previously stated, communities referable to this Sub-alliance occur in a marked zone across northern England and in western Ireland, and form a floristic link between the Classes Festuco-Brometea and Elyno-Seslerietea. The distribution pattern is similar to that of Sesleria caerulea shown in Figure 19, (from Perring & Walters 1962), with the exception of the Scottish localities. The Associations of this group are characterised by the dominance of this gregarious grass and the occurrence of

FIGURE 19. The distribution of *Sesleria caerulea* in the British Isles.

(Reproduced by permission of Dr. F. H. Perring for the B.S.B.I.).


B 682/1
SESLERIA
CAERULEA
(L.) Ard.
● 1930 onwards
○ Before 1930
KM
MILES
0
50
100

several of the more widespread Mesobromion character species, such as Poterium sanguisorba, Scabiosa columbaria, Helianthemum chamaecistus, Helictotrichon pratense, Koeleria cristata and Carlina vulgaris. In addition there are several differential species, some of which are also Elyno-Seslerietea Class character species in central Europe (K-ES):-

Galium sterneri Ehrend.	(K-ES) Euphrasia salisburgensis Funck.
Polygala amara L.	Gentiana verna L.
Viola rupestris Schmidt.	Epipactis atrorubens (Hoffm.) Schult.
(K-ES) Dryas octopetala L.	Rhytidium rugosum (Hedw.) Kindb.

Cornicularia aculeata (Schreb.) Ach.

Primula farinosa and Carex capillaris are also differential species but are less restricted than the above group. They indicate the damper nature of the grasslands of this Sub-alliance and their close relationship to calcareous flushes.

Three major Associations are described in the Sub-alliance:-

Seslerio-Helictotrichetum

Seslerio-Caricetum pulicariae

Asperulo-Seslerietum

ASSOCIATION SESLERIO-HELICTOTRICHETUM Table 11.

Synonymy. Magnesian Limestone Rough Pasture Heslop-Harrison & Richardson 1953.

Habitat details

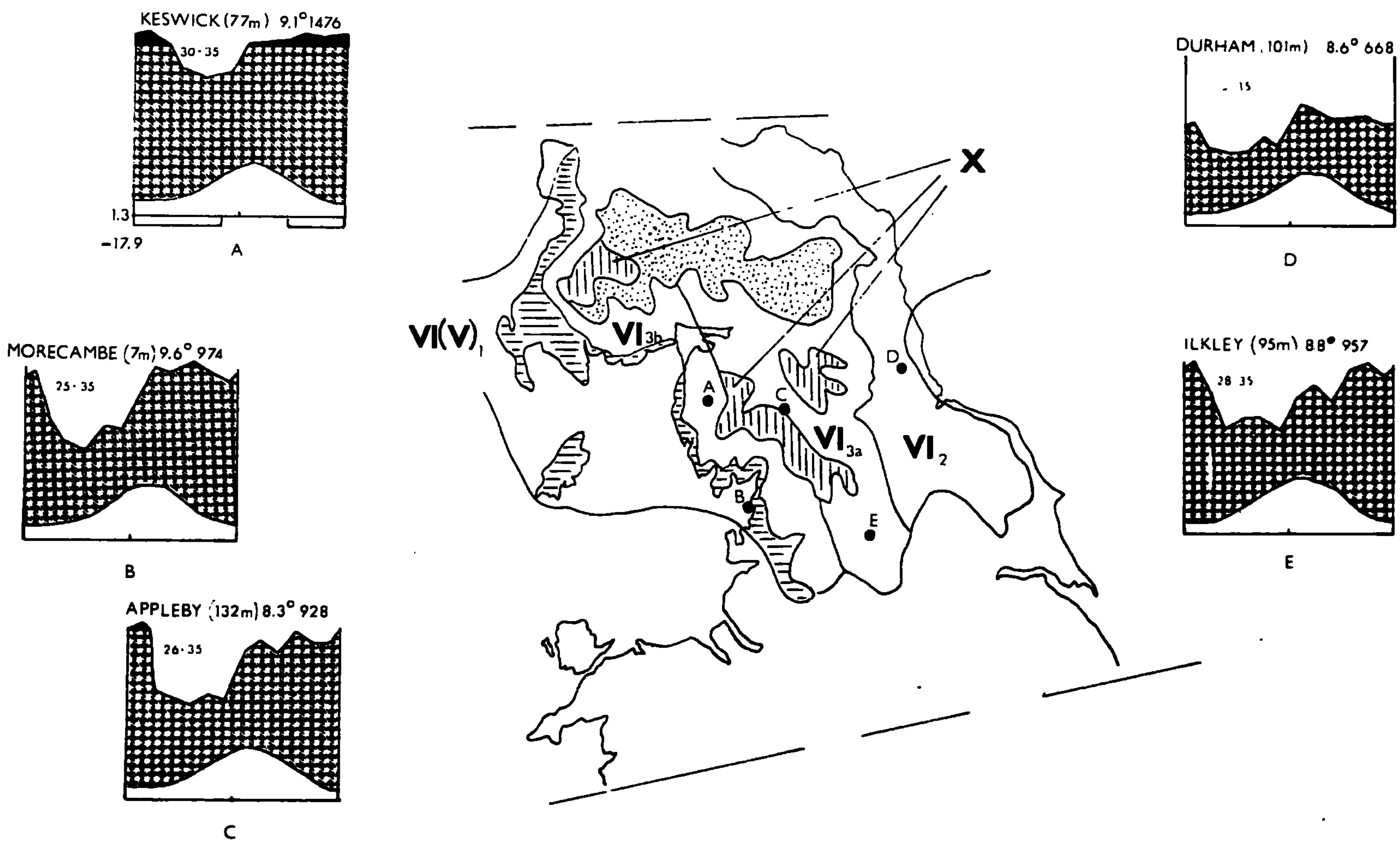
This Association is peculiar to the Magnesian Limestone escarpment of eastern Durham and a few localities in the plateau region further to the east. Representative stands have been recorded from Boldon and Tunstall Hills in the north to Bishop Middleham and Cornforth in the south at altitudes varying between 200 and 500 feet (60-160 m.).

On a broad regional basis the east Durham plateau represents an extension of the drier eastern climate of south England, e.g. Figure 15. type VI_{ib}. However, Walter & Lieth (1967) subdivide type IV so that the region in question is separated under IV_2. The reasons for this become clear when the climate diagrams for Durham (Fig. 20) and Cranwell (Fig. 15) are compared. In relation to the Durham city region and the plateau region, the west-facing escarpment has a considerably higher rainfall and cooler temperatures. At elevations of 500-600 feet (160-190 m.), the average annual rainfall is over 760 mm as opposed to 635-700 mm on the dip slopes. There is a longer snow-lie period and the most striking temperature differences are seen in the average minimum winter temperatures: 27.5 °F (-2.5 °C) compared to 32.5 °F (0.3 °C), (Durham University Observatory Records).

Over most of the eastern plateau the soils are never

FIGURE 20. Climate-types of the Seslerio-Mesobromion zone of northern England.

(Diagrams modified from Walter and Lieth, 1967).



KESWICK (77m) 9.1° 1476
30·35
1.3
−17.9
A
MORECAMBE (7m) 9.6° 974
25·35
B
APPLEBY (132m) 8.3° 928
26·35
C
DURHAM (101m) 8.6° 668
15
D
ILKLEY (95m) 8.8° 957
28 35
E
X
VI(V)1
VI3b
VI3a
VI2
A
B
C
D
E

free from the influence of drift and consequently, the deeper soils thus formed are mainly cultivated. The stands of the Association are found only in isolated localities on steep slopes, around quarries and rock outcrops along the western escarpment and in local areas on the undulating plateau, e.g. Thrislington Plantation and Thornley Hall Dene. Soils associated with these areas are all Rendzinas of the Cornforth and Middleham series, developed directly over the yellow lower limestone series. The nature of these soils is dealt with in detail in Part 3.

Characteristics of the Association

The Association is characterised by the occurrence of the Seslerio-Mesobromion differential species *Sesleria caerulea* and *Epipactis atrorubens* in combination with such Alliance and Order character species as *Poterium sanguisorba*, *Helictotrichon pratense*, *Anthyllis vulneraria*, *Scabiosa columbaria*, *Koeleria cristata*, *Helianthemum chamaecistus* and others. The gregariousness and dominance of *Sesleria* usually reduces the cover and abundance of these species and also many of the companion species. However, species such as *Carex flacca*, *Thymus drucei*, *Carex caryophyllea*, *Festuca ovina*, *Lotus corniculatus* and *Plantago lanceolata* maintain a high constancy.

The Seslerio-Helictotrichetum is the most thermophilous

Association in the Sub-alliance and forms an important link with the Eu-Mesobromion Associations to the south and the damper upland Associations of the Seslerio-Mesobromion to the west. These relationships are well illustrated in the Sub-associations that have been delimited.

Sub-ass. TYPICUM occurs in areas where anthropogenic influences have been minimal and is probably the most natural group of grasslands in the Association. The areas appear not to have been burned or disturbed and are generally free from species indicative of interference other than light grazing. The better areas are located at Thrislington Plantation, and on the escarpment above Pittington and the south side of Cassop Vale. Epipactis atrorubens is more or less restricted to this Sub-association and Betonica officinalis and Campanula rotundifolia occur more frequently here.

Sub-ass. CARICETOSUM PULICARIAE forms an important link with the Seslerio-Caricetum pulicariae described from the mountain limestones of the northern Pennines. It generally occurs on north- and west-facing slopes with a more humid microclimate. Carex pulicaris occurs as co-dominant with Sesleria and in several places at Thrislington almost replaces the latter. Two distinct variants are recognisable:- variant of Selaginella and Pinguicula is found only at

Cassop Vale on the steep, damp, north-facing slopes. The main localities appear to be on quarry spoil-banks, but doubtless the community survived here in a more natural habitat before quarrying began. The abundance of bryophytes such as _Ctenidium molluscum_, _Acrocladium cuspidatum_ and _Hylocomium splendens_, indicates the damper nature of the situation.

Variant of Antennaria dioica (x) has been recorded only at Thrislington and is differentiated by the extremely gregarious pattern exhibited by _Antennaria_. The population of this plant resembles the type description of _A. hibernica_ Br.-Bl., and it appears that effective reproduction is only by vegetative means, thus explaining the anomalous pattern of the species. _Ctenidium molluscum_, _Acrocladium cuspidatum_, _Rhytidiadelphus squarrosus_ and _Fissidens cristatus_ also show a high constancy to this variant. Although _Primula farinosa_ is reported from several localities in the Magnesian Limestone region of Durham, its only occurrence in this Association was at Thrislington in an Aufnahme of this variant.

Sub-ass. of Helictotrichon pubescens is fairly widespread along the escarpment and is differentiated by the presence of _Helictotrichon pubescens_, _Dactylis glomerata_ and _Daucus carota_. The Sub-association is found in small areas which have been disturbed in the past and are now grazed to varying extents. Indicator species of grazing which occur more commonly in this group are Centaurea nigra, Plantago media and Trifolium repens. These species and the differential species form a group which represents the first stage transition from a Mesobromion to an Arrhenatheretalia community. In general, the climate on the exposed hills such as Sherburn Hill is too dry and grazing too light to enhance further transition. On the damper slopes of Cassop Vale, H. pubescens assumes dominance and in combination with other tall grasses and herbs such as Arrhenatherum elatius, Heracleum sphondylium and Filipendula ulmaria, gives the characteristic community structure of an Arrhenatherion Association (q.v.).

A variant of Rosa pimpinellifolia is found in areas which are periodically burned, or where grazing pressures have been gradually lessened over a period of a few years.

A second variant of Bromus erectus is described from Tunstall Hills, and on raodsides at Catley Hill and near Bishop Middleham. This variant which forms an important link with the Eu-Mesobromion Associations to the south of Co. Durham is characterised by the dominance of Bromus erectus and the greatly reduced cover of Sesleria.

Sub-ass. of Encalypta and Plantago maritima represents the second stage of colonisation of quarry spoil-banks, replacing a weed community which includes Chamaenerion angustifolium, Hypericum spp., Erigeron acer and Equisetum arvense. The Sub-association was located in the quarries at Pittington, Sherburn Hill, Cassop and Bishop Middleham. The communities are typically open with large patches of Encalypta vulgaris often alternating with E. streptocarpa and occasionally Ceratodon purpureus. The areas in-between the moss patches are occupied mainly by tufts of Sesleria and three moderately good differential species - Hypochaeris radicata, Hypericum montanum and Plantago maritima. It is puzzling whether this latter species forms a link with the montane Seslerio-Caricetum pulicariae or with the common maritime grasslands.

This Sub-association is probably the seral stage below the Sub-association of Helictotrichon pubescens which develops as a more compact turf is formed.

Zonation and Succession

Many of the seral stages associated with this Association have been mentioned in the preceding text and these are summarised in Figure 21, (see Volume II). Part 3 of this thesis, which considers conservation problems associated with the Seslerio-Helictotrichetum deals with the seral stages of this successional series, and in order to avoid repetition, description is restricted to the Chapter in question.

ASSOCIATION SESLERIO-CARICETUM PULICARIAE Table 12.

Synonymy. Alpine and sub-alpine moorland, natural pasture Lewis 1904 *pro parte*;

Festuco-Seslerietum Balme 1954

Sugar limestone grassland Pigott 1956.

Limestone grassland Sinker 1960.

Kobresieto-Seslerietum Ratcliffe 1966 unpubl.

Thymo-Festucetum typical variant Williams & Varley 1967.

Habitat details

This Association is fairly widespread on the limestone uplands and fells of the northern Pennines from the Craven district of north Yorkshire to the Teesdale fells and the high fells of the Yorkshire-Lancashire-Westmorland borders. The representative Aufnahmen have been collected mainly from the regions around Malham and Gordale Scar and several localities in Wharfedale and Littondale in Craven; Cronkley and Widdybank Fells in Teesdale; the sub-alpine fells of Mickle, Little and Great Dun Fells; and the limestone scar region around Sunbiggin Tarn and Orton in Westmorland. Clearly this survey is by no means exhaustive and a more detailed survey of some of the extensive limestone uplands in the Whernside region and the region between Lunedale, Swaledale and Wensleydale should reveal further localities for the Association. A single locality at Ratcheugh Crag in east Northumberland is included in the Seslerio-Caricetum pulicariae though its relationships with this Association are not clear.

All the stands described from the Craven district are found at altitudes varying between 900 feet (290 m.) at Conistone Old Pasture and 2200 feet (730 m.) on the slopes of Great Whernside. The localities in the Sunbiggin area all fall within the range 900 to 1200 feet (390 m.), whilst the majority of the stands described from Cronkley and Widdybank Fells occur in the 1600-1800 feet (520-580 m.) range. Only the Sub-association of Cochlearia alpina and Saxifraga hypnoides shows any preference for high altitudes, occurring above 2000 feet (660 m.) on Mickle and Great Dun Fells. At Ratcheugh Crag, the stand described is at an altitude of 350 feet (113 m.).

Many of the stands are located in regions which fall within the climate-type VI_{3a} characteristic of the Pennine area from Ilkley to the Solway Firth and typified by the diagram from Appleby (Figure 20). Here there is an average annual temperature of 8.3 °C and an average annual rainfall of 928 mm. Most of the rain falls in the months of January and October and the highest average monthly temperatures are recorded for July. Similar recordings are reported by Manley (1957) for the region around Malham

Tarn. The main difference between this region and the lower regions around Appleby is that the average daily maxima are lower than the average night minima in the latter region, being 50 °F (10 °C) and 39 °F (4 °C) respectively. The mean annual rainfall is also higher, being about 1210 mm.

The distribution of rainfall in Teesdale has been measured by Glasspole (1932) who gives a transect moving upstream:- Middleton 890 mm; Cronkley Scar 1270-1400; Widdybank 1525; High Cup Nick 1780+. At higher altitudes, some idea of the climatic extremes of the Association may be obtained from the work of Manley (1942) from Great Dun Fell. The mean maximum temperature remains below 5.6 °C until May with average monthly minima of -0.7 °C in December and maxima of 9.3 and 9.1 °C in July and August respectively. The average monthly snow-lie period for December to March varies between 17 and 19 days, with periods of 13 days in November and April.

Grasslands of the *Seslerio-Caricetum pulicariae* are found predominantly on steep south- and west-facing slopes where the influence of glacial drift is minimal and where there is little or no accumulation of raw, peaty humus. The range of soil types described in Figure 6, are typical for the areas of sugar limestone on Cronkley and Widdybank Fells. The open type of habitat due to the coarse grain size of this metamorphosed limestone and the constant reassortment of particles and humus by moles gives rise to a "Calcareous Syroseum" in many areas. In other drift-free areas, the normal series from Rendzina to Brown Earth with some podsolisation is the usual range of soil type. This is the pattern on the unaltered limestones of the higher fells, the process of soil development being initiated alongside screes by the formation of Protorendzinas, e.g. on the south side of Mickle Fell. Surface pH varies between 7.6 and 6.8.

Characteristics of the Association

This Association is comparatively poor in Alliance and Order character species, due partly to the gregariousness of Sesleria and partly to the dampness and altitude of many of the stands. Only Helictotrichon pratense, Koeleria cristata, Helianthemum chamaecistus and Poterium sanguisorba are of high constancy, but never share dominance. Differential species of the Sub-alliance besides Sesleria, though frequent are not widespread throughout the Association and several occur only in one Sub-association or variant. Of these species only Galium sterneri attains a relatively high constancy.

Carex pulicaris is widespread throughout the Association. This sedge is frequently overlooked in its vegetative form because of its superficial resemblance to Festuca ovina and close examination often reveals it to be co-dominant with Sesleria. Along with species such as Primula farinosa, Carex hostiana, Molinia caerulea, Pinguicula vulgaris and Carex capillaris, it indicates the damp nature of the grasslands.

Companion species of high constancy are Carex flacca, Briza media, Thymus drucei, Linum catharticum, Festuca ovina, Lotus corniculatus, Anthoxanthum odoratum and Viola riviniana. The most notable regional difference is the replacement of Euphrasia nemorosa, which is common in the Craven region with E. curta on the higher Pennine fells to the north. Bryophytes are numerous in many Aufnahmen, but only Ctenidium molluscum, Pseudoscleropodium purum, Hylocomium splendens and Tortella tortuosa achieve a high constancy.

Four sub-associations have been recognised:-

Sub-ass. TYPICUM is by far the most widespread Sub-association occurring commonly in the Wharfedale and Malham regions, around Orton, and on both the sugar and unaltered limestones of Widdybank and Cronkley Fells mainly below the 1700 feet (560 m.) contour. Sesleria and Carex pulicaris usually dominate these communities, although Festuca ovina often occurs as co-dominant. Lotus corniculatus, Briza media, Scabiosa columbaria and Leontodon hispidus also play an important part in the structure of the compact sward.

In addition to the typical variant, there appear to be at least three distinct variants of this Sub-association:-

Calluna-Empetrum variant is recorded from Widdybank and Cronkley Fells on the gentler slopes. The occurrence of this variant is apparently associated with a greater accumulation of raw humus in the surface horizons of the soils (often 60% and 3 to 4 cms. deep), some drift influence, and the consequent transition from Rendzina to a slightly podsolised Red-Brown Calcareous soil. The physiognomy of Calluna creates different microenvironmental gradients to those normally functioning in grass and herb dominated grasslands and this enables bryophytes such as Pleurozium schreberi and Hylocomium splendens to assume a more important role.

Filipendula vulgaris-Geranium sanguineum variant is described from two localities in Wharfedale - Kilnsey Crag and below Dib Scar. This variant is recognised because it exhibits a floristic relationship with the Asperulo-Seslerietum of western Ireland. The occurrence of Dryas octopetala in the same region, and the old records for Craven (Lousley 1950) of Helianthemum canum and Euphrasia salisburgensis also support the evidence for this relationship.

Ditrichum flexicaule-Rhytidium rugosum variant is located at the margins of the grassland areas near the outcrops of sugar limestone. The variant is described from Thistle Green on Cronkley Fell and along Red Sike and Slapestone Sike on Widdybank Fell. The physical make-up of the substrate reflects that of maritime sand dunes and areas of the Breckland in East Anglia, hence the use of the "Calcareous Syrosem" for the primitive soils. The resemblance between these three habitats is best seen in their bryophyte composition, e.g. Ditrichum flexicaule, Tortella tortuosa, Entodon concinnus and Barbula fallax attain high cover in all three habitats whilst Rhytidium rugosum is common in the communities in Teesdale and the Breckland. Frullania tamarisci and Cornicularia aculeata are common only in the Teesdale habitat and also show a slight preference to this variant.

Viola rupestris, Carex ericetorum and Hieracium pilosella are found mainly in this variant, possibly due to the open nature of the community. Of these three species, only Viola rupestris does not occur in both localities.

Sub-ass. KOBRESIETOSUM is found exclusively on Widdybank Fell. Kobresia simpliciuscula, a plant of calcareous flushes of the Order Tofieldietalia in the Central Alps (cf. Braun-Blanquet 1949) is found in damp grassland where it assumes dominance from Sesleria. It also occurs in the neighbouring flushes in a community similar to that described by Braun-Blanquet.

Carex capillaris replaces C. pulicaris in many places, and Gentiana verna, Polygonum viviparum and Antennaria dioica (x) are found more frequently in this Sub-association. In damper areas where drainage is impeded and there is some gleying of the Red-brown Calcareous soils, there is a rapid transition to a calcareous flush community. A damper facies of the Sub-association kobresietosum, where Carex lepidocarpa assumes more importance in community structure, is often recognisable before the water table reaches the surface and serves to delimit the flush communities.

Sub-ass. DRYADETOSUM is described from three localities in Littondale and one on Cronkley Fell. It is recognised as a separate entity because of the characteristic structure that the Dryas plants give to the community. Like the variant of Filipendula and Geranium of the Sub-ass. typicum, this group of Aufnahme provides a phytogeographical link with the Asperulo-Seslerietum of western Ireland.

Sub-ass. of Saxifraga hypnoides and Cochlearia alpina is a sub-alpine Sub-association usually occurring above 2100 feet (690 m.) and described from the limestone slopes of Mickle, Little and Great Dun Fells, with a single locality on Widdybank. Cochlearia alpina and Saxifraga hypnoides are species which are fairly widespread in open communities at lower levels, e.g. gravel flushes on Widdybank Pasture, but only at higher altitudes where the climate is extremely damp and humid are they prominent constituents of a compact grass sward. The dominance in these communities is shared between Festuca ovina, Thymus drucei, Carex pulicaris and C. caryophyllea, and Sesleria, though of high constancy, rarely occurs as a dominant. Other indicator species of this Sub-association are the arctic-alpine plants Myosotis alpestris and Draba incana, whilst Carex capillaris is usually absent.

These grasslands are frequently heavily grazed and several nitrophilous weed species such as Cirsium vulgare, Bellis perennis, Cerastium holosteoides and Trifolium repens are abundant. There is also a significant reduction of Alliance and Order character species and only Helictotrichon pratense and Koeleria cristata are usually present.

Zonation and Succession

Figure 22 (back pocket) summarises the zonal and seral relationships of the Sub-associations and the Association.

Zonation within the Association is most marked on Widdybank Fell where the Ditrichum-Rhytidium variant on Calcareous Syrosems is replaced by the Sub-ass. typicum, typical variant and the Sub-ass. kobresietosum with the accumulation of humus and Rendzina formation. Downslope, as drainage is impeded and some gleying occurs the wet facies of Carex lepidocarpa is found. On the gentler slopes towards the top of the fell the Callüna-Empetrum variant occurs in the more leached areas.

On Widdybank and in upper Wharfedale the grassland is replaced by a calcareous flush community of the Alliance Eriophorion latifolii of the Order Tofieldietalia (see Chapter 5). In most of the regions surveyed the limestone grasslands are bounded by drift covered areas which are either covered with blanket peat and rough Nardus-Juncus squarrosus grasslands, or with heavily grazed Festuco-Poetum Association of the Alliance Ranunculo-Anthoxanthion in the Class Molinio-Arrhenatheretea (q.v.). The transition to this type of grassland is very gradual on the high northern fells and virtually every Intermediate between this Association and Seslerio-Caricetum Sub-ass. of Cochlearia and Saxifraga can be recognised.

This latter Sub-association is closely related to a scree community similar to the Sedum roseum-Arenaria hibernica Ass.Br.-Bl.&Tx.1952, described by these authors from Ben Bulben, Co. Sligo, and placed in the Alliance Cochlearion alpinae Br.-Bl.1950 of the Class Asplenietea rupestris Br.-Bl.1934.

On the limestone scars above Sunbiggin Tarn, the Sub-ass. typicum is bounded by the upland limestone pavements. In the shallow grikes Sesleria is the dominant and often the only species. Occurring with Sesleria in many places and replacing Carex pulicaris is the rare Carex ornithopoda. Table 13 comprises 6 Aufnahmen of these fragments, named the Sesleria-Carex ornithopoda fragment Community, and included here because the phytogeographical importance of the sedge species. Oberdorfer (1962) records this species as characteristic of Brometalia/Seslerietalia transition communities and also in woodland communities. This appears to be the case on the scars above Sunbiggin, where the relict woodland communities are represented in the deeper grikes and the grassland transition communities in the flat open areas and shallower grikes.

Similar fragment communities of the Seslerio-Caricetum pulicariae are reported by Ivimey-Cook (1965), Table 6, p.444 from solution-cups in the pavement limestones of Hutton Roof Crags.

ASSOCIATION ASPERULO-SESLERIETUM (Br.-Bl.&Tx.1952) comb.nov. Table 14.

Synonymy: Asperuleton-Dryadetum Br.Bl.&Tx.1952.

Antennarietum hibernicae Sub-ass. of Sesleria Br.-Bl.&Tx.1952.

Camptothecio-Asperuletum Sub-ass. of Sesleria Br.-Bl.&Tx.1952.

Helianthemum canum-Thymus drucei association, Sesleria facies Proctor 1958.

Dryas octopetela-Hypericum pulchrum Ass. Iv.-Ck.&Proct.1966.

Antennaria dioica-Hieracium pilosella Nodum Iv.-Ck.&Proct.1966.

In the author's opinion the Asperuleto-Dryadetum Br.-Bl. &Tx.1952 is too limited, and at the suggestion of Ivimey-Cook & Proctor (1966), the Sub-associations of Sesleria of the Associations Camptothecio-Asperuletum and Antennarietum hibernicae are united with this Association into the Asperulo-Seslerietum. Further strength to this nomenclature is lent by the inclusion of a group of Aufnahmen from the southern Lake District of England.

Habitat details

The Association occurs extensively on the Carboniferous Limestone of the Burren, Co. Clare from Black Head to Gort and Corrofin; in several localities around the city of Galway, on the eastern and northern coasts of Galway Bay near Portumna; and on the limestone scars of the southern Lake District - Scout, Underbarrow and Whitbarrow Scars and Humphrey Head. In most of these localities the altitudinal range is between 150 and 600 feet (45-190 m.), but in the Burren, communities have been recorded up to 900 feet (290 m.)

on Cappanawalla.

The climatic features of the western Irish region have already been reviewed for the Antennarietum hibernicae and in Figure 18. The conditions are exactly the same as those in the wetter localities (e.g. Ballyvaughan 1650 mm) described for this Association, and the north- and west-facing slopes on which many of these communities occur accentuate these features. The inland localities at Portumna fall into the same climate-type $VI(V)_i$ as the coastal areas of north Lancashire. Details of this climate-type are summarised in the diagram for Morecambe in Figure 20.

The soils on which the Association is found in western Ireland are all essentially the same type of dark organic Rendzina. These are shallow soils varying between 8 and 60 cms. in depth and characterised by a dark brown-black A horizon which is rich in humus (60% +). This grades diffusely into a C horizon of limestone fragments with small amounts of blown sand intermixed. The following profile was recorded at Black Head, Co. Clare:-

Grid ref. M16/12 Altitude 600 ft. Slope 5 °C NW

Drainage. Excessive.

0-8 cms A	Humus-rich, dark black/brown organic horizon. pH 7.4, compact root mat with few earthworms.

8-11 C/D Admixture of black humus and numerous limestone fragments with a small proportion of blown sand. Bedrock.

Less than one metre away from this profile and in the same community, the profile depth was recorded as 52 cms. This depth was marked by the presence of a *Calluna* bush and was presumably due to the presence of a grike in the limestone surface. Such an uneven depth of the sub-soil limestone causes a mosaic of grassland and heaths and poses problems of classification of the communities.

On the limestone scars of north Lancashire the soils are primitive and Rendzina-like. However, several profiles have a similar red-brown coloration to the *terra fusca* of the Gower series described by Robinson (1930) and Crampton (1966). The following profile was recorded at Humphrey Head:-

Grid ref. SD 391735 Altitude 150 feet Slope SW 15°

Drainage. Free

0-3 cms. A_0 Dark black-brown humus-rich layer with compact root mat and a few limestone fragments; pH 7.4.

3-16 A Red-brown moist clayey structure with numerous brashy limestone fragments and some blown sand.

C/D Limestone bedrock.

Characteristics of the Association

The Asperulo-Seslerietum is characterised by the dominance of Sesleria caerulea and the constancy of the Mesobromion character species Asperula cynanchica. Other Alliance character species of high constancy are Koeleria cristata and Carlina vulgaris, whilst species such as Anthyllis vulneraria, Helictotrichon pratense and Poterium sanguisorba are rare. Helianthemum canum replaces H. chamaecistus in western Ireland, but the two species occur together in several localities in the southern Lake District. The most common differential species of the Sub-alliance is Galium sterneri which is found throughout the Association. Other differentials such as Gentiana verna, Epipactis atrorubens and Euphrasia salisburgensis are less common.

The overall community structure is further characterised by four major components (based on Ivimey-Cook & Proctor 1966):-

(a) the co-dominance in many stands and constancy of Carex flacca, Thymus drucei, Succisa pratensis, Festuca ovina and Linum catharticum;

(b) the constancy of several pleurocarpus mosses such as Breutelia chrysocoma, Hylocomium brevirostre (Ireland only), Rhytidiadelphus triquetrus, Neckera crispa and Pseudoscleropodium purum;

(c) a group of bryophytes with preferences for open, stony habitats - Ctenidium molluscum, Tortella tortuosa and in the English localities Weissia spp.;

(d) in western Ireland, a group of species more or less characteristic of leached soils, e.g. Calluna vulgaris, Hypericum pulchrum and Sieglingia decumbens.

The features listed above are essentially those of the Sub-ass. TYPICUM, typical variant described from Co. Galway, and several localities in the Burren. Included in this part of Table 14 is Antennarietum hibernicae Sub-ass. of Sesleria Br.-Bl.&Tx.1952 and the Camptothecio-Asperuletum, Sesleria Sub-ass. of the same authors. A constancy table of 7 of the lists from the Antennaria dioica-Hieracium pilosella Nodum Iv.-Ck.&Proct.1966 is also appended, (see Appendix for individual details).

The Helianthemum variant of this Sub-association is described from the southern Lake District and is differentiated from the typical variant by the dominance of Helianthemum canum and the presence of H. chamaecistus, a species which is virtually absent from Ireland. Viola hirta is a third differential species.

A second Sub-association is described only from the Burren:-

Sub-ass. DRYADETOSUM. This unit is equivalent to the

Asperuleton-Dryadetum Br.-Bl.&Tx.1952 and to the Dryas octopetala-Hypericum pulchrum Ass. Iv.-Ck.&Proct.1966. The Sub-association has all the characters of the Sub-ass. typicum, typical variant except that Dryas is usually the physiognomic dominant. This feature and the paucity of Mesobromion character species indicate a close floristic link with the Class Elyno-Seslerietea.

Neither of the two Sub-associations described by Braun-Blanquet & Tüxen (1952) are recognisable as strict units, but the wide variation of cover of the dominant species such as Dryas, Breutelia, Sesleria and Helianthemum canum, produce definite facies. Since these variations are virtually continuous and aligned mainly with small changes of soil depth and humus content of the soils, no further classification is attempted.

Zonation and Succession

The three main successional trends of development from the Asperulo-Seslerietum in western Ireland are:-

(a) to an upland heath Association, Arctostaphylleto-Dryadetum (Arctostaphyllos-Dryas Nodum Iv.-Ck.&Proct.1966);

(b) to a scrubby Corylus avellana-Oxalis acetosella Ass. Iv.-Ck.&Proct.1966, (also in the Lancashire localities);

(c) to a scrub community dominated by Potentilla fruticosa.

These three successional communities are considered in more detail in Chapter 5. However, a number of fragment communities which fall between these Associations and the Asperulo-Seslerietum and which appear to be degradation stages of one or the other, are dealt with here.

Breutelia-Sesleria pavement communities occur mainly at lower levels in the Burren and in some of the Galway localities. They are mostly fragments of the Asperulo-Seslerietum and usually consist of patches of Breutelia and Sesleria with saxicolous species such as Mycelis muralis, Geranium robertianum, Asplenium spp. and Saxifraga tridactylites. Other areas comprise the occasional low Corylus bush and often a few woodland herbs such as Sanicula europaea and Brachypodium sylvaticum. These communities are adequately described by Ivimey-Cook & Proctor (1966), Table XL, and no table is included in this thesis.

Empetrum nigrum-Epipactis atrorubens Nodum Iv.-Ck.&Proct.1966 was not observed by the author. This Nodum apparently replaces the Asperulo-Seslerietum dryadetosum on exposed slopes and crests at higher altitudes near the west coast of the Burren. According to Ivimey-Cook & Proctor, the Nodum is differentiated by the absence of many of the Asperulo-Seslerietum species, notably bryophytes, and is typically an open community dominated by Dryas, Sesleria and Empetrum nigrum. Their Nodum is summarised in constancy table form in Table 14, where its comparison with the Asperulo-Seslerietum suggests that it may be a fragment of the Arctostaphylleto-Dryadetum rather than the former Association. Solution-cup communities have been described from the Burren in detail by Ivimey-Cook (1965). Table 4 in this work is perhaps the most interesting, since its floristic composition resembles that of the Seslerio-Caricetum pulicariae of northern England rather than the Asperulo-Seslerietum. Presumably, the damper microclimate -of the solution-cups favours the dominance of Sesleria and Carex pulicaris and the exclusion of the more thermophilous species such as Asperula cynanchica, Helianthemum canum and Dryas.

The Phytogeographical Relationships of the Associations of the Alliance Mesobromion

(a) Eu-Mesobromion

The most continental Association of this group described in the preceding section is the Cirsio-Brometum, and the closest related grasslands to this type in terms of overall floristic structure occur on the chalklands of southern England, from Salisbury Plain to the North and South Downs, and thence northwards through Hertfordshire and Cambridgeshire to the wolds of east Yorkshire. In spite of the voluminous literature on chalk grassland ecology there are few papers which facilitate comparison of these grasslands and Cirsio-Brometum. In the present survey, only one region of chalk grassland was studied in detail, and comparative data are based mainly on this survey and the work of Tansley & Adamson (1925, 1926), Hope-Simpson (1941), Perring (1960), Watt (1958) and Wells (1965), (1968 pers. comm.).

The region surveyed was that of the downs along the south-facing Pewsey Vale escarpment and the north-facing downs above Cherhill in Wiltshire. Table 15 presents the results of this survey.

The Association described has the same basic structure as the Cirsio-Brometum with three of the four character species, Cirsium acaulon, Bromus erectus and Asperula cynanchica present throughout. In addition there is a long list of Alliance and Order character species which the two grassland types have in common:- Poterium sanguisorba, Helianthemum chamaecistus, Helictotrichon pratense, Koeleria cristata, Gentianella amarella, Anthyllis vulneraria, Carlina vulgaris, Campanula glomerata, Blackstonia perfoliata and Brachypodium pinnatum. Other character species not recorded in the Cirsio-Brometum of the Jurassic Limestones, but quite frequent in this region, are Phyteuma tenerum, Thesium humifusum, Gentianella anglica and Orchis ustulata.

The variation within this regional type of Cirsio-Brometum is well marked and four Sub-associations are recognisable:-

Sub-ass. TYPICUM is similar to the Sub-ass. typicum described from the Cotswolds, but has two main differences:-

(a) the lack of Brachypodium pinnatum;

(b) the frequency of the two Alliance character species Phyteuma tenerum and Campanula glomerata.

This Sub-association is found mainly near the centre of the south-facing slopes on shallow Rendzinas.

Sub-ass. of Onobrychis and Serratula was recorded only on Knap Hill in the Iron Age fort disturbance zone near the summit. This Sub-association is closely related to the Sub-ass. astragaletosum of the Stamford region and appears to be characteristic of ancient disturbed sites. The differential species Onobrychis viciifolia and Serratula tinctoria are probably relics of old cultivation, whilst Thesium humifusum, Gentianella anglica, Orchis ustulata, Coeloglossum viride and Blackstonia perfoliata indicate an open habitat away from the more rank growth of the Sub-ass. typicum. The rare thistle, Cirsium tuberosum, is apparently confined to this Sub-association.

Sub-ass. BRACHYPODIETOSUM. Brachypodium pinnatum in the Pewsey region is only found on north- and west-facing slopes on Cherhill Downs and Beacon Hill. Here the grass is dominant, but there is no apparent reduction in numbers or vitality of Alliance character species as is seen in the Sub-ass. brachypodietosum described from the Jurassic Limestones. This evidence suggests that this group of Aufnahme should be placed as a variant of the typical Sub-association rather than with the distinct Sub-association brachypodietosum of disturbed ground.

Sub-ass. of Anthoxanthum and Holcus occurs on the deeper, less calcareous soils towards the top of the slope where leaching is greater, and where there is some influence of the clay-with-flints soil type. The sub-association is differentiated by the important part that Anthoxanthum odoratum, Holcus lanatus and Arrhenatherum elatius play in the composition of the sward.

The initial impression gained from this study and the literature on chalk grasslands, is that the Association name Cirsio-Brometum is applicable to the majority of chalk grasslands. However, there is much more variation in dominants than there is in the Jurassic Limestone grasslands. This is due to the fact that many of the Cirsio-Brometum stands described from these limestones, are lightly grazed and not as carefully managed as the extensive chalk downlands. Wells (1965) recognises four main chalk grassland types based on dominance:-

(a) Festuca ovina + rubra grassland complex are dominant in western chalk regions, but also occur commonly in the Chilterns and the North and South Downs. These were thought by Tansley (1939) to be the original grassland type which were replaced by other types, as the interference of man became more widespread.

(b) Zerna (Bromus) erecta grasslands are thought to be a sign of pasture deterioration and of low grazing; they are the dominant grasslands of the Chiltern escarpment, especially in Bedfordshire, Hertfordshire and Buckinghamshire. Bromus erectus has been shown to be extremely sensitive to grazing (Wells, loc. cit.).

(c) Brachypodium pinnatum grasslands are characteristic of more eastern downland and dominate large areas of the Kent chalk. This rhizomatous grass is extremely unpalatable to grazing animals.

(d) Arrhenatherum elatius grasslands are found chiefly on the flatter, top-slope, clay-with-flints soils. It is probable that most of these gently undulating grasslands have been ploughed and mown within living memory.

With the exception of the latter type, the other three fall within the Cirsio-Brometum. In the Festuca ovina + rubra type, though these two grasses dominate, three of the Association character species, Asperula cynanchica, Cirsium acaulon and Bromus erectus are usually present. Brachypodium pinnatum is apparently not as widespread on the chalk grasslands as on the limestones, but the Sub-ass. brachypodietosum seems valid when applied to grasslands dominated by this grass.

The Arrhenatherum elatius grasslands clearly fall within the Alliance Arrhenatherion of the Class Molinio-Arrhenatheretea and are not included here. However, the Cirsio-Brometum Sub-ass. of Anthoxanthum and Holcus described above, represents the first stage transition to this grassland type.

What appeared to be a different grassland type from those listed by Wells (1965), was located in the Salisbury Plain region. Unfortunately, time permitted only three Aufnahmen to be collected (Table 16). Subsequently, unpublished data made available by Mr. T. C. E. Wells of the Nature Conservancy, confirmed that these grasslands may be placed in the Cirsio-Brometum as a Sub-ass. CARICETOSUM HUMILIS. As the name suggests, this Sub-association is characterised by the dominance of Carex humilis. In Wells' table of 82 $1m^2$ quadrats from 34 sites in Wiltshire (1968 pers. comm.) (x), Asperula cynanchica and Cirsium acaulon

(x) As requested by Mr. Wells, details of these sites are not included in Association table form or in the form of a constancy table.

are of high constancy, whilst Bromus erectus is less common and Brachypodium pinnatum virtually absent. Other Alliance and Order character species of Constancy V or IV are Helictotrichon pratense, Koeleria cristata, Hippocrepis comosa, Campanula glomerata, Helianthemum chamaecistus and Poterium sanguisorba, and species such as Anthyllis vulneraria, Carlina vulgaris, Centaurea scabiosa, Gentianella amarella, Polygala calcarea, Senecio integrifolius, Onobrychis viciifolia and Filipendula vulgaris, are less frequent. Festuca ovina is often co-dominant and Cynosurus cristatus is of high constancy compared to other Sub-associations of the Cirsio-Brometum.

The inter-relationships of the Sub-associations of the British Cirsio-Brometa are summarised in Table 17 (A-J). Also included in this table are the details from Tansley & Adamson (1926), Table 1, which consists of site lists for the South Downs (K). Because these are site floristic data and not quadrat data, the species are recorded on a presence or absence basis, and not in constancy figures. The data of Watt (1958), Table 2 (L), is included using his constancy values out of a figure of 10.

The remainder of Table 17 (columns M-W) comprises constancy tables for various Mesobromion Associations from western Europe which resemble Cirsio-Brometum.

In the lists from north-east France (M-O), from de Litardiere (1928) and de Blangermout & Liger (1964), Brachypodium pinnatum is the dominant grass and Bromus erectus is of low constancy or absent. Both Cirsium acaulon and Asperula cynanchica are of high constancy. Other marked differences between these Associations and the Cirsio-Brometum is the low constancy of Helictotrichon pratense and the higher constancy of several Order character species, e.g. Galium pumilum, Gentianella germanica, Polygala calcarea and Bupleurum falcatum.

Columns P and Q are two variants of the Association Mesobrometum Koelerietum cristatae described by Diemont & Van den Ven (1954) from the sandy chalk region of South Limburg, Holland. As in the previous lists, Brachypodium pinnatum is dominant, Bromus erectus is absent and Cirsium acaulon is of high constancy. Asperula cynanchica is absent and Helianthemum chamaecistus is rare. The first variant (P), is characteristic of the more sandy areas and is similar to the list from Watt (1958) (column L). Both these lists comprise groups of communities which are transitory to communities of the Order Festuco-Sedetalia. The second variant (Q) consists of more mesophilous, grazed stands of typical Mesobromion. The bryophyte Associations for these grasslands are described separately by Barkman (1954) and bryophytes are represented only as presence and absence data.

The Association Gentiano-Koelerietum boreoatlanticum Knapp 1942, comprises columns R-W. The data for this Association is taken mainly from unpublished Aufnahmen from north-west Germany of Professor R. Tüxen (x), and from Bornkamm (1960), including his Association Euphorbio-Brachypodietum. Brachypodium pinnatum, Koeleria cristata, Cirsium acaulon and Potentilla tabernaemontani are of high constancy. Helianthemum chamaecistus, Asperula cynanchica, Anthyllis vulneraria, and Hippocrepis comosa are all uncommon. Columns R and S comprise the Sub-ass. brometosum characterised by the relatively high constancies of Bromus erectus, Medicago falcata and Centaurea scabiosa. An ungrazed variant of this Sub-association (S) is characterised by the constancy of the unpalatable Euphorbia cyparissias, the increase in constancy of Helictotrichon pratense and the occurrence of Tunica prolifera. This pattern is seen also in similar variants of the Sub-ass. typicum and the Sub-ass. sieglingietosum (columns U and W).

Though there are marked differences between these Associations, it becomes obvious that grasslands of the Cirsio-Brometum type are quite similar in structure and

(x) The constancy tables R-W are the results of the author's work with Prof. Tüxen at the Arbeitsstelle für Theoretische und Angewandte Pflanzensoziologie, Todenmann, West Germany.

floristic composition and are quite widespread on calcareous soils in the drier regions of western Europe. These sub-atlantic and sub-mediterranean grasslands are replaced by a series of damper, atlantic-type grasslands characterised by:-

(a) the absence of Brachypodium pinnatum, Bromus erectus and Cirsium acaulon;

(b) a reduction in the number of continental Alliance and Order character species;-

(c) the dominance of Helictotrichon pratense and Festuca ovina.

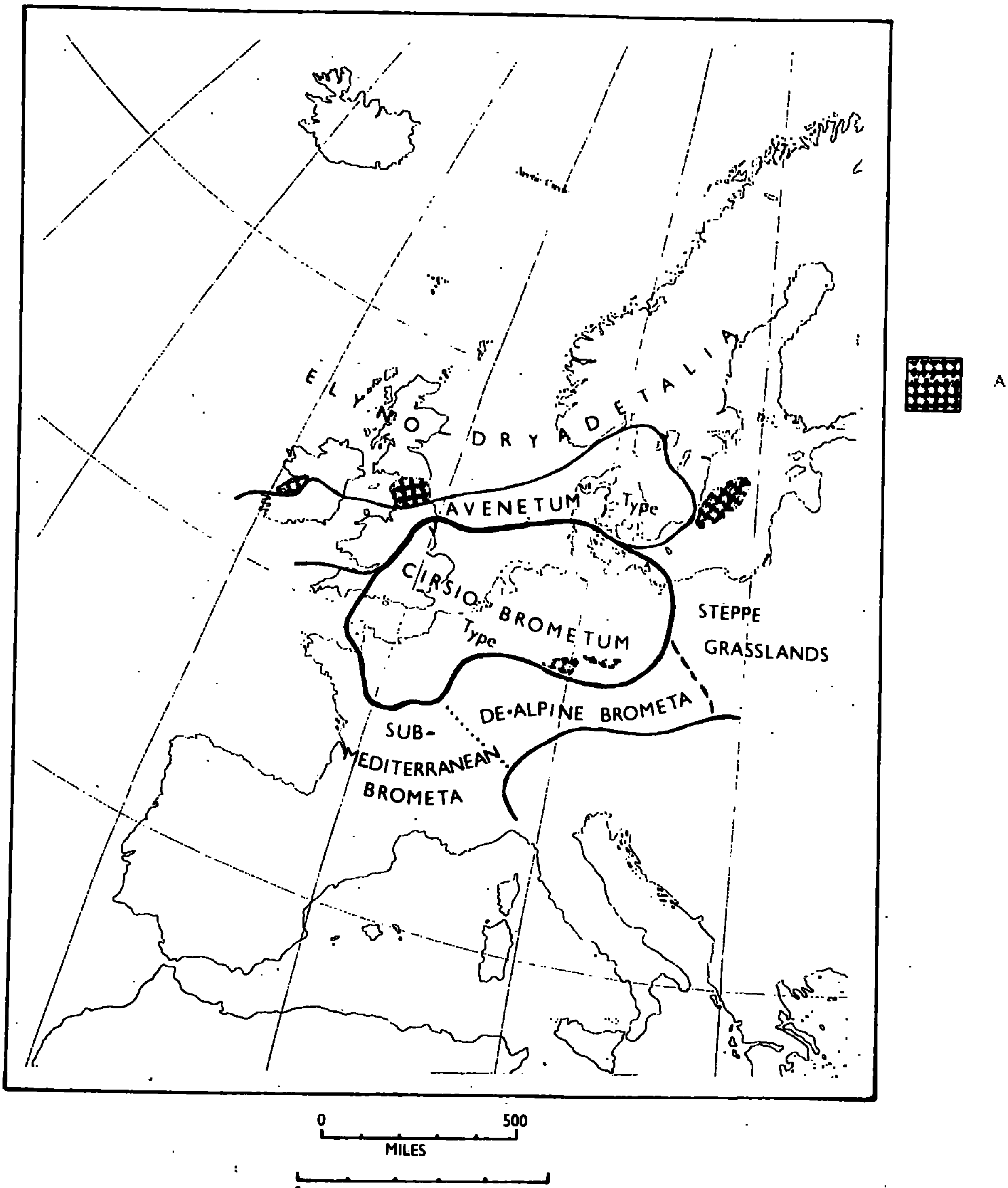
Representative Associations of this grassland type are summarised in Table 18. Columns A to L comprise the five Associations and their Sub-associations of this group described from the British Isles in the preceding text. Most of the differences have already been pointed out under the discussion of the Association characteristics. Table 18 emphasises these points and also indicates the close relationships of the Associations.

The remainder of Table 18 (M-P), is composed of calcareous grasslands from southern Scandinavia. Several communities described by Böcher (1946) from the Baltic Island of Møn, near Zealand, are intermediate between this type and the Cirsio-Brometum type. These lists are omitted from the table because Böcher describes a successional series with one Aufnahme representing each seral stage or zone. Column M however, contains a summary of an incomplete table of a similar grassland type from Böcher (1944) from north Denmark.

Most of the Scandinavian grasslands are found on calcareous sands and gravels. In the descriptions of these areas, there has been a tendency to include open communities of the Order Festuco-Sedetalia with Helictotrichon pratense dominant, along with good Mesobromion communities in one Association - the Avenetum pratensis Andersson 1950. With this fact in mind, column N includes only Mesobromion Aufnahmen of the Avenetum pratensis from Table 4 of Andersson (1950). In these communities Briza media and Helictotrichon pratense are dominant, with Camptothecium lutescens and Pulsatilla vulgaris of high constancy. Cirsium acaulon is also present here.

The lists which comprise column O are taken from an autecological study of Rhytidium rugosum, which dominates areas of calcareous sands in southern Sweden, (Hallberg 1959). This group has few Alliance and Order character species and represents a link community with the Seslerio-Mesobromion.

Similarly column P, consisting of unpublished Aufnahmen of Avenetum pratensis collected by Prof. Tüxen from southern


ELYNO-DRYADETALIA
AVENETUM Type
CIRSIO-BROMETUM Type
STEPPE GRASSLANDS
DE-ALPINE BROMETA
SUB-MEDITERRANEAN BROMETA
A
0 500
MILES
0 KMS. 1000

Sweden, provides a link with this latter Sub-alliance through the presence of Sesleria caerulea. Otherwise, this Association is by far the richest in terms of Alliance and Order character species in Scandinavia, and the presence of Asperula cynanchica and Cirsium acaulon link the Association to the Cirsio-Brometum type.

Figure 23 shows the approximate limits of these two grassland types along with the distribution of Seslerio-Mesobromion and Elyno-Seslerietea in western Europe.

(b) Seslerio-Mesobromion

The phytogeographical relationships of the Associations of this Sub-alliance in the British Isles, and the phyto-sociological relationships to Eu-Mesobromion and Elyno-Seslerietea have been considered in the sections for the individual Associations.

The distribution of the Sub-alliance in western Europe is intriguing and poses several interesting problems as to the origin of the communities. Unlike the two grassland types of the Eu-Mesobromion described above, there is no marked distribution zone which can be equated with climate. The disjunct distribution pattern (Figure 24) suggests that any interpretation on the origin of the communities, should be based on the study of the vegetation history of the region. The evidence revealed by such an approach is

FIGURE 23. The Distribution of related grassland types within the Class Festuco-Brometea in western Europe.

Legend:

A. Seslerio-Mesobromion.

	CRAVEN	TEESDALE	N/LANCS.	I. o. MAN	W. IRELAND	ÖLAND AND GÖTLAND	PRE-ALPINE GERMANY
Sesleria caerulea	x	x	x	.	x	x	x
Dryas octopetala	x	x	.	F	x	x	x
Galium sterneri	x	x	x	.	x	x	(x)
Epipactis atrorubens	x	x	x	.	x	x	x-
Breutelia chrysocoma	x	x	x	x	x	.	x
Tortella densa	x	x	x	x	x	x	?
Helianthemum canum	(x)	x	x	.	x	x	x
Primula farinosa	x-	x	x	.	.	x	x
Orobanche alba	x	(x)	(x)	.	x	x	x
Hippocrepis comosa	x	x-	x-	.	.	x	x
Carex ericetorum	.	x	x	.	.	x	x
Viola rupestris	.	x	x	.	.	x	x
Euphrasia salisburgensis	(x)	.	.	.	x	x	x
Bartsia alpina	x-	x	.	.	.	x	x
Gentiana verna	.	x	.	.	x	.	x
Polygala amara	x	x	.	.	.	x	x
Potentilla fruticosa	.	x	(x)	.	x	x	.
Neotinea intacta	.	.	.	x	x	.	.

(x) Doubtful status or old records.

F Fossil.

(*Tortella* details from CRUNDWELL & NYHOLM ex *Trans. B.B.S.* 1962)

FIGURE 24. The phytogeographical relationships of British regions of Seslerio-Mesobromion and the Baltic islands of Öland and Götland and the pre-alpine region of southern Germany: selected species.

obscure and often conflicting, but the basic details are outlined below.

The present distribution of the Sub-alliance is as follows:-

(a) Western Ireland, Lake District, northern Pennines, east Durham (Shimwell);

(b) Belgium - on Jurassic Limestone cliffs at Montauban, (Mosseray 1938);

(c) N. W. Germany - scattered localities on Jurassic Limestone cliffs, (Tüxen unpubl.);

(d) Öland and Götland, (Pettersson 1965);

(e) the pre-alpine region of southern Germany, (Oberdorfer 1957).

The problems of distribution under consideration here are essentially the same as those of the much discussed Upper Teesdale region, the only difference being that Teesdale has a much richer relict flora than most of the other areas (Figure 24). The general concensus of opinion on the origin of the relict flora of this region favours survival from the Late-glacial period (Pigott 1956, Godwin 1956), though there are conflicting theories of survival from an Inter-glacial period (Raistrick 1931). The subsequent Post-glacial events are summarised by Pigott & Walters (1954):-

(1) During the Late-glacial many species achieved a

more or less continuous distribution, preceding the spread of Boreal birch-pine and Atlantic deciduous forest, and have since been eliminated by forest and bog competition, so that they exhibit a relict distribution pattern.

(2) With the creation of open habitats by indirect or direct human activity, some species have been able to spread into habitats with an ecological similarity to those in which they survived, whilst others have remained in their *refugia*. *Sesleria caerulea* seems to fit the former category and *Dryas octopetala* the latter.

Evidence in support of the first part of this hypothesis involves a description of Post-glacial events and then comparison of the information obtained with present-day situations. Godwin (1956) and Iversen (1954) have shown that the climatic climax woodland type for the British Isles and western continental Europe from the Alps to southern Sweden, in the Atlantic period (Zone VII), was mixed thermophilous deciduous woodland. In certain regions, woodlands of this type exist today, and though they cannot be considered to be primeval, their structure and composition reflects that of the original climax.

Such an example occurs at Hohenstein in the Weser Gebirge of north-west Germany. In the middle of these climax woodlands of *Fagus* and *Fraxinus*, is a ridge of

Jurassic Limestone cliffs with communities referable to the *Seslerio-Mesobromion* occurring on the ledges and declivities where there is no tree cover. Amongst the relict species found in these communities are *Sesleria caerulea*, *Dianthus gratianopolitanus*, *Biscutella laevigata*, *Hippocrepis comosa*, *Pulsatilla vulgaris* and *Cotoneaster integerrima*. Aufnahmen from this locality and similar ones in the region are represented in the Association *Vincetoxico-Seslerietum* R. Tx. 1967, in columns M and N, Table 19. This Association shows quite a close relationship to the *Seslerio-Koelerietum* (Kuhn 1937), Oberd. 1957 (column O) from southern Germany, but lacks many of the high alpine and Order character species of the latter.

A second climatic climax woodland type has been recorded in northern Scandinavia (Fries 1965), and this Boreal Birch-Pine-Hazel type probably extended into Scotland, northern England and north-west Ireland. Recently, Hewetson (1968) has produced evidence for a climax Pine-Birch-Juniper woodland from profiles on Widdybank Fell, Teesdale. The closest resemblance to this calcicolous Pine-Juniper woodland at the present day, is to be found in the communities of the alvar or limestone plateaux of the islands of Götland and Öland, described by Du Rietz

(1925) and Pettersson (1965). Amongst these fragmentary woodlands are Sesleria-dominated grasslands and open patches of crystalline limestone dominated by Tortella spp., mainly T. tortuosa, but also the interesting species T. densa, which is found throughout the Seslerio-Mesobromion "zone". Further similarities in the flora of Teesdale and these islands (Figure 24), and the work of Iversen (1954) on Öland, indicate that the two regions have had a similar Post-glacial history.

Pettersson (1965) reports a second type of pinewood with a dominant understorey of Arctostaphylos uva-ursi and Juniperus communis. This community, but without the Pinus sylvestris, is found at higher altitudes in the Burren, western Ireland, where Seslerio-Mesobromion communities are also common, (see Arctostaphylleto-Dryadetum, Chapter 5). Similar communities are reported on south- and west-facing limestone slopes in the high Pyrennees (Rivas-Martinez 1968 and pers. comm.). In the Arctostaphilo-Pinetum uncinatae Rivas-Mart 1968, Pinus mugo replaces P. sylvestris, but associates in common with western Ireland are Juniperus communis and Dryas octopetala.

From the above evidence it seems reasonable to conclude that communities of the Late-glacial "steppe-tundra" vegetation survived forest maxima and on the removal of the forest by

Man, spread to similar habitats where they were invaded by Mesobromion character species to give the characteristic structure of the Seslerio-Mesobromion.

B. CLASS ELYNO-SESLERIETEA Br.-Bl.1948

This Class comprises most of the calcicolous grass-heath communities of the arctic-alpine zones of the Alps, Pyrenees, several of the mountain regions of Norway, Sweden and Finland (to 68-70° north), Iceland and northern Scotland. In addition, there are a few other localities in the British Isles, e.g. Snowdonia, the Lake District and Co. Sligo, Ireland, where fragmentary relict communities are found. In the majority of these regions the grass-heaths are found above 2000 feet (660 m.) but in north-west Scotland they occur down to sea level. In central Europe the grass-heaths occupy a zone of between 4200-4500 feet (1400-1500 m.) in the Jura Mountains and up to 5500 feet (1800 m.) in the central Alps (Braun-Blanquet 1948).

In the Alps and the Pyrenees the communities are usually dominated by *Sesleria caerulea*, *Kobresia* (*Elyna*) *myosuroides*, *Carex ferruginea* and *Dryas octopetala*, while those of Scandinavia are dominated mainly by *Dryas*, *Kobresia*, *Cassiope tetragona*, *Carex rupestris* and *Carex nardina* (Nordhagen 1955). The British communities fall midway between these two types. Only *Dryas* and *Carex rupestris* occur as dominants and of the other species, only *Sesleria* is present in a few isolated localities.

Because of the occurrence of a similar type of calcicolous

CLASS ELYNO-SESLERIETEA Br.-Bl. 1948

(a) Alps

ORDER SESLERIETALIA COERULEAE Br.-Bl. 1926

ALLIANCE CARICION FERRUGINEAE Br.-Bl. 1931.
SESLERION COERULEAE Br.-Bl. 1926.

ORDER OXYTROPIDO-ELYNETALIA Oberd. 1957

OXYTROPIDO-ELYNION Br.-Bl. 1948.

(b) Pyrenees

ORDER SESLERIETALIA COERULEAE Br.-Bl. 1926

ORDER OXYTROPIDO-EYNETALIA Oberd. 1957

(c) Scandinavia

ORDER ELYNO-DRYADETALIA Br.-Bl. 1948
(Syn: Elyno-Seslerietalia Nordh. 1936).

ALLIANCE KOBRESIO-DRYADION (Nordh. 1936) emend? Dahl 1956 (McV & Rat. 1962).
(Syn: Elynion bellardii Nordh. 1936.
Caricion nardinae Nordh.1936.
Kobresieto-Dryadion Nordh. 1936.
Dryadion Kalliola 1939.

ALLIANCE POTENTILLETO-POLYGONION VIVIPARI Nordh. (1928) 1936.

FIGURE 25. Syntaxonomy and synonymy within the Class Elyno-Seslerietea.

grass-heath in widely separated geographical regions, there has been considerable confusion over the nomenclature of the constituent Orders and Alliances of this Class. Figure 25 summarises and clarifies the syntaxonomy and synonymy of the Class Elyno-Seslerietea for the three main regions - the Alps, the Pyrenees and Scandinavia (including Scotland and Iceland).

The adoption of the Order names Seslerietalia coeruleae (x) or Elyno-Seslerietalia for Scottish and Scandinavian grass-heaths, convey an erroneous impression, because Sesleria caerulea is infrequent or absent in most of the communities. In order to avoid confusion with the Seslerio-Mesobromion and to emphasise the arctic-alpine nature of the communities, the name Elyno-Dryadetalia Br.-Bl. 1948, is adopted. As Braun-Blanquet suggests (1948, p.149), "........ the high number of exclusively nordic species indicate in favour of a special nordic order (Elyno-Dryadetalia), which also comprises a comparatively unknown number of boreo-arctic groups, analogous (to the Alps)".

ORDER ELYNO-DRYADETALIA Br.-Bl.1948

Comprises the alpine and arctic-alpine calcicolous grass-heaths of Scotland and Scandinavia. Two Alliances are recognised in both these areas:-

(x) Again coeruleae rather than caeruleae.

ALLIANCE POTENTILLETO-POLYGONION VIVIPARI Nordh (1928) 1936 is reported from Scotland by McVean & Ratcliffe (1962), but not with any certainty. It appears that several of their base-rich, damp grasslands of the Dwarf Herb Nodum and the Saxifrageto-Agrosto-Festucetum belong to this Alliance, but this remains to be verified. No data of this Alliance was collected.

ALLIANCE KOBRESIO-DRYADION (Nordh.1936) emend.? McV. & Rat.1962.

This Alliance contains all the familiar Dryas-heaths of Scotland and Scandinavia and a variety of grass-heaths dominated by Cassiope tetragona, Carex rupestris etc. Character species of the Alliance and Order in Scotland are:-

(All.) Dryas octopetala L.
Carex rupestris All.
Minuartia rubella (Wahlenb.) Hiern.
Arenaria norvegica Gunn.
Salix reticulata L.
Salix myrsinites L.

(O.) Silene acaulis (L.) Jacq.
Potentilla crantzii (Crantz) G.Beck ex Fritsch
Saxifraga oppositifolia L.
Carex atrata L.
Sesleria caerulea (L.) Ard. (rarely)
Cerastium alpinum L.
Astragalus alpinus L.

Order differential species (from Seslerio-Mesobromion)

Saxifraga aizoides L.
Polygonum viviparum L.

The limestone areas of Scotland were visited primarily to ascertain the northern limits of the Class Festuco-Brometea. It soon became apparent that the grasslands of the Seslerio-Mesobromion of northern England showed quite close similarities with several of the Scottish Dryas-heaths. Individual Aufnahmen of the Seslerio-Caricetum pulicariae from Cronkley Fell could quite easily be placed in the Kobresio-Dryadion, mainly because of the dominance of Dryas. However, these lists are retained in the Seslerio-Caricetum pulicariae in the Seslerio-Mesobromion because:-

(a) Sesleria, the gregarious dominant of these pastures, apparently survived forest maxima in refugia and then spread to suitable habitats to give communities which are uncharacteristic of the Elyno-Seslerietea and closer to Mesobromion. A similar survival is envisaged for Sesleria on the mica-schists of the Lawers range, but here, the grass has not spread from its refugia to form extensive grasslands;

(b) the stands of the Seslerio-Caricetum pulicariae in the Craven have a richer complement of Mesobromion character species and form a line of continuous variation through to the impoverished Carex pulicaris-Festuca ovina dominated pastures of the high Pennines;

(c) the communities in several areas of Teesdale, though more closely related to Kobresio-Dryadion than any of the other stands of this Association, form an important link in the variation of the Association and with the Seslerio-Helictotrichetum to the east;

(d) the absence or paucity of arctic-alpine indicator species of the *Elyno-Seslerietea* recommend the Association be retained in the *Seslerio-Mesobromion*.

Similar arguments apply to the status of *Asperulo-Seslerietum*.

Two distinct Associations and a series of relict *Dryas* communities are described for the *Kobresio-Dryadion* in the British Isles:-

ASSOCIATION PLANTAGINO-DRYADETUM. Table 20.

Synonymy. *Dryas* Heaths Poore & McVean 1957.
Dryas-Carex rupestris Nodum McVean & Ratcliffe 1962.
Dryas-Carex flacca Nodum McVean & Ratcliffe 1962.
Dryas octopetala localities Elkington 1962. *pro. parte*.

Habitat details

The Association is restricted to the lowland Cambrian limestones and *machair* or blown shell sand of the north and west coasts of Scotland. The Aufnahmen in Table 20 have been collected from pastures between Durness and Smoo Cave and from Druim Chuibhe, near Bettyhill, Sutherland, on the north coast, and inland from Inchnadamph in Sutherland and Glas Cnoe, Kishorn in Ross-shire. Lists are also included from the island of Raasay (Elkington 1962). McVean & Ratcliffe (1962) also report similar stands at Heilam and

Borralie in Sutherland and Monadh Dubh on the Isle of Rhum. The altitudinal distribution of the Association varies between 50 feet (16 m.) at Bettyhill and 1700 feet (550 m.) above Inchnadamph, though the majority of stands fall within the 100-250 feet (30-80 m.) range.

The climate is an extremely oceanic type with high rainfall figures of 1203 mm. at Cape Wrath, but with relatively warm average annual temperatures of 47 °F (8.2 °C), (Walter & Lieth 1967). The higher temperatures of the lowland coastal regions results in a much shorter snow-lie period and enhances the performance of this Chionophobous Association. Dahl (1951) has shown that in Fennoscandia the distribution ranges of most arctic-alpine species are closely related to maximum summer temperatures isotherms. The critical temperature calculated by Dahl is 22-29 °C for different species, but this can not be the case with Dryas which withstands average summer maxima of about 50 °F in its localities at Bettyhill and Durness. The presence of Dryas at low levels is probably due to the minimal snow-lie period and also the presence of open calcareous habitats where it can compete effectively with other shrubs.

The soils on which the Association occur are mainly Rendzinas and Brown Rendzinas overlying brashy limestones.

There is frequently a large proportion of black-brown humus in the A_0 horizon, the accumulation of which eventually gives rise to a Calluna-Empetrum heath. The soils at Bettyhill are primitive "Calcareous Syrosems" similar to those of Upper Teesdale, but the main source of calcium carbonate is shells. In these machairs the percentage of free calcium carbonate by weight varies between 40 and 58 (Gimingham et al., 1949), and there is a small amount of humus accumulation in the surface horizons.

Characteristics of the Association

The Association is characterised by the dominance of Dryas octopetala and its co-dominance with Carex rupestris in many localities. The only other Alliance character species is Arenaria norvegica, and Silene acaulis is the sole Order character species. The two Order differential species, Saxifraga aizoides and Polygonum viviparum, are of high constancy.

The Association is differentiated by a marked group of character species, most of which indicate the grazed, lowland nature of the majority of the stands:- Plantago lanceolata, P. maritima, Carex flacca, Bellis perennis, Cynosurus cristatus and Cerastium holosteioides. These species differentiate the Association from all others so far described from Scandinavia, and the mountains of

Scotland, and relate the Association to communities of the Seslerio-Mesobromion to the south. The sporadic occurrence at Durness of the Mesobromion character species Gentianella amarella, Scabiosa columbaria, Koeleria cristata and Anthyllis vulneraria is a further link with Mesobromion.

The Association has a remarkably uniform structure with respect to companion species and of the many constants some of the more important ones in determining structure are:- Festuca ovina, Thymus drucei, Carex pulicaris, Antennaria dioica (x), Lotus corniculatus, Ditrichum flexicaule and Hylocomium splendens.

Two Sub-associations are recognisable. The Sub-ass. TYPICUM comprises the majority of the lists from inland localities and has a lower average species number of 35. The Maritime Sub-association is differentiated by the presence of Cerastium atrovirens, Leontodon autumnalis, Sieglingia decumbens, Achillea millefolium and Scilla verna, and is generally more floristically rich than the latter. The Mesobromion character species mentioned above are more common in this Sub-association.

Zonation and Succession

In many places the Plantagino-Dryadetum is replaced by a calcicolous Empetrum nigrum-Calluna heath, which on the accumulation of peaty humus, gives rise to a blanket-bog community. At Bettyhill where Machair overlays acidic cliffs the zonation proceeds to a community dominated by Arctostaphylos uva-ursi and Juniperus communis and resembling the Juniperetum nanae of McVean & Ratcliffe 1962.

ASSOCIATION SALICO-DRYADETUM (McV.&Rat.1962) emend. Table 21.

Synonymy. Dryas-Salix reticulata Nodum McV.&Rat. 1962.

Habitat details

The Salico-Dryadetum is described from mica-schist cliff ledges between 2250 and 2800 feet (700-900 m.) on Meall nan Tarmachan, Ben Lawers and Cairnwell, Perthshire and Caenlochan Glen, Angus. McVean & Ratcliffe (1962) report similar communities up to 3000 feet (950 m.) on Creag Mhor, Loch Lyon, Perthshire, and within the above range at Glen Doll, Clova, Angus, and on Ben Lui, Argyllshire.

The most significant feature of climate relative to the distribution of this Association seems to be the fact that stands are found on cliff ledges facing east or south where insolation is maximum and consequently the snow-lie periods are reduced. Otherwise the distribution pattern of the Association appears not affected by climate, but is due to substrate and vegetation history.

The soils of these mica-schist ledges are mainly damp, humus rich Rankers or Rendzinas with a pH of 6.8 to 7.8.

McVean & Ratcliffe (1962) describe an Alpine Rendzina from Cairnwell in Perthshire, overlying crystalline metamorphic limestone which is atypical of this Association, because of it depth, parent rock and sandy nature.

Characteristics of the Association

The Association is characterised and differentiated from the *Plantagino-Dryadetum* by the co-dominance with *Dryas octopetala* of several arctic-alpine willow species, mainly *Salix reticulata*, but also *S. arbuscula* and *S. myrsinites*. The more widespread *Salix herbacea* is also present. The absence of a group of species characteristic of grazing differentiates the Association from the previous one and the presence of a group of arctic-alpine Order character species; amongst them *Saxifraga oppositifolia*, *Silene acaulis*, *Potentilla crantzii* and *Cerastium alpinum*, also serves to differentiate between the two Associations and confirm the relationships to Scandinavian communities. *Sesleria caerulea* is also quite frequent in this Association and in one Aufnahmen from Meall nan Tarmachan is co-dominant with *Salix reticulata*. Other Alliance character species present are *Minuartia rubella* and *Carex rupestris*. The most prominent constant companion species are those recorded for the *Plantagino-Dryadetum*.

Zonation and Succession

In all the localities these communities are fragmentary and zonation is obscured by rock-exposures and cliffs. On Cairnwell, the zonation from broken outcrops and sands of sugar limestone, through eutrophic heath to oligotrophic heath has been described by McVean & Ratcliffe (1962), Fig. 6, p.49). The most interesting community here is the open rocky area which may be referable to the *Arenarion norvegicae* Nordh. 1936 (see Chapter 5).

Related Communities

Also included in Table 21 is one Aufnahme from 2750 ft. (880 m.) on the base-poor rocks of Ben Vrackie, Perthshire. This fragmentary grassland community is dominated by *Carex rupestris* and *Festuca* spp. and has *Oxytropis halleri*, *Astragalus alpinus*, *Saxifraga oppositifolia* and *Silene acaulis* as notable companions.

Fragmentary *Dryas* communities have been recorded in Snowdonia and the Lake District, and Elkington (1962) records the following list at Llyn Idwal, Glyder Fawr, Caernarvon:-

Grid ref. 23/648594 Altitude 1750 ft., SSW 75°,
Cover 40%, 2m^2.

Kobresio-Dryadion species	Companions
3 Dryas octopetala	4 Calluna vulgaris
3 Saxifraga oppositifolia	3 Festuca ovina
4 Silene acaulis	3 Thymus drucei

2	Succisa pratensis	1	Amphidium mougeotii
1	Antennaria dioica	1	Ctenidium molluscum
1	Alchemilla glabra	1	Grimmia doniana
1	Veronica officinalis	1	Tortella tortuosa
1	Lycopodium selago	1	Trichostomum brachydontium
3	Rhacomitrium lanuginosum	1	Frullania tamarisci

(Figures on the Domin scale).

The Breutelio-Seslerietum Br.-Bl.1952 from Ben Bulben, Co. Sligo, is not so closely related to the Salico-Dryadetum as this latter fragment. The dominance is shared between Breutalia and Sesleria similar to some of the Burren Asperulo-Seslerieta, but Dryas is absent and arctic-alpine species such as Silene acaulis and Saxifraga aizoides differentiate these communities from the latter; (see Braun-Blanquet & Tüxen 1952, Table 38, p.317).

The Phytogeographical Relationships of the Associations of the Alliance Kobresio-Dryadion. Table 22.

The Plantagino-Dryadetum (columns A and B) appears to have no lowland, grazed counterpart in Scandinavia. McVean (1955) reports lowland Dryas Heaths at 200 ft. (60 m.) at Lodmundarfjordur in Iceland, but even at this low level arctic-alpine species such as Kobresia myosuroides, Cerastium alpinum, Erigeron borealis, Potentilla crantzii and Silene acaulis, are common.

The Salico-Dryadetum has a closely related counterpart in the Species-rich Dryas-Association of Nordhagen (1928) from Sylene in Norway. As McVean (1964) states, besides

Dryas and Salix reticulata, the two Associations have a number of species in common (cf. Table 22, columns C and D).

Other Associations and Sociations of Kobresio-Dryadion are summarised admirably in Table XIV, p.38 of Nordhagen (1936). Of these groups only the Elyna-Certraria nivalis-Ochrolechia tartarea-Soc. and the Arctostaphylos uva-ursi-Dryas-Soc. are included in Table 22 (columns E and F). The former is included to give some idea of the structure of communities where Kobresia myosuroides is co-dominant. The latter Sociation is particularly interesting because of its apparent close relationship to the Arctostaphylos-grass heath recorded by McVean and Ratcliffe (1962) at Blair Atholl, Perthshire.

Column G in Table 18 comprises two lists of the Species-rich Diapensia-Association Nordhagen 1928, which is closely related to the previous Sociations. It seems possible that a survey of the Diapensia lapponica locality in Scotland may reveal a community similar to this.

C. CLASS MOLINIO-ARRHENATHERETEA R.Tx.1937.

This Class includes many of the west European lowland, cultivated grassland communities of anthropogenic origin. Typically, they occur in flat areas of regularly enclosed land - the pastures and the hay meadows of the farmer. Grasses and rushes dominate the sward and the combined management effects of mowing and grazing by domestic animals maintain the communities in theirfamiliar form.

The problems associated with the conservation of these grassland communities are different from those of the *Festuco-Brometea*. Hay meadows and permanent pastures are not generally useful for recreation and, unlike the areas of *Festuco-Brometea* communities, these pastures do not fulfil the two-fold conservation requirements of amenity and scientific interest. Any conservation measures taken for the purpose of scientific investigation alone are usually agriculturally biassed and aimed at pasture improvement by controlled grazing, reseeding and the use of selective weedkillers.

In addition, these meadows and pastures are fairly uniform in floristic composition, irrespective of soil type or underlying rock strata, e.g. O'Sullivan (1965) describes five Associations from 580 Aufnahmen of Irish lowland pastures. Many of the component species of the pastures are quite widespread and only a few such as Fritillaria meleagris and Alchemilla glomerulans occupy precarious positions and require conservation.

With the above considerations in mind, plus the problems of time and access, the communities of "cultivated pastures and meadows" were omitted from the limestone grassland survey. However, where there was a rapid visible transition from a Festuco-Brometea to a Molinio-Arrhenatheretea community the transition was studied in detail. It was found that these communities fall mainly into the Order Arrhenatheretalia. In addition, several Molinietalia communities were studied, mainly in Derbyshire, in order to obtain some idea of the full range of basic structure of the grassland types. These and pastures of the Alliance Cynosurion cristati are summarised in synopsis form only. The choice of character species is based on the work of O'Sullivan (1965).

The following Class character species are recognised in western Europe:-

Holcus lanatus L.
Festuca rubra L.
Poa trivialis L.
P. pratensis L.
Alopecurus pratensis L.
Festuca pratensis Huds.
Helictotrichon pubescens (Huds.) Pilg.
Cerastium holosteioides Fr.
Rumex acetosa L.
Ranunculus acris L.
Cardamine pratensis L.
Rhinanthus minor L.
Ophioglossum vulgatum L.
Lathyrus pratensis L.
Vicia cracca L.

ORDER MOLINIETALIA COERULEAE (x) W.Koch 1926.

This Order is a floristically and ecologically distinct group of communities subjected to little anthropogenic influence and considered to be semi-natural by O'Sullivan (1965). The range of communities included within this Order is wide but all are damp or wet and characterised by the dominance of tall herbs. Amongst the Order character species are:-

- *Juncus effusus* L.
- *Cirsium palustre* (L.) Scop.
- *Lotus uliginosus* Schkuhr.
- *Filipendula ulmaria* (L.) Maxim.
- *Juncus acutiflorus* Ehrh.
- *Juncus conglomeratus* L.
- *Myosotis caespitosa* K.F.Schultz.
- *Lychnis flos-cuculi* L.
- *Angelica sylvestris* L.
- *Deschampsia caespitosa* (L.) Beauv.
- *Achillea ptarmica* L.
- *Equisetum palustre* L.
- *Galium uliginosum* L.
- *Hypericum tetrapterum* Fr.

Though several of the Alliances of this Order are found in calcareous districts, mone of the communities were observed growing on calcareous soils. The Alliance *Molinion coeruleae* W. Koch 1926, is apparently a calcifuge Alliance, but two other Alliances exhibit closer relationships to calcicole habitats:-

ALLIANCE CALTHION PALUSTRIS R.Tx 1937.

This Alliance includes moist meadow communities of west and central Europe. Braun-Blanquet & Tüxen (1952) describe the Association *Senecioni-Juncetum acutiflori* from

(x) The specific name for *Molinia* is spelt *coerulea* in continental literature and *caerulea* in Dandy (1958).

Ireland but this Association was not observed in England. In Derbyshire a community similar to the "Molinietalia Community" O'Sullivan 1965, is common with Senecio aquaticus, Juncus effusus and J. conglomeratus the most prominent components. This community occurs frequently at the junction of the gritstone and impervious shale, where a chalybeate spring forms a flush with the characteristic red-brown coloration, which runs on the surface over the shale. At the limestone-shale junction the water disappears and the community changes abruptly. The best examples are to be seen on the hills to the south of Youlgrave and to the north of Eyam. The more frequent character species of the Alliance are:-

Caltha palustris L.
Senecio aquaticus Hill.
Myosotis scorpioides L.
Crepis paludosa (L.) Moench.
Polygonum bistorta L.
Bromus racemosus L.
Polygonum hydropiper L.

ALLIANCE FILIPENDULO-PETASITION Br.-Bl. 1947.

Communities of this Alliance are found commonly along the sides of drains and rivers on the eutrophic flood levels and valley alluvium. Character species are:-

Epilobium hirsutum L.
Epilobium parviflorum Schreb.
Valeriana officinalis L.
Eupatorium cannabinum L.
Stachys palustris L.
Petasites hybridus (L.) Gaertn., Mey. & Scherb.

The most common community type is dominated by one of the Epilobium species and Filipendula ulmaria and occurs frequently along the river banks of most of the Derbyshire rivers. Another type of leaf-rich Petasites-dominant community is more restricted and was seen only in two localities in Derbyshire. The following Aufnahme was recorded in Tideswell Dale on the alluvial flood plain of a small stream:-

Grid ref. SK 154734 Altitude 700 ft., $10m^2$ Cover 100%

5.5	Petasites hybridus	+	Heracleum sphondylium
1.1	Galium aparine	+	Chamaenerion angustifolium
+	Urtica dioica	+	Poa annua
+	Arum maculatum	3.4	Eurynchium praelongum
+	Anthriscus sylvestris	+.2	Mnium hornum
+	Stachys palustris	+	M. undulatum
+	Bromus ramosus	+	Lophocolea bidentata

ORDER ARRHENATHERETALIA ELATIORIS Pawl. 1928.

This Order contains the majority of lowland permanent pasture and meadow, hay meadow and rough grassland of basic, neutral and slightly acidic soils. The composition of these communities is usually made up of species with a wide ecological range such Anthoxanthum odoratum and Agrostis spp., but there are a number of species of narrower amplitude which serve as Order character species:-

Trisetum flavescens (L.) Beauv.
Bromus mollis L.
Daucus carota L.
Knautia arvensis (L.)
Chrysanthemum leucanthemum L.
Taraxacum sect./vulgaria B.P.L.
Bellis perennis L.
Veronica chamaedrys L.
Veronica officinalis L.

ALLIANCE CYNOSURION CRISTATI R.Tx. 1947.

The greater percentage of the unseeded permanent pastures and hay meadows on loamy soils in the British Isles fall into this Alliance. Preliminary observations revealed that most of the pastures on the undulating plateau areas of the Derbyshire Limestone Dome and the rich meadows of Upper Teesdale fall within this Alliance. The Alliance is confined to western Europe, from north-west Germany to Holland and Belgium and the British Isles. Nearly one-third of the total land surface of Holland has been described as a single Sub-association of a *Cynosurion* Association and consequently the pastures are best known in this country (de Vries *et al*. 1942, etc.). Continuous pasturing and mowing on a rotation system results in the appearance and maintenance of those species most suited to grazed situations. The more or less uniform management practice over a wide geographical range has resulted in the formation of much the same communities in all regions. Thus, the two Associations described for Ireland by Braun-Blanquet & Tüxen (1952) and O'Sullivan (1965) are recognisable in several regions of England.

The character and differential species of *Cynosurion cristati* are as follows:-

Character.	*Cynosurus cristatus* L.	*Phleum pratense* L.
	Trifolium repens L.	

Differential. Lolium perenne L. Cirsium arvense (L.) Scop.
Achillea millefolium L.

Lolium perenne and Cirsium arvense appear to be indicative of long and intensive grazing and are the main character species of the ASSOCIATION LOLIO-CYNOSURETUM Br.Bl. & de Leeuw 1936. "These rye-grass-white clover pastures show more clearly than any other community the effects of human management" (O'Sullivan 1965). This Association is common on the enclosed plateau land of the Derbyshire limestones and on the higher pastures in Teesdale and Weardale. It appears to be completely unrelated to Festuco-Brometea communities except in small areas of rock outcrops where Thymus drucei and Festuca ovina tend to replace the dominant Lolium, Trifolium repens, Poa pratensis and Agrostis tenuis.

No lists for this Association are included in Table form, but the following Aufnahme from Bee Low, Youlgrave, Derbyshire, illustrates the type of grassland structure:-

Grid ref. SK 193648 Altitude 1000 ft., $40m^2$ Cover 100%, E 2°.

3.3	Lolium perenne	1.1	Ranunculus acris
+	Poa pratensis	+	R. bulbosus
3.4	Agrostis tenuis	+	Poa annua
+	Trisetum flavescens	+	Cerastium holosteioides
1.1	Dactylis glomerata	+	Medicago lupulina
+	Briza media	+	Veronica chamaedrys
2.3	Trifolium repens	+	Cirsium palustre
1.2	Cirsium arvense	+	C. vulgare
+	Galium saxatile	+	Urtica dioica
+	Festuca ovina	+	Bellis perennis
+	Achillea millefolium		
		+.2	Rhytidiadelphus squarrosus
		+	Lophocolea bidentata

ASSOCIATION CENTAUREO-CYNOSURETUM Br.Bl.&Tx.1952.

This Association was first described for Ireland by Braun-Blanquet & Tüxen (1952), and the later research of O'Sullivan (1965) and Ivimey-Cook & Proctor (1966), has shown that the Association is widespread. The *Centaureo-Cynosuretum* is characteristic of lightly grazed pastures and hay meadows and is recognisable from the *Lolio-Cynosuretum* by the presence of a group of differential species:-

Rhinanthus minor L.
Luzula campestris (L.) DC.
Lotus corniculatus L.
Senecio jacobaea L.
Crepis capillaris (L.) Wallr.
Lathyrus pratensis L.
Carex flacca Schreb.
Briza media L.
Vicia cracca L.
Trifolium dubium Sibth.
Rhytidiadelphus squarrosus (Hedw.) Warnst.
Pseudoscleropodium purum (Hedw.) Fleisch.

This group of species are common in many of the Associations of the *Festuco-Brometea* described previously, and is generally indicative of light grazing pressures and a varying amount of manuring. These species in combination with *Mesobromion* character species give the characteristic limestone grassland community structure, but where grasses such as *Cynosurus cristatus*, *Bromus mollis*, *Poa pratensis* and *Poa trivialis* are dominant, the Association certainly belongs to the *Cynosurion* Alliance, and is probably a *Centaureo-Cynosuretum*.

The complete transition from a *Mesobromion* Association to *Centaureo-Cynosuretum* was not observed on the rough grasslands of steeper limestone slopes, and the latter Association is apparently confined to flatter meadows, where the annual mowing favours its maintenance. However, in western Ireland, O'Sullivan reports a contact zone between Antennarietum hibernicae Br.-Bl.&Tx.1952 and Centaureo-Cynosuretum recognisable as Centaureo-Cynosuretum Sub-ass. of Galium verum sub. var. of Thymus drucei O'Sullivan 1965.

ALLIANCE ARRHENATHERION ELATIORIS W.Koch 1926.

This Alliance includes most of the lowland and sub-montane oatgrass meadow communities of the Atlantic region of Europe. They are usually taller and rougher grasslands than those of the previous Alliance, are more fragmentary, e.g. found on roadsides etc., and are usually lightly grazed. The drainage of these pastures is consistently free and the infrequent mowing gives rise to a tall herb-rich grassland.

Character species.

Arrhenatherum elatius (L.)Beauv	Anthriscus sylvestris (L.)
Heracleum sphondylium L.	Tragopogon pratensis L.

Differential species.

Vicia sepium L.	Trisetum flavescens (L.) Beauv.

Helictotrichon pubescens (Huds.) Pilg.

Of the four character species, Anthriscus and Tragopogon are more or less restricted to eutrophic habitats, especially roadsides and hedgebanks. Arrhenatherum, Trisetum and

Helictotrichon pubescens occur frequently in the Aufnahmen from the Helictotricho-Caricetum flaccae (Table 6), and it is in the humid coombes and dales that the transition from a Mesobromion to an Arrhenatherion community occurs.

ASSOCIATION CENTAUREO-ARRHENATHERETUM O'Sullivan 1965.
Table 23.

Synonymy. None. Not Centaureo-Arrhenatheretum Oberd. 1957.

Habitat details.

The Association is described in England from Cheddar Gorge, in Somerset, from several of the Derbyshire Dales and in three localities on the eastern limestone escarpment of Co. Durham. The altitudinal range varies between 500 and 900 feet (160-280 m.) in Derbyshire, between 200 and 500 feet (60-160 m.) in Durham, and at approximately 500 feet in Cheddar Gorge.

The conditions of climate are essentially those described for the Helictotricho-Caricetum flaccae and Seslerio-Helictotrichetum with which the Association is in contact. The range of soil types is fairly narrow, being mainly in the range Red-brown Calcareous to Brown Earth, and surface pH varies between 6.8 and 7.4.

Characteristics of the Association

The Association is characterised by the dominance of Arrhenatherum elatius or the co-dominance of this grass with

with Helictotrichon pubescens. Alliance species of high constancy are Heracleum sphondylium, and Trisetum flavescens, whilst common Class character species are Cerastium holosteioides, Holcus lanatus, Poa pratensis, Lathyrus pratensis, Ranunculus acris and Rumex acetosa. Other constant companion species are Dactylis glomerata, Centaurea nigra, Lotus corniculatus and Pseudoscleropodium purum. The rare species Silene nutans occurs frequently in the Derbyshire localities for this Association.

The community structure is more or less the same as that of Centaureo-Arrhenatheretum Sub-ass. of Galium verum O'Sullivan 1965, which is differentiated by Galium verum, Lotus corniculatus, Agrimonia eupatoria and Pimpinella saxifraga. According to O'Sullivan (1965), this Sub-association is characteristic of species-rich, freely drained, calcareous localities. These Aufnahmen lend support to his tentative classification which is based on only four Aufnahmen.

Zonation and Succession

The Association appears to be derived from the Seslerio-Helictotrichetum Sub-ass. of H elictotrichon pubescens in eastern Durham, in damper areas where there is more raw humus and light grazing. In other regions, more humid conditions, light manuring and grazing seem to be important factors in affecting the transition from Helictotricho-Caricetum flaccae.

ARRHENATHERUM-MERCURIALIS Community. Table 24.

In many of the Derbyshire Dales and in Burrington Coombe, Somerset, a peculiar community has developed alongside screes, where Arrhenatherum elatius is dominant, and where woodland relict species such as Mercurialis perennis, Teucrium scorodonia and Brachypodium sylvaticum are constants. These communities are undoubtedly derived from woodland and scrub degeneration and probably represent the furthest point of the degradation series. Table 19 contains six Aufnahmen of this community and it seems possible that the Caricetum montanae Sub-ass. of Galium and Melica is more closely related to this community than to Caricetum montanae typicum (Table 8).

ASSOCIATION FILIPENDULO-ARRHENATHERETUM. Table 25.

Synonymy. Polemonium caeruleum localities pro parte Pigott 1958.

Habitat details

The Filipendulo-Arrhenatheretum is described from steep-sided, humid dales and crags in Derbyshire, the Craven district of Yorkshire, a stream bank in Teesdale, and one locality reported by Pigott (1958) from Alwinton in

Northumberland. The majority of localities are found on north-facing slopes between 600 and 800 feet (190-260 m.), but the Association also occurs on east-facing crags at Kilnsey Crag and west-facing slopes at Malham Cove in Yorkshire at about 800 feet.

In his autecological study on Polemonium caeruleum, Pigott (1958) reports a pronounced microclimate on the steep north-facing slopes characterised by an annual reduction of air temperature maxima of 5 to 8 °C, and an even greater reduction in soil temperature maxima. Garrett (1956) records a period of only two hours sunshine on either side of the dale near the bottom where these communities occur, and the severe night temperature inversions may be as low as -10 °C. Pigott's experiments suggest that temperature is an important factor in these communities, mainly because its reduction of transpiration and evaporation from the simple Protorendzina and Brown Rendzina soils, where drainage is normally free. The reduction of temperatures and the consequent diminished evaporation gives the impression that drainage is impeded, but there is no gleying and little humus accumulation in these shallow soils.

Characteristics of the Association

The Filipendulo-Arrhenatheretum occupies a unique position in the Molinio-Arrhenatheretea, in that it falls midway between the Molinietalia and Arrhenatheretalia in terms of floristic composition. The mixed nature of the Association is reflected in the presence of the following character species:-

Molinietalia - Filipendula ulmaria, Angelica sylvestris, Cirsium palustre and Valeriana officinalis.

Arrhenatheretalia - Arrhenatherum elatius, Helictotrichon pubescens, Veronica chamaedrys and Heracleum sphondylium.

The constancy of a further group of species comprising Mercurialis perennis, Silene dioica, Dryopteris filix-mas, Epilobium montanum and Plagiothecium denticulatum, indicates the affinities of the communities to Alnus-Prunus padus woodland and explains their heterogeneity. A similar explanation also fits the European ecological distribution pattern of Polemonium caeruleum, which is characteristic of damp ash-alder woodlands of the Alliance Alno-Padion Knapp 1942 emend. Mat. et Roz. 1957. This relationship is also reflected by the occurrence of scattered trees of Fraxinus and Prunus padus in several of the lists, and the two woodland lists appended to Table 25 (Aufnahmen MA47, MB2) illustrate these affinities.

Two Sub-associations are recognised:-

Sub-ass. TYPICUM is characterised by the co-dominance of the tall herbs and grasses Arrhenatherum, Helictotrichon pubescens, Filipendula ulmaria and Heracleum sphondylium, and the constancy of the Molinio-Arrhenatheretea character species Festuca rubra and Poa trivialis. Other species of high constancy are Mercurialis perennis, Silene dioica, Cruciata chersonensis, Epilobium montanum, Anthriscus sylvestris and the bryophytes Acrocladium cuspidatum, Eurynchium swartzii, Mnium undulatum, Plagiothecium denticulatum and Lophocolea bidentata.

Sub-ass. POLEMONIETOSUM is characterised by the co-dominance of Polemonium caeruleum with the dominants of the Sub-ass. typicum. The best stands of this Sub-association are seen on the damp north-facing slopes of Lathkill Dale, Derbyshire and in Malham Cove, where the Polemonium is more or less dominant.

Zonation and Succession

In many localities the Association is a woodland fringe community which passes into a mixed Fraxinus-Ulmus woodland. At Kilnsey Crag, the ledge communities are in contact with the open grasslands of the Seslerio-Caricetum pulicariae.

-o-o-o-O-o-o-o-

The survey of a group of montane, sub-alpine limestone grasslands in Breconshire and on the higher fells of the Craven and northern Pennines, revealed a type of grassland composition atypical of both the Festuco-Brometea and the lowland Alliances of Molinio-Arrhenatheretea. The absence of Mesobromion character species and of the familiar dominant grasses, e.g. Arrhenatherum, Cynosurus, Bromus mollis and Helictotrichon pubescens of the Arrhenatheretalia have led to the provisional adoption of the Scandinavian Alliance Ranunculo-Anthoxanthion Gjaerevoll 1956 as a component Alliance of the Arrhenatheretalia.

ALLIANCE RANUNCULO-ANTHOXANTHION (Gjaerevoll 1956) emend.

Synonymy. Nardeto-Agrostion tenuis Sillinger 1933, pro parte.
Ranunculeto-Oxyrion digynae Nordhagen 1943 emend. Dahl 1956.

Though the Scandinavian interpretation of the term Alliance is slightly different from that of the Z-M School, the name of this Alliance seems to be applicable to several British communities, because of similar dominants and overall floristic composition. Gjaerevoll (1965) describes the communities as "late snow-free meadow communities .... the unpretentious flower garden of the mountain built up by acid rocks". McVean & Ratcliffe (1962) adopt the Alliance in their description of Scottish vegetation and include several Noda and Associations in this group. Their Agrosto-Festuceta have basically the same physiognomic and floristic structure and resemble the Nardeto-Agrostion tenuis Sillinger 1933 (Nordhagen 1943), which in turn differ mainly in dominant only from the Ranunculo-Anthoxanthion sensu Gjaerevoll.

Thus, in Britain, the Alliance Ranunculo-Anthoxanthion is amended to include damp montane and sub-alpine meadows and pastures dominated by Deschampsia caespitosa, Festuca ovina, F. rubra, Agrostis tenuis, A. canina or Anthoxanthum odoratum. The Alliance is differentiated from other Arrhenatheretalia Alliances by the absence of any of their grass character species, and by the presence of the following Class character species:- Deschampsia caespitosa, Festuca rubra, Ranunculus acris, Bellis perennis, Cerastium holosteioides, Trifolium repens, Rumex acetosa, Achillea millefolium and Poa subcaerulea.

Of lower frequency are Holcus lanatus, Cardamine pratensis, Geum rivale and Veronica chamaedrys. The prefix Ranunculo- is adopted primarily because of the constancy of Ranunculus acris and R. repens in most of the Associations described. Table 26 summarises the Associations described by McVean & Ratcliffe (1962), which are considered to belong to this Alliance and gives a good example of the range of structure and floristic composition. Also included are the "Festuca-Agrostis complex" grasslands from the Southern Uplands of Scotland, described by King & Nicholson (1964). Williams & Varley (1967) give details of several pasture types where Holcus lanatus is a prominent constituent, and suggest the name Holco-Cynosuretum. Unfortunately, Table 1 of this paper seems incomplete and Cynosurus cristatus is not recorded in these or any other lists from continental Cynosurion Associations. Because of these facts and numerous other inaccuracies in the text, none of their data is included here.

The Alliance Ranunculo-Anthoxanthion fills a regional lacuna in the Z-M system of classification and is broadly, the northern, sub-boreal counterpart of the sub-alpine Alliance Polygono-Trisetion Br.-Bl.1948, of the central European region. One of the Associations of this latter Alliance, the Meo-Festucetum Bartsch 1940, described by Oberdorfer (1967) from the Black and Thüringer Forest regions of south Germany, resembles several of the Ranunculo-Anthoxanthion communities through the dominance of Festuca rubra and Agrostis tenuis.

One Association is described from the montane limestone regions of England and Wales.

ASSOCIATION FESTUCO-POETUM. Table 27.

Synonymy. Agrosto-Festucetum typicum Eddy, Welsh & Rawes 1968 unpubl.

Habitat details

The Association is included and described from limestone pastures to the south of the Brecon Beacons, Wales, in one locality from Derbyshire, three localities on Ingleborough, Great Whernside and Malham Lings, in Craven, and on the Teesdale National Nature Reserve from Mickle Fell and the north side of Dufton Fell. The Association is undoubtedly much more widespread on the northern Pennine fells than the representative Aufnahmen indicate. The lowest recorded stand is at 1000 ft. (300 m.) in Breconshire, and in all the other localities the Association is found at altitudes of 1250 to 2200 feet (400-700 m.).

The climate-type is that characteristic of the adverse montane zones described for the Seslerio-Caricetum pulicariae, and falls within Walter & Lieth's type X. Soil-types vary widely from Rendzina to podsolised Brown-Earths with varying drift influence. The following profile was recorded on Mickle Fell at the transition of the Association to degraded Nardus-Juncus squarrosus peat surface:-

Grid ref. NY 802240 Altitude 2300 ft. Slope SW 10°

Drainage. Fair to good.

0-4 cms. Ao	Raw black-brown humus accumulation with compact root mat. Few earthworms. pH 6.4.
4-10	Red-brown, loamy, moist fine crumb structure with small amount of intermixed humus.
10-16 B	Dark red-brown "iron-pan" zone with compact structure acting as a barrier to most roots; a few drift fragments and pebbles of small size.

C/D Limestone scree. Bedrock.

The occurrence of drift here seems to be anomalous and does not appear to have been reported at this altitude previously.

On the Moorhouse Nature Reserve, the Association is reported on alluvial river gravels and silt of the numerous sikes and becks which flow over limestone into the River Tees.

Characteristics of the Association

The dominant species of the Association are Festuca ovina, F. rubra, Anthoxanthum odoratum and Agrostis tenuis, with a group of Class character species such as Ranunculus acris, Achillea millefolium, Cerastium holosteioides, Rumex acetosa, Bellis perennis and Trifolium repens of high constancy. Companion species of high constancy are Prunella vulgaris, Thymus drucei, Carex caryophyllea, Galium saxatile, Viola riviniana, Selaginella selaginoides etc. The Association is differentiated from other Associations of this Class by:-

(a) the abundance of bryophytes and the important part they play in the composition of the turf; species of high constancy are Hylocomium splendens, Hypnum cupressiforme, Rhytidiadelphus squarrosus and Lophocolea bidentata;

(b) the high constancy of Poa subcaerulea which replaces the familiar P. pratensis of lower pastures in all but one

Aufnahmen;

(c) the presence of Saxifraga hypnoides and Galium sterneri;

(d) the absence of most Cynosurion and Arrhenatherion companion species such as Centaurea nigra, Lolium perenne and Rhinanthus minor;

(e) the constancy of Thymus drucei and Ctenidium molluscum, two species more or less characteristic of calcareous habitats.

Two Sub-associations are recognised:-

Sub-ass. CYNOSURETOSUM is found at lower altitudes in Brecon and Derbyshire and is differentiated by the presence of Cynosurus cristatus and Holcus lanatus. This Sub-association is a transitory group of pastures between the familiar lowland pastures and the sub-alpine pastures, and is probably equivalent to the Holco-Cynosuretum Williams & Varley 1967.

Sub-ass. SUB-ALPINUM is found at higher altitudes where the grasslands are more moist, and species such as Ranunculus acris and Achillea millefolium are partly replaced by R. repens and A. ptarmica. There is also an abundance of leafy liverworts, the most common being Barbilophozia barbata, Tritomaria quinquedentata and Plagiochila asplenioides.

Zonation and Succession

The Association is usually in contact with acidic Nardus-Juncus squarrosus grasslands on peat or deep drift, and a grassland mosaic occurs quite frequently. The Sub-ass. Sub-alpinum on Mickle Fell grades gradually into the Seslerio-Caricetum pulicariae Sub-ass. of Cochlearia and Saxifraga as Sesleria and Carex pulicaris assume more importance on the shallower Rendzinas.

The Phytogeographical Relationships of Arrhenatherion and Ranunculo-Anthoxanthion

The relationships of the latter Alliance have been considered in detail in the type description and Table 26 summarises the available British material.

The distribution of the Arrhenatherion Alliance in continental Europe coincides with that of Fagus sylvatica woodland (Ellenberg 1963). As the altitude increases, the Arrhenatherion species are gradually replaced by species of the montane Alliance Polygono-Trisetion at about 2,000 feet. An analogous situation is seen in the British Isles. Here the oatgrass meadows show roughly the same distribution pattern as natural Fraxinus woodland, and at higher altitudes (1000 ft.+) are replaced by Agrostis-Anthoxanthum-Festuca pastures, which have been referred to the Alliance Ranunculo-Anthoxanthion.

The only anomalous Association is Filipendulo-

Arrhenatheretum which occurs around the fringe of natural *Fraxinus* woodland, and hints that the communities are derived from a different woodland type. The *Sub-ass. polemonietosum*, which appears to have no European counterpart, indicates the relationships to damp alluvial *Alno-Padion* woodlands.

D. CLASS VIOLETEA CALAMINARIAE R.Tx. 1961

The communities of metalliferous strata and metal mine spoil-heaps were originally included in the Class Festuco Brometea in the Alliance Violion calaminariae Schwick 1933, but the lack of Festuco-Brometea character species led to the erection of a special Class. Such communities are widespread but local in central and western Europe from north-west Germany and Belgium to northern Spain (Ernst 1965). In Britain, these communities are found in the Mendip H ills of Somerset, north Wales, Derbyshire and the northern Pennines from Craven to the Tyne valley.

ORDER VIOLETALIA CALAMINARIAE Br.-Bl.&R.Tx.1943

The Class and Order are named for the species Viola calaminaria Lej., a member of the V. lutea group and as yet, not recognised in the British Isles. The plant was first described as V. lutea ssp. elegans var. calaminaria by de Candolle (1824), and Schulz (1912) reported the taxon from Germany with n = 26 chromosomes as opposed to n = 24 in V. lutea.

Of the three Alliances recognised by Ernst (1965), only one occurs in Britain:-

ALLIANCE THLASPEION CALAMINARIAE Ernst 1965

The adjective calaminaria is applied because of the high proportion of zinc (calamine) in the soils on which the communities occur. The character species cited by Ernst (1965) for the Alliance are doubtful taxa, which are not recognised in "Flora Europaea", Vol. I, Tutin, T.G. et al. (ed.) (1964), e.g.

Thlaspi alpestre ssp. calaminare (Lej.) O. Schwarz
Minuartia verna ssp. hercynica (L.) Hiern
Silene cucubalus var. humilis (Wibel) Schwick.

It seems that sub-specific rank is given mainly because of the tolerance of high concentration of zinc by what appear to be ecological races.

The communities of this Alliance are open and seldom merit the term "grassland", but because of their former inclusion in the Class Festuco-Brometea they are considered here. Only one Association is recognised in the British Isles:-

ASSOCIATION MINUARTIO-THLASPEETUM. Table 28.

Synonymy. None.

Habitat details

The Association includes Aufnahmen from the Mendips, Derbyshire, and the northern Pennines at Altitudes varying between 500 and 2250 feet (160-730 m.). Despite the low altitude of a few sites, the Association is essentially one of the upland zone of Britain. The majority of localities have less than 1300 hrs. sunlight, and rainfall varies between 900 and 1250 mm in the Mendips and Derbyshire, and up to 2500 mm in the northern Pennines (Garrett 1956 and Manley 1942).

Minuartio-Thlaspeetum occurs only on disturbed open habitats of lead mine spoil-heaps which are composed mainly of shale, fluorspar and barytes and other gangue minerals. There is usually some humus accumulation in the surface layers, but there is seldom a recognisable soil profile. Whereas lead is the important mineral commercially, zinc is the mineral which is responsible for the restriction of vegetation growth. Ernst (1965) reports a content of 5060 ppm zinc in soils near Osnabrück, with figures of up to 6790 ppm and 2460 ppm in the leaves of Thlaspi alpestre ssp. calaminare and Minuartia verna ssp. hercynica respectively. Only these species and heavy metal tolerant strains of Agrostis tenuis (Bradshaw 1952) and probably Rumex acetosa are capable of colonising and reducing the toxicity of extreme metal-rich habitats. Where the heavy-metal concentration of the soils is less, or where these species have reduced the concentration by prolific absorption, a more compact sward occurs.

Characteristics of the Association

The two character species of the Association are Thlaspi alpestre and Minuartia verna which in the Sub-ass. TYPICUM are the dominants with Agrostis tenuis and Rumex acetosa. This Sub-association is described mainly from younger spoil-heaps and from heaps which overlie acid rocks, such as those at Eyam in Derbyshire and Grassington in Yorkshire.

Sub-ass. CLADONIETOSUM is found at higher altitudes on Eyam and Bonsall Moors in Derbyshire at circa 1250 feet (400 m.), Moorhouse in the northern Pennines at 1850 feet (590 m.) and on Grassington Moor at 1250 feet. The Sub-association is differentiated by the constancy and co-dominance of Cladonia rangiformis, C. chlorophaea, Cornicularia aculeata and the presence of Calluna vulgaris.

Sub-ass. ACHILLETOSUM is found on older spoil-heaps or those with a high proportion of ordinary limestone debris and is characterised by a more or less closed sward. The differential species are Achillea millefolium, Anthoxanthum odoratum, Euphrasia nemorosa, Plantago lanceolata and Rhytidiadelphus squarrosus. This Sub-association is found at lower altitudes in Derbyshire and the Mendips and several Aufnahmen have Mesobromion character species such as Anthyllis vulneraria, Koeleria cristata, Helictotrichon pratense and Scabiosa columbaria occurring sparsely in the turf.

The Association is usually dominated by Minuartia verna, Festuca ovina and Agrostis tenuis. Species of high constancy are Campanula rotundifolia, Cerastium holosteioides, Rumex acetosa, Linum catharticum and Thymus drucei.

Zonation and Succession

In lowland areas the open habitats of Sub-ass. typicum is replaced by Sub-ass. achilletosum, which then gives way to a meadow community of the Alliance Cynosurion. At higher altitudes the Sub-ass. typicum is replaced by the Sub-ass. cladonietosum and finally by Calluna-dominated moorland.

Phytogeographical Relationships of the Association

The pattern of the three Sub-associations described above is repeated on the continent of Europe in the Violetum calaminariae Schwick. 1931, described by Ernst (1965) from north-west Germany, Belgium and Holland. A fourth Sub-association, cardaminopsidetosum, not recorded in Britain is reported from Sauerland in Westphalia.

The main differences between this Association and the Minuartio-Thlaspeetum are the presence of Viola calaminaria, Armeria maritima ssp. calaminaria and Silene cucubalus var. humilis in the former, and the occurrence of Thymus drucei in place of T. pulegioides in Minuartio-Thlaspeetum.

In the Violetum calaminariae achilletosum Ernst (1965) recognises a *Koeleria* variant with *Koeleria cristata* and *Scabiosa columbaria* representing a transitory community to *Mesobromion*.

PART III

Chapter 5.

Succession and zonation in relation to Limestone Grasslands.

Limestone grasslands are generally regarded as a biotic plagioclimax. Because they are maintained in a more or less stable state, it is difficult to visualise their role in the dynamo-genetic classification systems of Tansley (1939), e.g. Scree - Grassland - Scrub - Climax woodland (see Figure 7), and only long-term experiments and observations such as those of Hope-Simpson (1940, 1941b), and Watt (1958), can claim to elucidate some of their individual relationships to other communities.

However, if it is assumed that grasslands are themselves, a climax state, there are several important factors which cause comparatively short-term changes in grassland structure, which may be identified as succession:-

(a) Climate (especially its pedogenic manifestations, see Figure 3);

(b) Drainage;

(c) Grazing;

The multidimensional effects of these three factors on limestone grasslands are summarised in Figure 25, and Figures 21 and 22 include actual examples of their influence. Many of the communities described in these figures can only be observed as zones of contact with the grasslands and the mechanism or speed of succession from one community to another must remain as a hypothesis.

The successional trends from *Mesobromion* pastures to

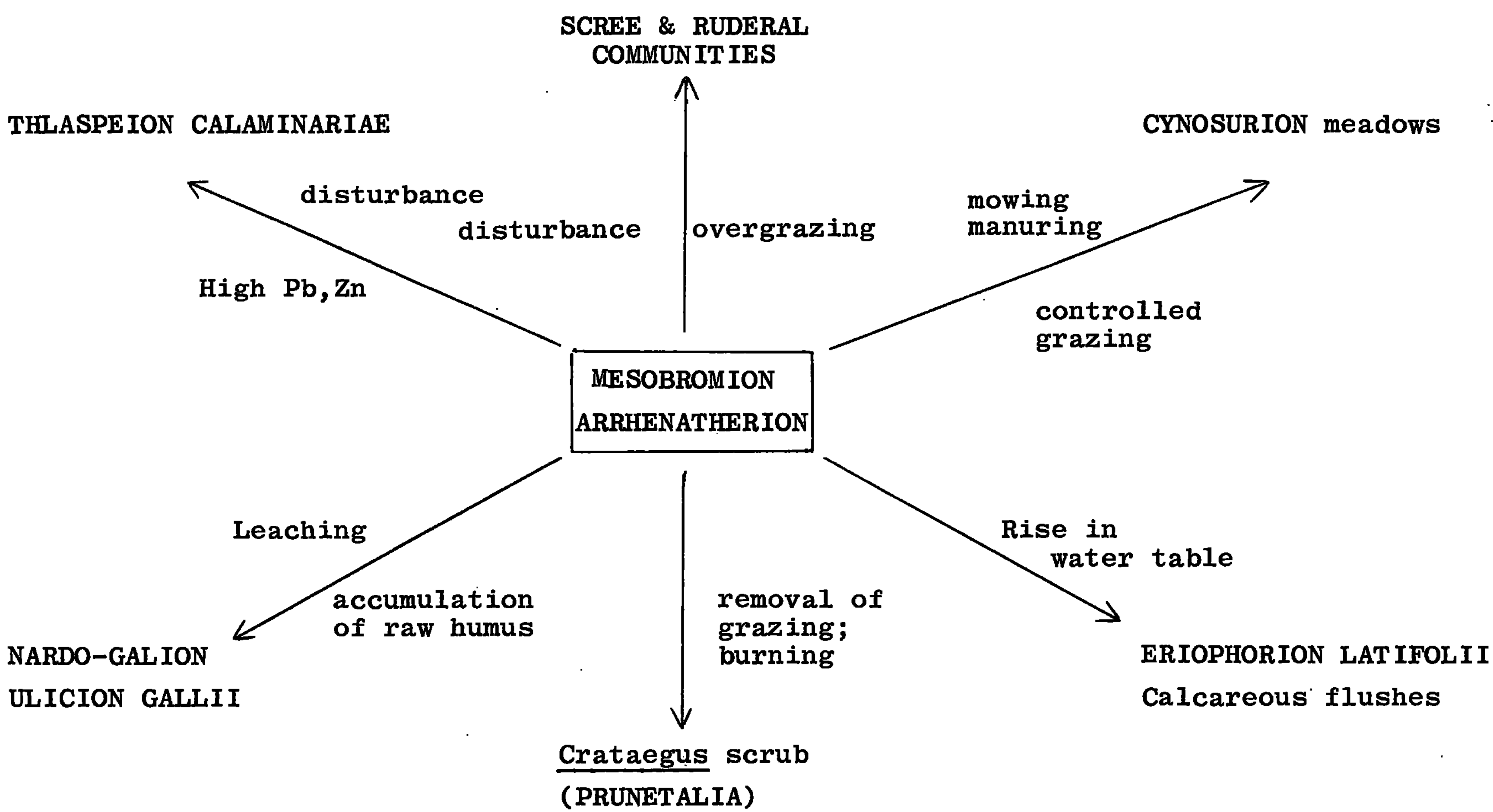


FIGURE 26. A summary of the short-term seral relationships of limestone grasslands.

Cynosurion meadows and Thlaspeion calaminariae communities have already been considered in the relevant sections of Chapter 4. The remaining seral and zonal communities related to limestone grasslands can be considered under four broad habitat or community types, e.g. (1) Screes, (2) Calcareous flushes, (3) Calcareous heaths, (4) Scrub and woodland border vegetation.

A. Communities of Screes and open ground

(1) Arrhenatherum-Mercurialis Community, (Table 24) is probably a derivative of a retrogressive woodland or scrub community. It forms marked zones at the edge of screes in Derbyshire in contact with Helictotricho-Caricetum flaccae.

(2) The Class Thlaspeetea rotundifolii Br.-Bl. 1947 includes alpine communities of open screes and rocks, which are often pioneer or conversely, relict fragments of higher Associations. The most common Association is the Dryopteridetum robertianae (Kuhn 1937) Tx. 1937, which occurs locally in the Alps and in scattered localities throughout northern Europe, including the British Isles. Table 29 comprises lists of this Association from Breconshire, Somerset, Derbyshire, Westmorland, and one locality in N.W. Germany. The Association is characterised by the dominant Thelypteris robertiana - the Limestone Fern, and

this plant is frequently the sole member of the community. Three Sub-associations are recognised:- Sub.-ass. typicum; Sub-ass. of Rubus saxatilis described from Derbyshire only; and Sub-ass. mesobrometosum indicating the trend of colonisation of limestone grassland plants such as Helictotrichon pratense and Carex flacca. A single list from the grikes above Sunbiggin Tarn, Westmorland, indicates relationships to humid woodland via the presence of Poa nemoralis and Phyllitis scolopendrium. The three constant species of the Association, Mercurialis perennis, Brachypodium sylvaticum and Teucrium scorodonia suggest that the Association is a retrogressive derivative of a scrub community.

This Association is placed in the Alliance Stipion calamagrostis Jenny-Lips 1930. A second Alliance, the Thlaspeion rotundifolii Br.-Bl. 1926, is recorded for the Alps. Oberdorfer (1957) cites Carex ornithopoda as a character species of this Alliance and it may be that the Sesleria-Carex ornithopoda Community (Table 13) falls into this category.

(3) Nordhagen (1936) describes a nordic-alpine Alliance Arenarion norvegicae for the Class Thlaspeetea rotundifolii, and communities related to this Alliance were recorded from two localities in Scotland. On the limestones above Inchnadamph, Arenaria norvegica is found in a community

which has been placed in the Plantagino-Dryadetum (Table 20), but at Cairnwell in Perthshire, the other Alliance character species Minuartia rubella occurs in an open sugar limestone community with the following composition:-

1.2	Minuartia rubella	+	Distichum capillaceum
1.2	Dryas octopetala	+.2	Rhytidium rugosum
1.1	Festuca ovina	+	Campanula rotundifolia
+.2	Ctenidium molluscum		

Grid ref. NO 135774; Altitude. 3050 ft.; $2m^2$; Slope 5 °SE; Cover 40%.

Neither of these communities are closely related to the typical Arenarion communities described by Nordhagen, but both indicate the close relationships of the Alliance to the Kobresio-Dryadion.

(4) Sedum fosterianum community (Table 30) is described from two localities on screes in the Cheddar Gorge and at Craig Breidden in Montgomeryshire. The systematic relationships of this community are obscure, and it is placed provisionally in the Alliance Sedo-Scleranthion Br.-Bl. 1949 of the Class Sedo-Scleranthetea.

B. Calcareous flush communities

The majority of calcareous flush communities fall within the Alliance Eriophorion latifolii Br.-Bl. & Tx. 1943 of the Order Tofieldietalia Prsg. apud Oberd 1949. In order of increasing wetness, the sequence of communities from calcareous grasslands to flush in the north of England runs:-

Seslerio-Caricetum pulicariae

Caricetum lepidocarpae-hostianae

Eriophorion latifolii   Schoenetum nigricantis

Gymnostomum-Cratoneuron bryophyte flush

Cratoneurion commutati (calcareous and tufaceous bryophyte communities)

Cratoneuron spring-head

This sequence was not seen in an adjacent series of zones, but all communities are present in the flush/grassland complex to the north-east of Sunbiggin Tarn, Westmorland.

Alliance Character species	Differential species
Eriophorum latifolium Hoppe	Carex pulicaris L.
Carex hostiana DC.	C. capillaris L.
C. lepidocarpa Tausch.	Primula farinosa L.
Tofieldia pusilla (Michx.) Pers.	

Order Character species	Differential species
Scorpidium scorpioides (Hedw.) Limpr.	Pinguicula vulgaris L.
Campylium stellatum (Hedw.)	Selaginella selaginoides (L.) Link
Carex dioica L.	Parnassia palustris L.
C. flava agg. L.	Thalictrum alpinum L.
Bartsia alpina L.	
Eleocharis quinqueflora (F.X. Hartmann) Schwarz	
Equisetum variegatum Schleich.	
Juncus triglumis L.	
J. alpino-articulatus Chaix	

A second Alliance, Caricion bicoloris-atrofuscae Nordh. 1936, is predominantly nordic-alpine and has amongst its character species Carex saxatilis, C. microglochin and C. atrofusca. Communities of this Alliance are recorded mainly from the Ben Lawers mica-schist flushes in the Bredalbane Range of Scotland (McVean & Ratcliffe 1962).

(1) Association Caricetum lepidocarpae-hostianae Table 31a.

Synonymy: Carex hostiana-Ges Br.-Bl.&Tx. 1952.

Habitat details

The Association is recorded from one locality in Derbyshire, several in Craven, Widdybank Fell, Teesdale, and Sunbiggin Tarn, Westmorland. In all the areas except Derbyshire, the communities form a contact zone with Seslerio-Caricetum pulicariae. The first stage of transition is usually recognisable by the abundance of Molinia caerulea, which gradually replaces Sesleria, and the occurrence of Primula farinosa and Pinguicula vulgaris. In the Derbyshire locality, the community is found in a calcareous seepage zone formed due to the intrusion of an igneous layer of toadstone between the limestone strata. The Association is essentially one of the sub-montane fringe in the limestone regions of the northern Pennines, between 700 and 1600 ft. (230-530 m.). Braun-Blanquet & Tüxen (1952) record a similar community at 250 m. on the north-west slopes of Ben Bulben, Co. Sligo.

The soils are usually primitive peaty gleys overlying calcareous brash or strata and the water table seldom falls more than a few centimetres below the surface. The pH of the water varies between 6.8 and 7.8.

Characteristics of the Association

The Association is characterised by the dominance and constancy of *Carex hostiana*, *C. lepidocarpa* and/or *C. pulicaris* and *C. dioica*. In several stands *C. demissa* partly replaces *C. lepidocarpa*, and whilst *Eriophorum latifolium* is frequent in the Craven stands it is replaced by *E. angustifolium* in Teesdale. *Campylium stellatum*, *Scorpidium scorpioides* and *Cratoneuron commutatum* often form a compact moss-layer in flushes where water movement is not so rapid. Two Sub-associations are recognised:-

(a) Sub-ass.*molinietosum* is described from Derbyshire, Craven and Westmorland and is differentiated by the co-dominance.of *Molinia caerulea* with the sedge species;

(b) Sub-ass. *kobresietosum* is described only from Widdybank Fell, Teesdale in the Red and Sand Sike areas. It is differentiated by the replacement of *Molinia* by *Kobresia simpliciuscula* and the presence of *Carex nigra*, *C. panicea* and *Equisetum variegatum*.

The Phytogeographical Relationships of the Association

The variation in calcareous flush communities seems to be greater than in any other series of related communities. Oberdorfer (1967) lists several communities for the pre-alpine region of southern Germany, which have numerous facies and variants. Amongst these are:- Juncetum alpini Phil. 1960 - a pre-alpine Association with an optimal Equisetum variegatum variant derived from an intermediate Carex lepidocarpa-rich facies; Parnassio-Caricetum pulicaris (Oberd 57.) Görs 1963 - a lowland Association dominated by Carex pulicaris and C. demissa.

Both Phillipi (1960) and Görs (1963) remark on the variation within these communities and relate all the different variants of dominance to a single Association in each case. This is probably the best solution for the wide variation exhibited by sedge-flushes in the northern Pennines.

The Caricetum lepidocarpae-hostianae Kobresietosum is closely related via the dominance of Kobresia simpliciuscula (bipartita) to the Association Kobresietum bipartitae Br.-Bl. in Nadig 1942. Oberdorfer (1967) places this Association in the Alliance Caricion bicoloris-atrofuscae, but the Teesdale communities lack any of the character species of this Alliance and also show too close a relationship to other Carex hostiana-lepidocarpa communities to merit a separate Association.

Association-group Schoenetum nigricantis W. Koch 1962.
Table 31b.

Synonymy: Schoenus nigricans-Cirsium dissectum Ass. Br.-Bl. & Tx. 1952.

(2) A group of open, calcareous flush communities dominated by Schoenus nigricans comprise the next stage in terms of wetness in the series from calcareous grassland to sprigs. Table 31b comprises constancy tables for Aufnahmen from Westmorland, Kishorn in Wester Ross, Lough Derg and the Burren in western Ireland. Two Sub-associations are recognisable in all regions:- Sub-ass. typicum where Schoenus is dominant and the bryophyte layer is composed mainly of Scorpidium and Campylium stellatum; Sub-ass. eleocharietosum where Eleocharis quinqueflora is more or less co-dominant with Schoenus. Oberdorfer (1957) divides Schoenetum nigricantis up in to separate Associations based mainly on the differing floristic composition of the stands in sub-alpine and lowland regions. His Primulo-Schoenetum shows close affinities to several stands with Primula farinosa from Sunbiggin Tarn, Westmorland. The lowland stands from western Ireland form part of a different zonation series around a lake, e.g.

Open water

Cladietum marisci Zobrist 1935

Phragmition W. Koch 1926 | Caricetum elatae W. Koch 1926

Scirpo-Phragmitetum W. Koch 1926

Eriophorion latifolii | Schoenetum nigricantis

Cynosurion pasture

along the south-eastern shores of Lough Bunny, Co. Clare. These stands fall within the Schoenus-Cirsium Ass. of Braun-Blanquet & Tüxen (1952), but because of insufficient data are left with the sub-alpine stands in the Schoenetum nigricantis.

(3) Several of the Gymnostomum recurvirostrum dominated bryophyte flushes of Upper Teesdale show affinities to the Eriophorion latifolii, but initial impressions suggest that they are more closely related to the Alliance Cratoneurion commutati W. Koch 1928 of the Class Montio-Cardaminetea Br.-Bl. & Tx. 1943.

C. Communities of Leached Grassland and Calcareous Heaths

(1) The Class Nardo-Callunetea Prsg. 1949, contains most of the lowland and sub-montane leached grasslands and heaths which are dominated by coarse grasses, ericaceous shrubs and gorse. The Order Nardetalia Prsg. 1949 and the Alliance Nardo-Galion saxatilis Prsg. 1949, comprise most of the familiar species-poor acidic grasslands dominated by Nardus

stricta, Agrostis spp., Deschampsia spp., Potentilla erecta and Galium saxatile.

Association Nardo-Galietum saxatilis Prsg. 1949 Table 32.

Synonymy. Leached grasslands p.p. Balme 1951, Grime 1963a.
Neutral/Acidic grasslands p.p. Moss 1913, Tansley 1939.

Habitat details

The Association occurs commonly at the tops of the dale sides in Derbyshire and on higher plateaux above 1200 ft. (380 m.) in Derbyshire, Breconshire, Yorkshire and Westmorland. These stands are only fragmentary when compared to the extensive areas of Nardo-Galietum, which occur in many parts of sub-montane Britain on non-calcareous soils. In the limestone regions, the Association occurs on leached, acidic slopes in areas where the precipitation component of the climate is pronounced, e.g. Grime (1963a) describes a soil catena in Cressbrook Dale, Derbyshire, and Bryan (1967) a climosequence of soil formation due to the high precipitation. As a result, podsolised Brown Earths develop and the vegetation develops hand in hand from a calcareous Helictotricho-Caricetum flaccae community to an acidic Nardo-Galietum community.

Characteristics of the Association

Dominance in most stands of the Association is shared between Agrostis tenuis, Nardus stricta, Galium saxatile, Potentilla erecta, Festuca rubra and Deschampsia flexuosa. Heath species such as Calluna vulgaris and Vaccinium myrtillus are constant, but never attain dominance as in the familiar heath-type communities on peat or Iron-Humus Podsols.

No Sub-associations are recognisable in the Aufnahmen collected, but it is probable that a more representative sample from non-calcareous regions and upland areas may reveal several Sub-associations.

(2) The second Order of the Class Nardo-Callunetea, Calluno-Ulicetalia (Quantin 1935) R.Tx. 1937, is not widespread on limestone in the British Isles, and only one Association, Agrosto-Ulicetum gallii of the Alliance Ulicion gallii Des Abb. & Corillon 1949, is detected.

Association Agrosto-Ulicetum gallii (Tansley 1939) Table 33.

Synonymy: Ulicetum gallii Tansley 1939.
Agrostis setacea localities p.p. Ivimey-Cook 1959.
Ulex heath Nodum 2 Moore 1960.
Ulex gallii heaths Clark 1968.

Habitat details

The Association is described from the leached podsolic soils overlying the limestones in the west of England and Wales - in Somerset, Gower and Ewenny, Anglesey and Great Ormes Head and two localities in Derbyshire. As is the case with most of the Associations of the Nardo-Callunetea, their maximum expression and distribution is on siliceous soils and rocks, and the Aufnahmen used here as representatives of the Association are probably a fragment of a greater variation.

Characteristics of the Association

The Association is dominated by *Ulex gallii* and/or *Ulex europaeus* with *Agrostis tenuis*, *A. stolonifera* and *A. canina*, forming a compact sward where the *Ulex* is less dense. *Erica cinerea*, *Sieglingia decumbens* and *Festuca rubra* are often co-dominant while *Galium saxatile*, *Potentilla erecta*, *Hypericum pulchrum*, *Anthoxanthum odoratum* and *Pseudoscleropodium purum* are constants. In all the localities in which it was observed, the Association formed a mosaic zone between a pure heath and limestone grassland. Consequently, many species characteristic of *Mesobromion* hang on in this Association, e.g. *Poterium sanguisorba*, *Helianthemum chamaecistus* and *Filipendula vulgaris*. The mosaic is exaggerated in places by drift as at Long Dale, Derbyshire, and blown sand at Ewenny Down. The presence of Calcicoles in this seemingly acidic habitat is probably due to the rooting depths of these plants in the deeper calcareous horizons of the sub-soil.

Two provisional Sub-associations are recognised:-

(a) *Sub-ass. of Agrostis setacea* is described from S. Wales and is differentiated by the presence of *Agrostis setacea*.

These communities are probably at the northern limits of the range of a widespread community type in western France and Spain and in several localities in southern England.

(b) Sub-ass. typicum includes all the stands to the north and west of the distribution zone of Agrostis setacea. This Sub-association is probably more widespread in the mountains of Wales and in S.E. Ireland (Clark 1968), and as far north as the Scottish Borders. Derbyshire is probably its easternmost locality.

(2) In limestone regions in the north and west of the British Isles where the post-glacial climax forest was probably Pinus sylvestris woodland as opposed to mixed deciduous (Godwin 1956), several shrub/heath communities referable to the Alliance Juniperion nanae Br.-Bl. 1939 of the Class Vaccinio-Piceetea Br.-Bl. 1939, occur.

Association Arctostaphyleto-Dryadetum (Iv.Ck. & Proct. 1966)
Table 34.

Synonymy: Arctostaphylos uva-ursi-Dryas octopetala Nodum Iv. Ck. & Proct. 1966.

This Association probably represents a calcicolous Sub-association of a more widespread Association similar to the Juniperetum nanae McV. & Rat. 1962.

Habitat details

The Association is described mainly from the higher mountains of Black Head and Gleninagh in the Burren, Co. Clare.

Related communities included in Table 34 are recorded on the Dalradian limestones below Ben Schiehallion, Perthshire, and near Kishorn, Ross-shire on Cambrian limestone. In the Burren, the Association descends to low altitudes, but is found predominantly above the 200 m. contour. In Scotland the sites are both around 330 m. on primitive humus rich soils over limestone pavement.

Characteristics of the Association

The Association is dominated by the dense growth of Arctostaphylos and the prostrate form of Juniperus communis, ssp. nana, Dryas octopetala and other calcicolous herbs of the Seslerio-Mesobromion, such as Galium sterneri, Koeleria cristata, Sesleria caerulea and Thymus drucei. These latter species are usually absent in the Scottish localities, but Helianthemum chamaecistus occurs in the Schiehallion locality.

The reltionships to the Juniperetum nanae McV. & Rat. 1962, is indicated by the addition of a constancy table for their data to Table 34.

D. Communities of calcareous scrub

(1) Müller (1962) proposed the Class Trifolio Geranietea to include all the heterogenous "Saumgesellschaft" or woodland border communities, which show obscure relationships to "Mantel" or true, natural woodland. These communities

contain species which, though they are frequently present in the woodland or the open grassland, seem to have their maximum expression in the border zone, e.g. Corylus avellana, Populus tremula, Geranium sanguineum, Origanum vulgare, Trifolium medium, Epipactis helleborine, Aquilegia vulgaris and Lithospermum purpureocaeruleum. The sole Order Origanetalia Th. Müller (1962), contains two Alliances, only one of which, the Geranion sanguinei R.Tx.1961, was encountered in this survey.

Association Geranio-Coryletum. Table 35.

Synonymy: Retrogressive Corylus Scrub Moss 1913.

This Association is described only from the Derbyshire Dales in north and west-facing localities on dry protorendzina soils (see Figure 5). The community appears to be extremely thermophilous and is found towards the tops of the dale sides forming a fringe community around semi-natural ash-woodland (Campanulo-Fraxinetum Shimwell & Bellamy 1967).

The Association is characterised by the presence of low bushes of Corylus avellana, often less than one metre tall, in a semi-scree habitat which is extremely floristically diverse. Many Mesobromion species such as Poterium sanguisorba, Helianthemum chamaecistus, Gentianella amarella etc., are common in the community. Species characteristic of these border areas are Epipactis helleborine, Geranium sanguineum, Silene nutans, Origanum vulgare and Aquilegia vulgaris. The dominant grasses in the Association are usually, Brachypodium sylvaticum or Melica spp.

The Association shows close floristic affinities to Geranio-Anemonetum silvestris Th. Müller 1961, described from southern Germany. The Aufnahme from Cressbrook Dale with a canopy of Populus tremula does not appear to have a counterpart in Derbyshire or anywhere in the British Isles, and seems to be closely related to the alpine Association Coryleto-Populetum Br.-Bl. (1919) 1938, (see Braun-Blanquet 1949).

(2) The majority of scrub and scrubby woodland types are placed in the Order Prunetalia R.Tx. 1952 of the Class Querco-Fagetea Br.-Bl. & Vlieger 1937. These embrace most types of shrubby hedgerows, thickets and dune scrubs dominated by a number of species such as Prunus spinosa, Crataegus monogyna, Salix repens, Hippophäe rhamnoides and Rubus fruticosus agg. Table 36 is a constancy table which summarises 20 Aufnahmen from four Associations in three of the Alliances of the Order Prunetalia:-

(a) Prunion fruticosae R.Tx. 1952 is an Alliance which contains all the familiar hawthorn-blackthorn dominated communities which occur widely throughout the British Isles in marginal habitats along hedgerows and woodland borders.

(i) Crataegus-Rosa pimpinellifolia Ass. is described from the Magnesian limestone of Co. Durham, and from Derbyshire. It tends to be a northern Association and is probably much more widespread. Rosa pimpinellifolia characterises the Association and also relates it to several dune communities dominated by this species and Geranium sanguineum.

(ii) Clematito-Prunetum is essentially the southern equivalent of the Crataegus-Rosa Ass. and is characterised by the dominance of the climbing Clematis vitalba, which smothers other shrubby species such as Prunus spinosa and Sambucus nigra. The northernmost locality recorded for the Association is at Ticknall in southern Derbyshire.

(b) Salicion arenariae R.Tx. 1952, the common Alliance of dune slacks throughout the British Isles, was only recorded in three localities on limestone in Co. Durham. The provisional Association Salicetum repenti-nigricantis is a low scrub usually comprising a hybrid swarm between the two willows Salix repens ssp. argentea and S. nigricans. The Association is predominantly coastal in Co., Durham and it seems that the only other possible localities for this community type, can be in the coastal areas of east-central Scotland, where the ranges of the two willows overlap again (cf. Perring & Walters 1962).

(c) Rubion subatlantici R.Tx. 1952 contains the familiar Rubus fruticosus-Ligustrum vulgare dominated impenetrable coastal scrub of cliffs in south and west England and Wales and Ireland. The Association Ligustro-Rubetum ulmifolii (Table 36 (4)), is based on $50m^2$ square quadrats from, S. Wales, Somerset, Devon and Sark in the Channel Island. Ligustrum, Lonicera periclymenum and Rubus sect./discolores (frequently R. ulmifolius) are dominant over large areas, whilst Pteridium aquilinum and Iris foetidissima differentiate the Alliance from others in the Order Prunetalia.

(3) ALLIANCE POTENTILLION FRUTICOSAE Comb. nov. Table 37.

The rare and localised "Saumgesellschaften" dominated by Potentilla fruticosa, show affinities to no other Alliance of the Order Prunetalia, and it is proposed to erect a new Alliance. These communities appear to be related to the "Mantel" of the Alliance Alno-Padion and the lists in Table 37 from Teesdale, indicate this relationship. In one locality Potentilla was observed growing on an alluvial stream bed under a closed canopy of Fraxinus, Alnus and Prunus padus. The Alliance is probably restricted to the Burren district of W. Ireland, the English Lake District, Upper Teesdale and the islands of Öland and Gotland in the

Baltic Sea. Braun-Blanquet (1948) records the shrub in two Associations of the Caricion davallianae Alliance (Eriophorion latifolii) in the valleys of the eastern Pyrenees. The British and Irish communities show few resemblances to this Alliance but the three geographic regions have several species in common, e.g. Gentiana verna, Sesleria caerulea, Saxifraga aizoides, Primula farinosa, Bartsia alpina, etc.

The high complement of species of damp meadows in Irish localities led Ivimey-Cook & Proctor (1966a) to place the communities in the Class Molinio-Arrhenatheretea. However, the more dense stands show few relationships to any Class or Order other than the Prunetalia and then only via the occurrence of Prunus spinosa and the general physiognomy of the community. These features and the apparent "Saum-Mantel" relationships to Alno-Padion have led to the erection of the Alliance Potentillion fruticosae.

Association Potentilletum fruticosae Table 37.

Synonymy: Potentilla fruticosa associated species Elkington & Woodell 1963.
Potentilla fruticosa stands Ivimey-Cook & Proctor 1966.

Habitat details

The Association occurs on damp, alluvial soils and pebble banks which are periodically irrigated with flood water. This feature further relates the Alliance to the

Alno-Padion. In Teesdale, the localities are predominantly riverside communities in dolerite rock crevices or on alluvium, whilst the Irish localities are around small turloughs which vary greatly in area and often flood the lower zone of the Potentilletum fruticosae. Ivimey-Cook & Proctor (1966a) report that they are found at a few metres above the summer water level to above the lower level of Crataegus and Prunus spinosa. In the Lake District localities the Association occurs on screes above Wastwater lake.

The distribution pattern of the Association is similar to that of the Seslerio-Mesobromion communities described previously, and the only possible interpretation of this pattern is again left with survival from Late glacial times.

Characteristics of the Association

The Association is characterised by the dominance of Potentilla fruticosa and the high constancy of species such as Sesleria caerulea, Briza media, Thymus drucei and Festuca ovina. The damp nature of the environment enhances the performance and diversity of Molinietalia species, such as Succisa pratensis, Filipendula ulmaria, Deschampsia caespitosa, and Heracleum sphondylium, and Potentilla often occurs sparingly in a community referable to this Order (Table 37, lists 1 and 2). Interesting alpine species which occur in the Teesdale localities and which relate to the communities to those of the Pyrenees, are Galium boreale, Thalictrum alpinum and Polygonum viviparum. Crataegus monogyna, Prunus spinosa and Rosa pimpinellifolia are the only three Prunetalia character species which occur in the Association.

Two provisional Sub-associations are recognised:-

Sub-ass. typicum includes the majority of the stands described and is characterised by a continuous shrub layer of Potentilla fruticosa. Prunetalia character species are most common in this Sub-association.

Sub-ass. salicetosum phylicifoliae is recorded only on the banks of the River Tees and is differentiated by the co-dominance of Salix phylicifolia with Potentilla. This Sub-association indicates the "Saumgesellschaft" relationships to the Alno-Padion Alliance, and the final list in Table 37 is an example of an Alnus-Fraxinus woodland with Potentilla in the understorey on alluvial soils in Teesdale, which is referable to this Alliance.

PART IV

Chapter 6.

Discussion.

(A) Introduction - the Phytosociological bases for Conservation

The Z-M system of plant sociology has long been advocated as a thorough technique for the initial survey of a region or of a particular vegetation type. Like the surveys of Braun-Blanquet & Tüxen (1952) and O'Sullivan (1965) in Ireland, this present survey emphasises its value in the production of a manual of qualitative data which serves as a factual background of information on which conservation proposals can be based. The similarity of the format of the thesis to a catalogue is unavoidable and is necessitated by the desire for ready reference to a set of data for a particular site. The subsequent comparison of this data with that for similar sites enables a broad overall view or "Überblick" of a vegetation type by reference to an abstract synthetic representation of the stand descriptions - the Association Table.

AS THE BASIS OF THE SOCIOLOGICAL AND HIERARCHICAL CLASSIFICATION SYSTEM OF THE Z-M SCHOOL, THE ASSOCIATION COULD ALSO BE ADOPTED AS TH E BASIC UNIT FOR A SYSTEMATIC APPROACH TO THE CONSERVATION OF A REPRESENTATIVE SAMPLE OF ALL VEGETATION TYPES FOR THE PURPOSE OF SCIENTIFIC INVESTIGATION.

Reference to an Association Table immediately details the range of variation within the Association, the most typical stands and the trends away from the median type. These multidimensional trends are frequently associated with small changes in soil properties and in several cases, are apparently identifiable with short term successional trends.

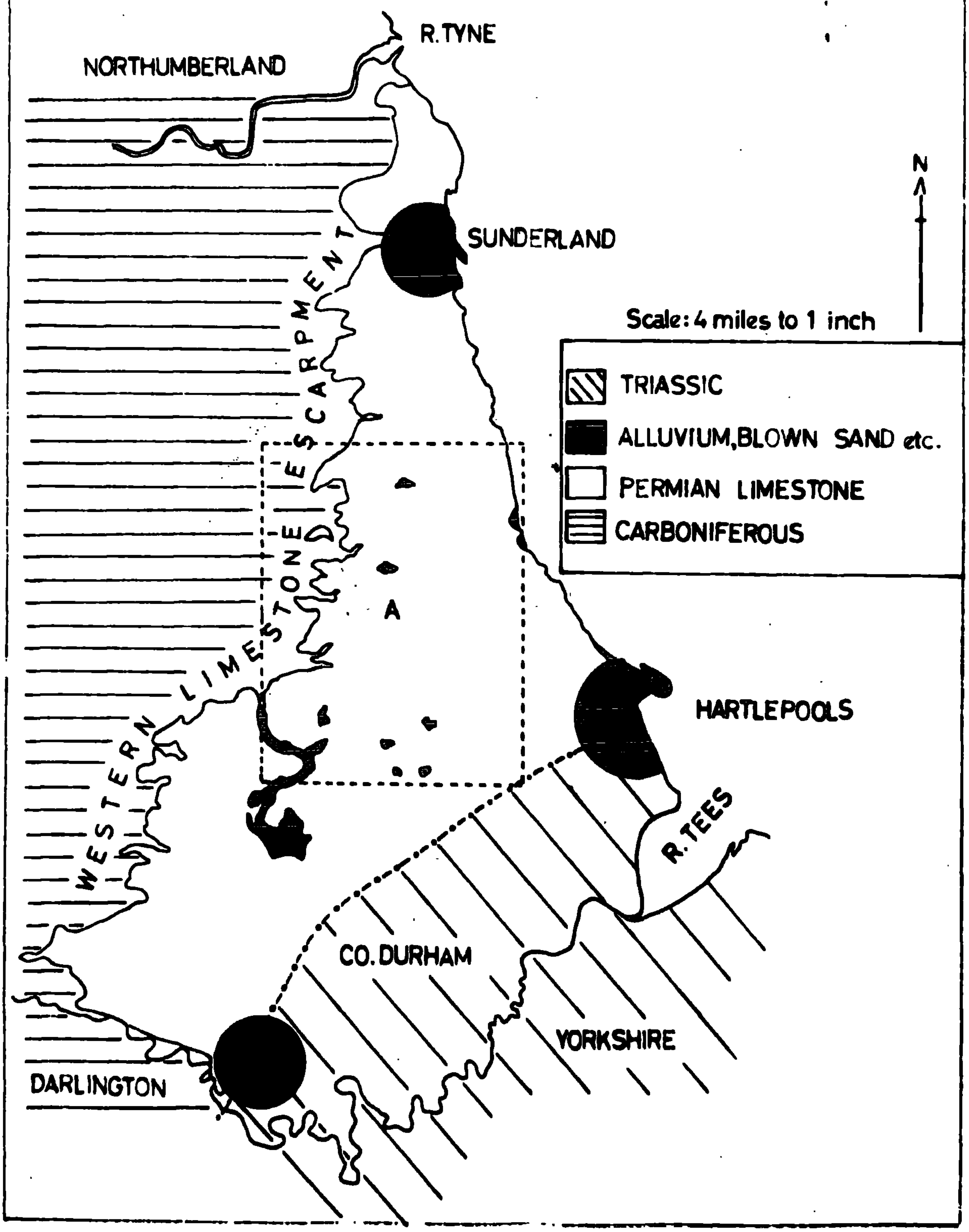
On a broader regional basis, Association structure and type can frequently be related to climatic trends. This phenomenon has been pointed out by Bellamy (unpubl.) and used to emphasise the change in floristic composition and structure of ombrophilous mire communities with climatic change in western Europe. Similarly, with grassland types, broad relationships between climate type and grassland composition are evident, e.g. the relationships of the North and South Wales grasslands of the Helianthemo-Koelerietum with the same climate type of Walter & Lieth (1967).

Whilst climatic differences are important factors affecting community structure and change on a regional basis, and are important at the level of the recently proposed International Commission for Nature Conservation (International Colloquium, Todenmann, 1968), the more practical problems of community management and conservation can only be answered by detailed floristic and experimental ecological investigations based on an initial vegetation and soil survey.

FIGURE 27. Map of the Magnesian Limestone outcrop in eastern Co. Durham.

THE MAGNESIAN LIMESTONE OF COUNTY DURHAM

MAP 1: SOLID GEOLOGY



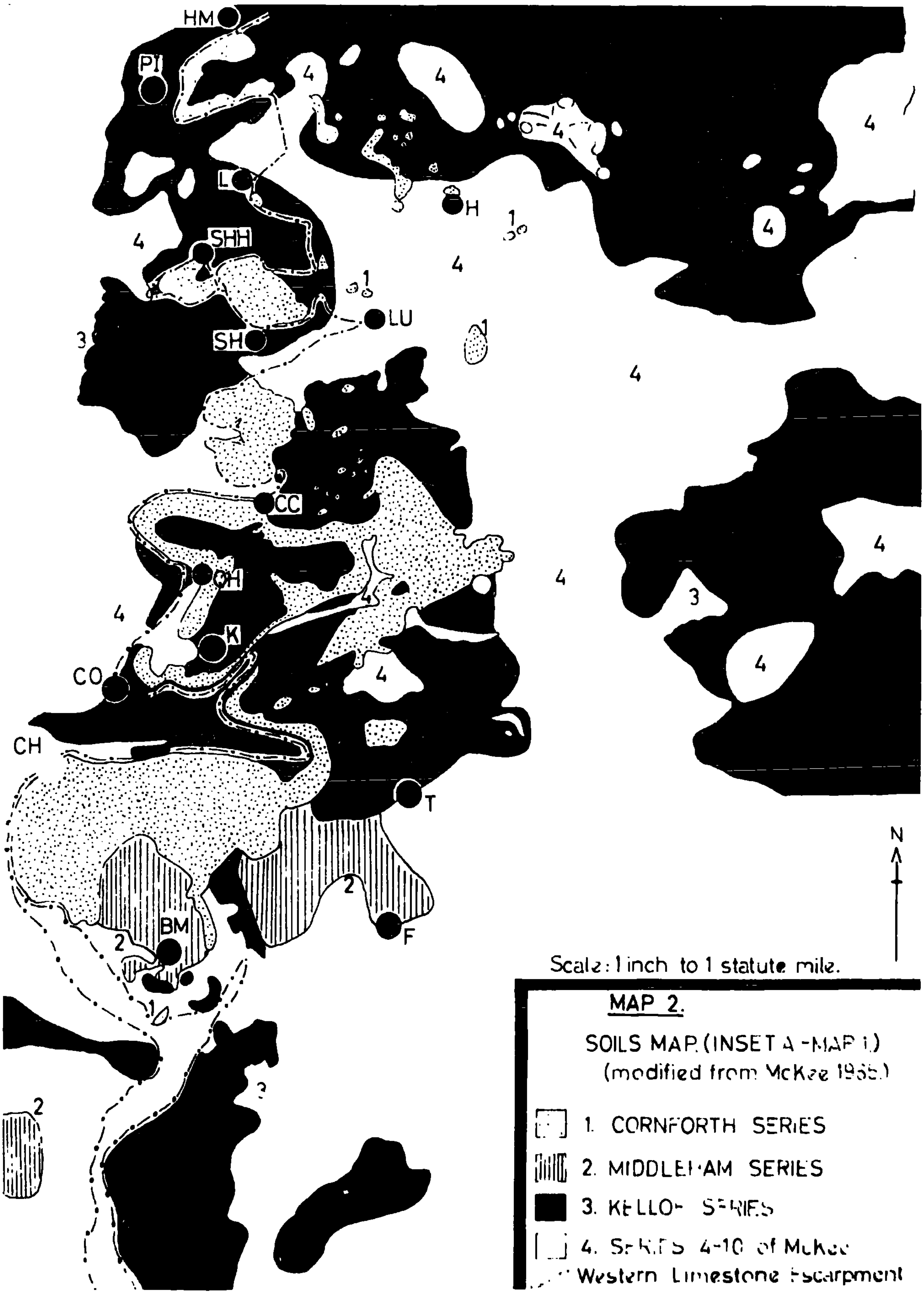
W. H. Pearsall (1950) summed up the problem thus - "It is not enough to conserve blindly, because the trends of soil and vegetation operating today determine what the conserved site will be in the future, and will often be unlike what is there now". With a basic soil and vegetation survey accomplished and with most of the minor variations of a vegetation type elucidated in Association Tables and an overall Synoptic Table (Figure 14), hypotheses on the nature of management practice and the type of experimental approach required can be formulated to produce a programme for conservation of that particular vegetation type at its present status. The foregoing points are best illustrated by a specific example - the Association *Seslerio-Helictotrichetum* described from the Magnesian Limestone escarpment of Co. Durham (Figure 27).

(B) Proposals for the conservation of localities for Seslerio-Helictotrichetum

(i) Available Vegetation Data. From the floristic and ecological data presented in the appropriate section of Chapter 4 and Table II, it may be concluded that the Association *Seslerio-Helictotrichetum* is a grassland type unique to the limestones of eastern Durham. Reference to Table 19 also suggests that this lowland thermophilous Association of the *Seslerio-Mesobromion* Alliance has no

FIGURE 28. Soil types in an area of the Magnesian Limestone escarpment (from Figure 27, Inset A).

(Modified and reproduced by permission of Dr. R. F. McKee, University of Sierra Leone).



MAP 2.

SOILS MAP (INSET A - MAP 1)
(modified from McKee 1965)

close counterpart in western Europe. Such conclusions are only possible when a broad "Überblick" has been obtained from the application of a survey system which is in common usage throughout Europe.

(ii) Available Pedological Data. The east Durham plateau region has been surveyed in detail by McKee (1965) and Figure 28 (redrawn from the work of this author) illustrates the more important soil types relative to the *Seslerio-Helictotrichetum*. Over most of the undulating plateau the soils are affected by drift and the deeper profiles promote extensive arable farmland. On the steeper western escarpment the soils are generally free from drift and the shallow rendziniform profiles of the Cornforth and Middleham Series, are developed from the parent friable, yellow lower limestones. Both soil types are exceptionally thin, uniformly sandy loams directly over limestone with little or no drift influence and good drainage. The Middleham Series differ mainly in that they are brash-like throughout with diffuse boundaries between horizons and are developed over the upper beds of the lower limestone series around Bishop Middleham and Fishburn. The maximum profile depth in both soil types is around 24" (60 cms.) with a typical profile A:C/D, but a B horizon may appear as a shallow weathered drift. The pH range is between 7.2 and 7.8 and there is a high content of sand (60-70%) and low (3-20%) humus content. The Kelloe Series (Fig. 28, Type 3) are thin drift soils transitional between the former types and the deeper drift soils (Type 4), and are located mainly in the arable areas of the plateau.

(iii) Correlations between vegetation and soil. Once the correlations between vegetation and soil are better understood it becomes possible to hypothesise on the stability of the vegetation, its longevity, i.e. status with regard to disturbance, and the form of management needed to maintain the vegetation at its present level of community organisation. In the past there has been little correlation between broad soil and vegetation surveys. On the one hand, the Soil Survey of Great Britain shows a distinct bias toward an agricultural rather than a potential natural vegetation/ soil type relationship, whilst on the other hand, the present ecological trend is towards the autecological correlations of plant and environment.

The relation between vegetation and soils seems to be best studied according to a set procedure which logically is:-

(a) Qualitative vegetation and soil surveys, to establish the basic trends of vegetation development and stability and the related general soil properties.

(b) The study of the available soil nutrients and mineral cycling via autecological and detailed synecological studies.

In the present survey, several of the general soil properties of the soils of the Seslerio-Helictotrichetum were studied, e.g. pH, total carbonates, % humus, calcium and magnesium. The choice of these properties was based entirely on an initial impression obtained from the vegetation survey that variation in some of the properties could be responsible for observable changes in vegetation. The validity of these impressions is only partly tested by the following results (Figures 30, 33) and full investigation of the importance of the effects of these soil properties on the vegetation requires a more detailed soil analysis technique. (For full results and details of methods refer to Appendix).

The method of representation chosen for the correlations of vegetation and soil properties within the Association Seslerio-Helictotrichetum, was the ordination technique proposed by Bray & Curtis (1957), which was successfully used by Gittins (1965a,b) for this purpose. Although this method has been criticised by Austin & Orloci (1966) as an inaccurate method of construction of axes, its creation of a "theoretical hyperspace" (Whittaker, 1962, 1967), on which can be superimposed various sets of ecological data seems to be a useful tool in the interpretation of vegetation to habitat relationships. Moreover, Bannister (1968) concludes that the Bray & Curtis similarity coefficient (C) method produces a more readily interpreted ordination when dealing with a wide range of species-richness and abundance than the Euclidean distance (D) method of Austin & Orloci (1966).

Figure 29 represents an ordination of some 45 stands or Aufnahmen of the Seslerio-Helictotrichetum and the various symbols indicate the different Sub-associations and variants recognised within the Association. The similarity coefficient used was of the form:

$$C = 2w/(a + b)$$

where w is the sum of the species common to both stands and a and b are the number of species for each stand under comparison. The corrected measure of interstand distance of Bray & Curtis (1957) C max-C, where C max is the highest value of C found within the matrix of comparison, was used for the ordination. The calculated C max was 85 and the greatest interstand distance of 56 units was between stands 57 and 8, which loci were used for construction of the X axis. Stands 52 and 5, which were 50 units apart and close on the X axis, were used for the construction of the Y axis.

The ordination of an abstract unit produces a scatter

FIGURE 29. Ordination of an Abstract Unit - the Association Seslerio-Helictotrichetum.

Legend:

1. Sub-ass. typicum.
2. Sub-ass. of Helictotrichon pubescens.
3. Sub-ass. of Encalypta and Plantago maritima.
4. Sub-ass. of Helictotrichon, Rosa variant.
5. Sub-ass. Caricetosum pulicariae, Selaginella variant.
6. Sub-ass. of Helictotrichon, Bromus variant.

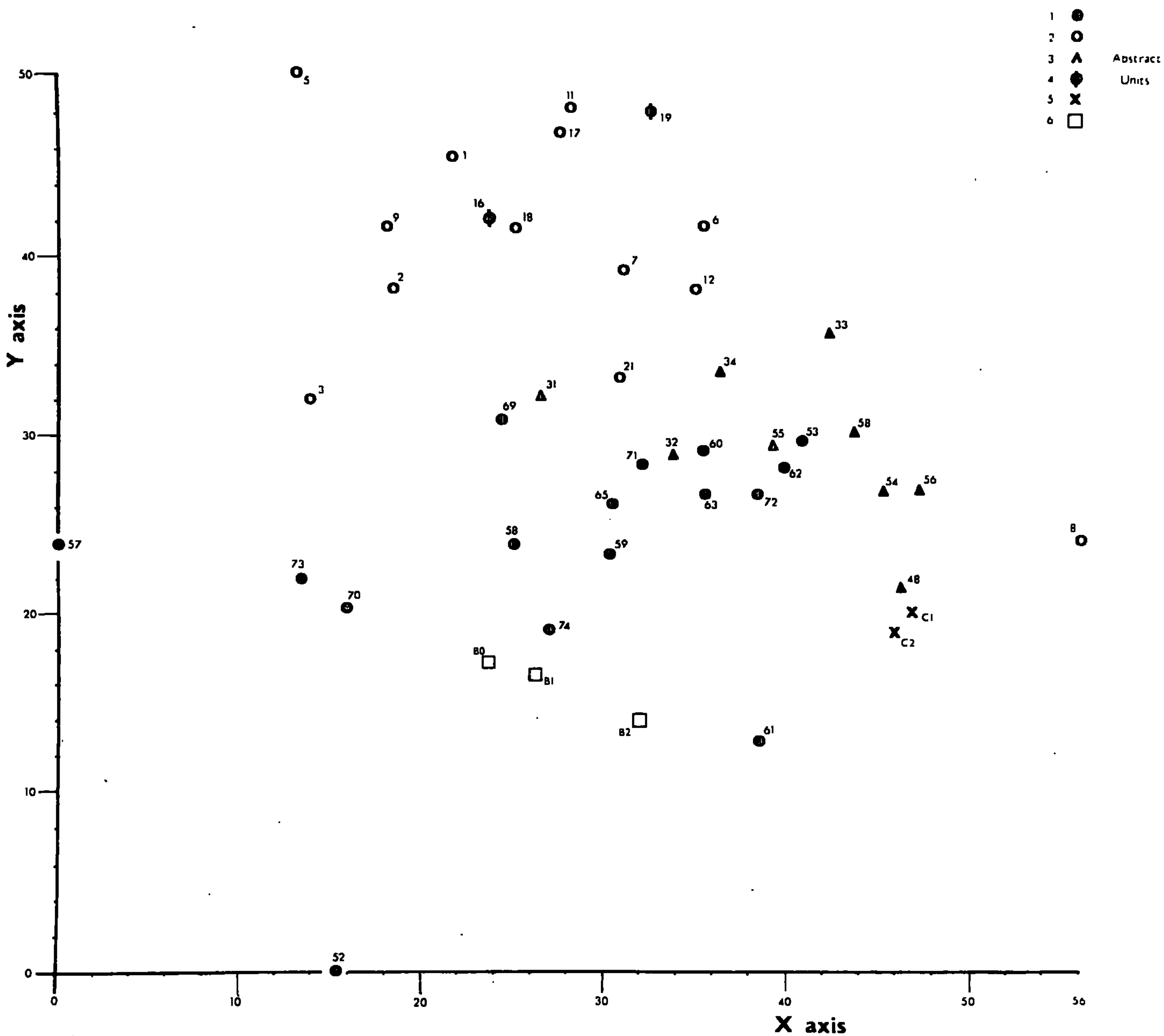

1
2
3 Abstract
4 Units
5
6
Y axis
X axis
0
10
20
30
40
50
56

diagram effect, probably because of the low dissimilarity figures (C max - C = 56 being the greatest), and the familiar ordination patterns produced by adjacent quadrats along observable ecological gradients (e.g. Figure 32) are not depicted. Neither does the superimposition of soil factors indicate discreet ecological or pedological units, but the range of variation of a particular soil property within the Association is apparent at a glance. However, several broad vegetation/soil correlations are evident (Figure 30).

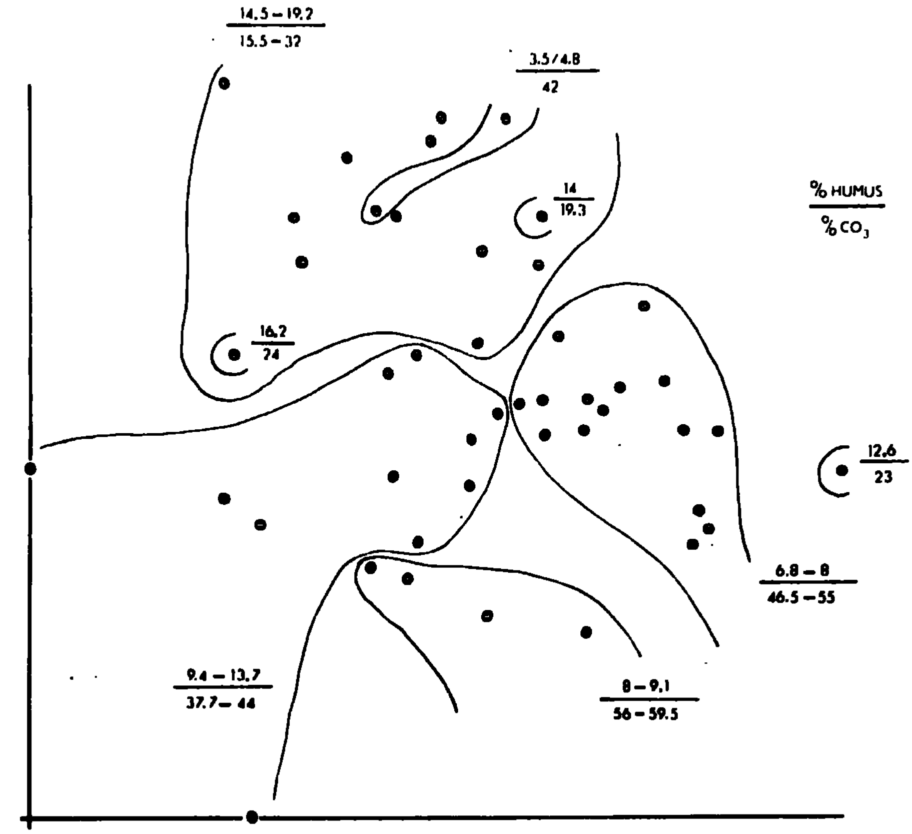
The majority of the stands of the Sub-ass. typicum and Sub-ass. of Helictotrichon pubescens, typical variant (Fig. 30, closed and open circles referred to as Types 1 and 2) show a wide variation in all the four factors shown in Figure 31. The component stands of Type 2 have a higher percentage of humus than other types, whilst the figures for total carbonates are generally smaller than in Type 1, and the pH range of 6.8-7.4 has the lowest mean of any group (Fig. 31A). The isolines for measurements of calcium and magnesium expressed as gms/100 gms dry soil do not follow the same division of stands, but it will be noticed that the figures for Types 1 and 2 are considerably lower than those for other floristic units.

Type 4 (closed circle with protruding diameter), Sub-ass. of Helictotrichon pubescens, Rosa variant, shows an

FIGURE 30. Correlation of environmental and vegetation variables within the ordination of the Association Seslerio-Helictotrichetum.

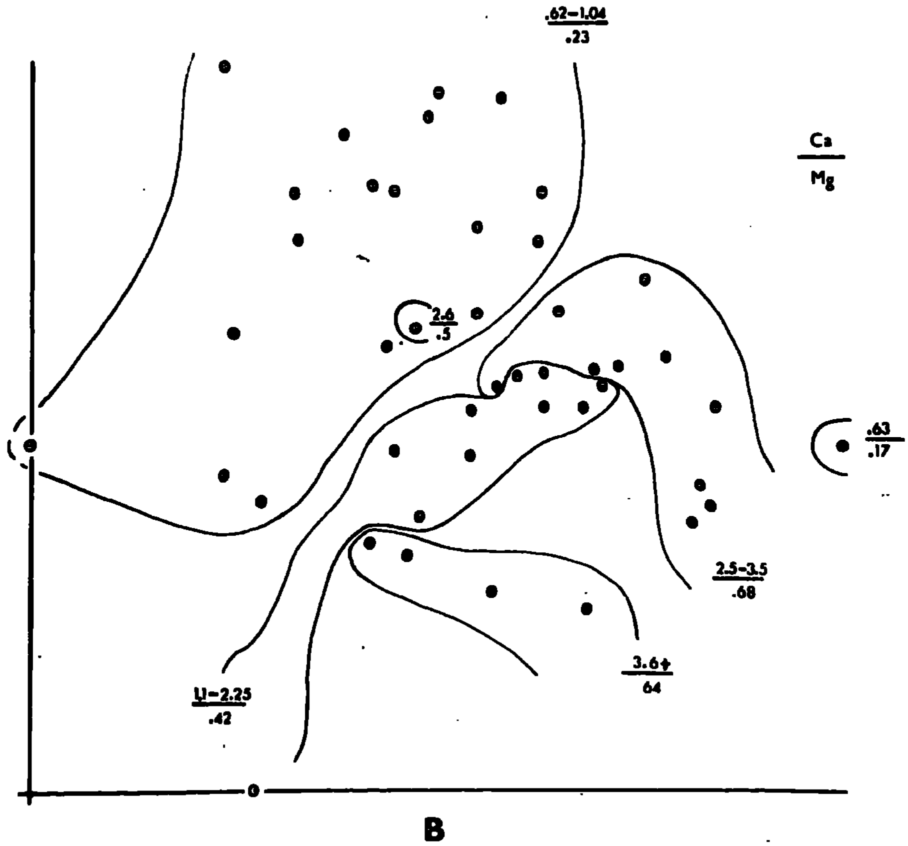
A. Humus/total carbonates relationships.

B. Calcium/Magnesium relationships.



14.5 – 19.2 / 15.5 – 32
3.5/4.8 / 42
14 / 19.3
% HUMUS / % CO3
16.2 / 24
12.6 / 23
6.8 – 8 / 46.5 – 55
9.4 – 13.7 / 37.7 – 44
8 – 9.1 / 56 – 59.5

A



.62–1.04 / .23
Ca / Mg
2.6 / .5
.63 / .17
2.5–3.5 / .68
3.6+ / 64
1.1–2.25 / .42

B

unusually low humus percentage and a relatively high carbonate figure of 42. Subsequent investigations have revealed that the area had been burnt some years previously, which event probably led to the invasion of the shrubs.

Type 3 (closed triangle) Sub-ass. Encalypta and Plantago maritima, Type 5 (cross) Sub-ass. Caricetosum pulicariae, Selaginella variant and Type 6 (open square), Sub-ass. of Helictotrichon pubescens, Bromus erectus variant, have four features in common:-

(a) relatively low % humus;

(b) high % total CO_3;

(c) (d) high calcium and magnesium figures.

With the exception of Aufnahme 53 and B0, B1, B2, all these stands are located on quarry spoil-banks which are probably less than one hundred years old, and where the amount of humus accumulation and soil formation is small. In this respect, no pedological distinction is apparent between Types 3 and 5. Type 4 however, and Aufnahme 61 of Type 1 are all recorded from the brashy soils of the Middleham Series and, though located on and near roadsides, appear to be comparatively undisturbed sites. These soils and stands are picked out in the ordination by their extremely high carbonate and calcium figures, being 59.5% and 4.9 gms/100 gms dry soil respectively.

(iv) Vegetation/Soil correlations and their relationships to theories of succession. The variation in edaphic factors within the Association *Seslerio-Helictotrichetum* and the parallel variation in vegetation enables several tentative suggestions to be made with regard to the mechanisms involved in some stages of the theoretical succession on the Magnesian Limestone as outlined in Figure 21, (see folder volume). On disturbed sites the initial colonisers of quarry waste are ruderals such as *Hypericum* spp. and *Chamaenerion angustifolium*. Several mosses such as *Encalypta* spp. and *Ceratodon purpureus* colonise damper, more shaded habitats and form a patchy carpet which gradually adds more humus to the habitat. The subsequent colonisation of the habitat by the coarse grass *Sesleria caerulea* and herbs which require semi-open, unstable habitats, gives the characteristic structure of the Sub-ass. of *Encalypta* and *Plantago maritima*. On older disturbed habitats where there has been, (a) considerable humus accumulation; (b) some nitrogenous enrichment via grazing; (c) reduction in pH and decrease in total carbonates due to leaching;
(d) development of a deeper soil profile, coarse grasses, such as *Helictotrichon pubescens* and *Dactylis glomerata*, and mesophilous indicators of grazing, e.g. *Daucus carota* and *Briza media*, begin to replace the acrocarpous bryophytes

and Sesleria to give the Sub-ass. of Helictotrichon pubescens typical variant. In other areas this stage in succession is prevented by the invasion of Salix capraea and S. atrocinerea bushes to produce a low hybrid scrub, a seral stage where development mechanisms seems to be unanswerable via the above pedological data.

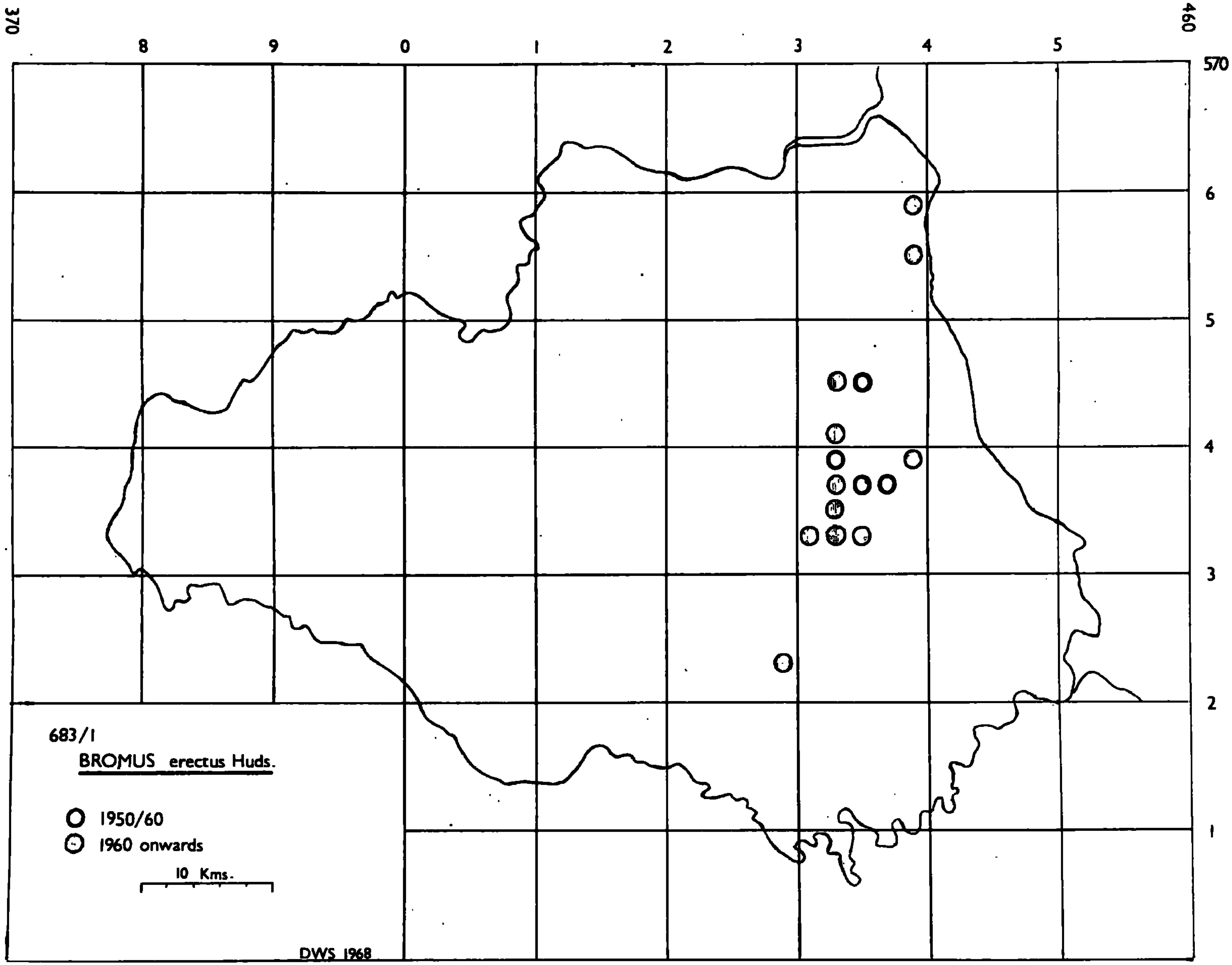
It cannot be suggested that there is a successive step from Sub-ass. of Helictotrichon pubescens to Sub-ass. typicum, because the community organisation and edaphic factors controlling development are more or less the same. The decrease of floristic diversity in Sub-ass. typicum and hence the appearance of a more stable community indicate the grasslands are older and perhaps semi-natural. For similar reasons, it is difficult to envisage the short-term development of this grassland type in recent times from the disturbed Sub-ass. of Encalypta and Plantago maritima.

It appears that burning and the consequent destruction of much of the raw humus in the habitat probably causes invasion of Rosa pimpinellifolia and Crataegus monogyna, and observations over three years have indicated that this step may proceed when grazing pressures are relieved.

The communities of the Sub-ass. of Helictotrichon pubescens, Bromus erectus variant appear to have no place in the disturbed succession sequence, in spite of the

FIGURE 31. The distribution of *Bromus erectus* in Co. Durham.

(Mapped on a 2 km^2 (tetrad) basis).


683/1
BROMUS erectus Huds.
1950/60
1960 onwards
10 Kms.
DWS 1968
370
460
570
8
9
0
1
2
3
4
5
6

relationships suggested by their brash-like soils. In fact, Bromus erectus was observed growing on similar soil types over Jurassic limestone, throughout the Cotswold Hills and on the Magnesian Limestone of Yorkshire and Derbyshire. It seems that in eastern Co. Durham the interface overlap between two otherwise distinct calcareous grassland plagioclimax-dominant zones occurs - Sesleria to the north and west and Bromus erectus to the south. Here both species appear to be at their climatic extremes and a study in the change of plagioclimax structure (see below) should prove interesting. For this reason and because several of the localities for this grassland type were threatened by motorway operations, the distribution of Bromus erectus in Co. Durham has been mapped on a "tetrad" basis (Figure 32).

(v) Choice of Conservation Sites. Today only four extensive areas of semi-natural inland Magnesian Limestone vegetation exist in Co. Durham, namely, Pittington, Sherburn Hill, Thrislington Plantation and Cassop Vale. The former two are scheduled for quarrying which will completely destroy a large part of them and will greatly alter that part which is left. This leaves Cassop Vale and Thrislington Plantation, both of which are already unique. Attempts should be made to conserve both these sites because virtually seventy-five per cent of the variation exhibited by the

Magnesian Limestone vegetation is seen at these two sites. Of the two, Thrislington is the only large area of semi-natural calcareous grassland, and because of this fact and the diversity of the communities, this site was chosen as a Proposed National Nature Reserve. The following communities were recorded there:-

Seslerio-Helictotrichetum S-a. typicum
" " S-a. caricetosum pulicariae, Antennaria variant.
" " S-a. of Helictotrichon pubescens, Rosa variant.
Salicetum repenti-nigricantis (fragment).
Crataegus-Rosa pimpinellifolia Ass.

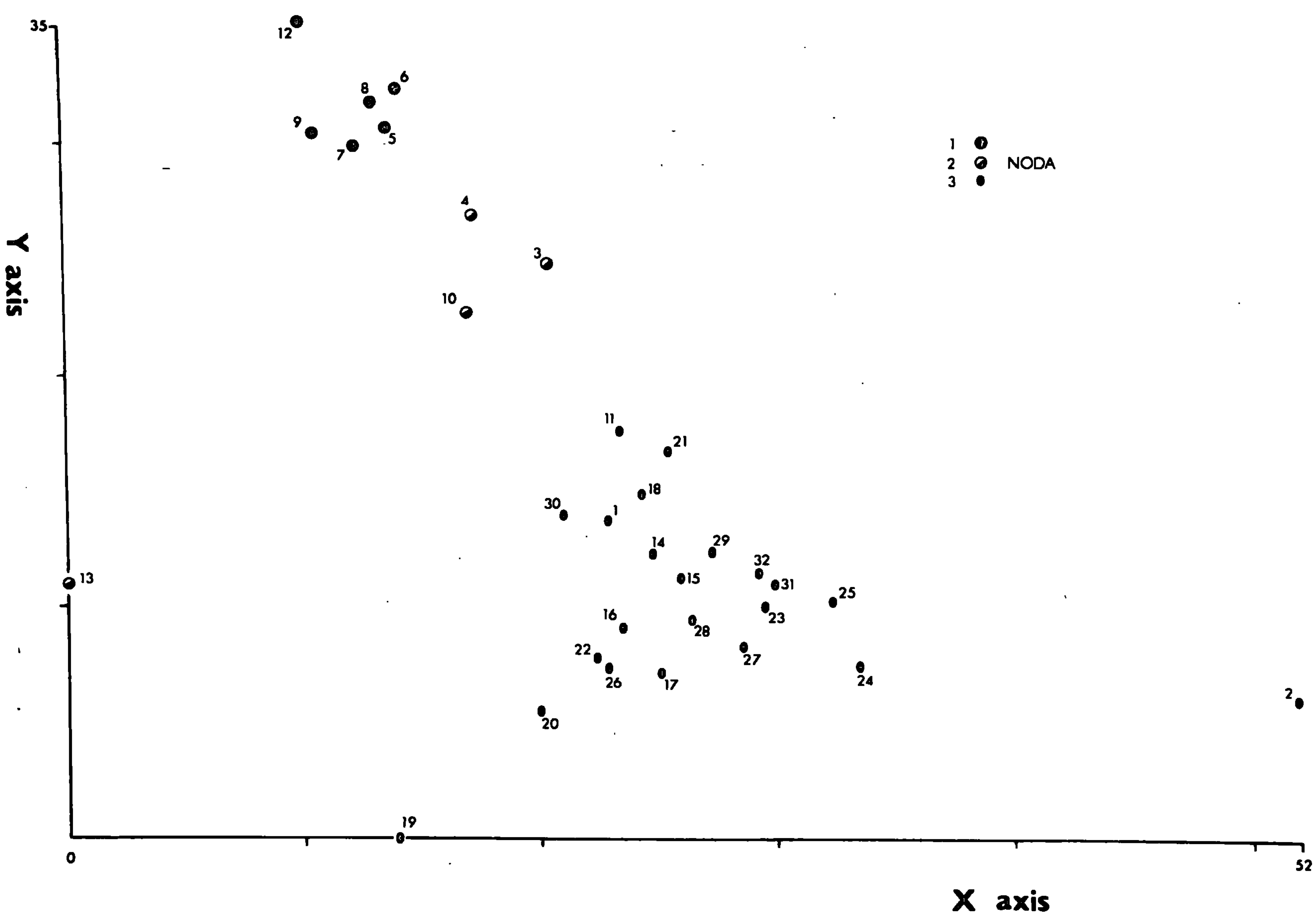
(vi) Collection of Site Information. During the three years of the research it was not possible to collect all the necessary site information required to formulate a detailed conservation proposal. However, several problems of community/habitat relations were studied and a plan developed for future investigations.

The ordination techniques of Bray & Curtis (1957) as adopted by Gittins (1965a, b) were again used for the correlation of vegetation and habital along an observable ecological gradient. Thirty two $1m^2$ quadrats were taken along a belt transect from an area of Seslerio-Helictotrichetum typicum downslope across Helictotricho-Caricetum flaccae and

FIGURE 32. Ordination of stands of vegetation along an observable environmental gradient at Thrislington Plantation, Co. Durham.

Legend:

1. Helictotricho-Caricetum flaccae typicum.
2. Mixed Scrub/grassland stands.
3. Seslerio-Helictotrichetum.

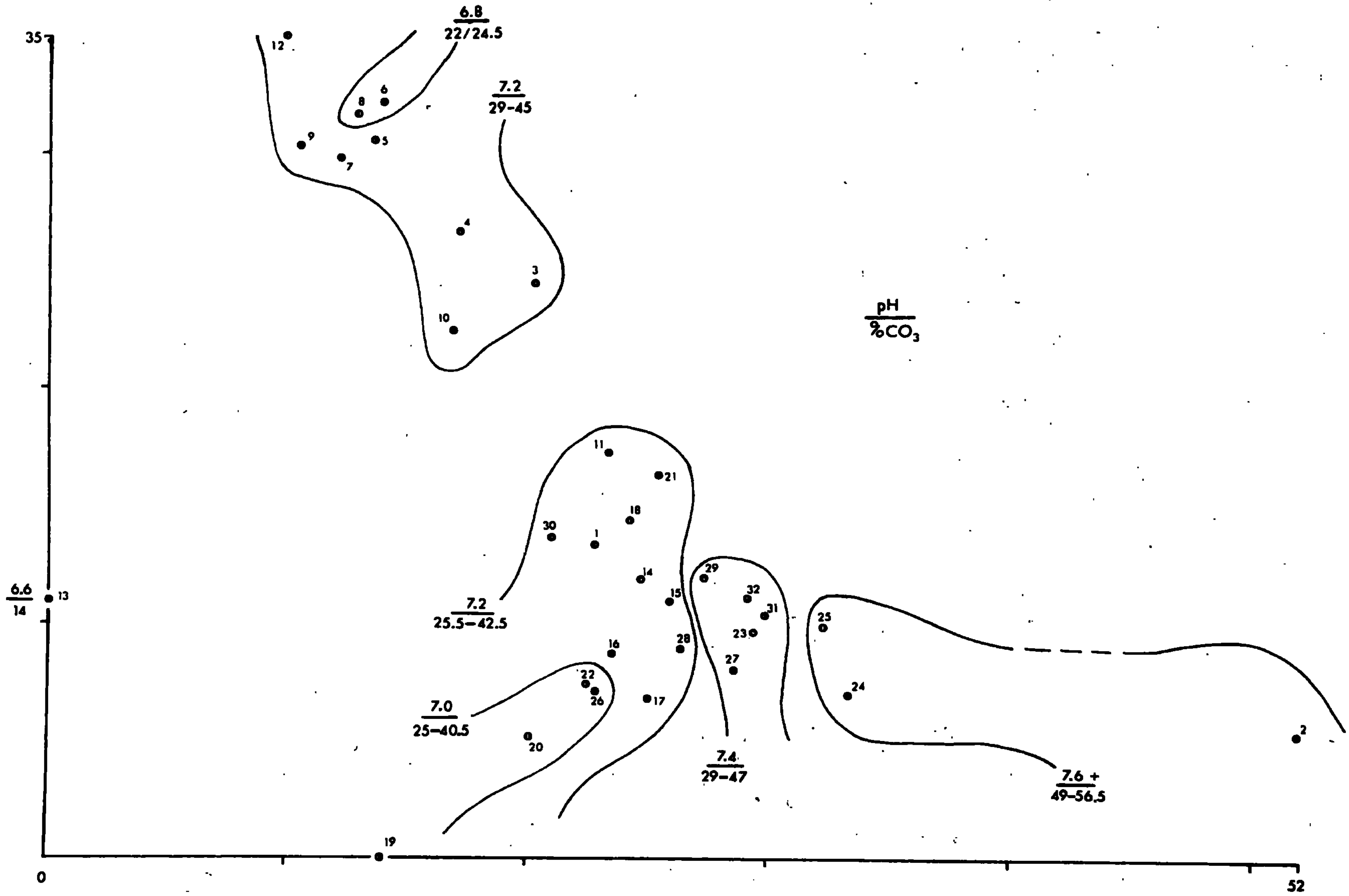


35
Y axis
0
52
X axis
1
2
3
NODA
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32

mixed scrub communities to an area of Seslerio-Helictotrichetum caricetosum pulicariae. As in the previous example the ordination was based on total floristic similarity using species presence and absence values, and the results are shown in Figure 32. The maximum interstand distance (C max-C) was 52 units between stands 13 and 2 and these were used for the construction of the X axis. Stands 19 and 12 which were 35 units apart were used for Y axis construction. Instead of a scatter diagram type of representation such as the one produced in Figure 29, three distinct noda are distinguishable as compared to the four units recognised in the initial survey. Nodum 1 comprises stands of the Helictotricho-Caricetum flaccae; 2 the unclassified mixed scrub/grassland stands; 3 includes the two Sub-associations of the Seslerio-Helictotricetum.

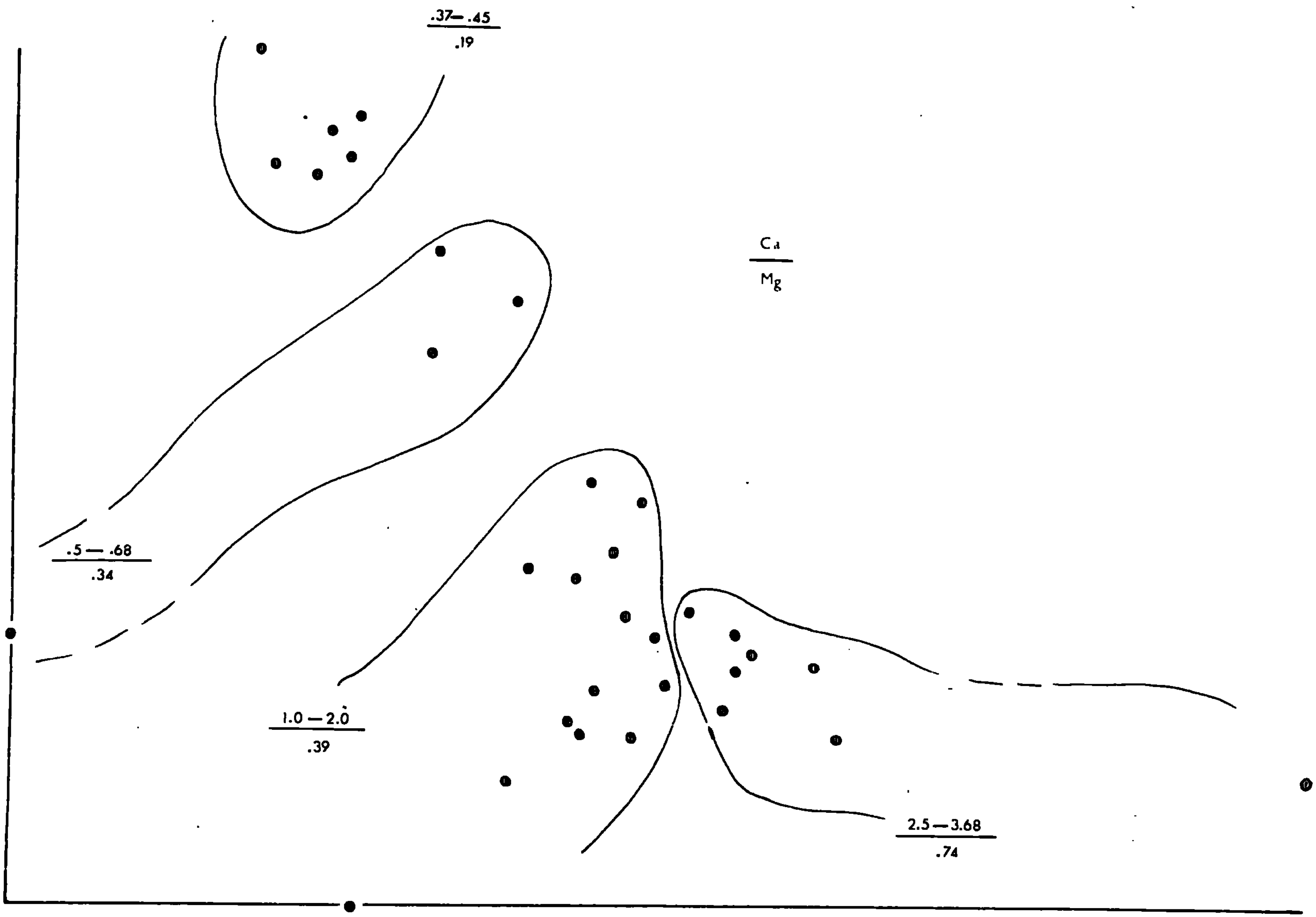
The separation pattern of the three Noda according to the four habitat factors represented in Figures 33 and 34 is not as clear-cut as might be hoped. But one interesting pattern emerges. Stands 23, 24, 25, 27, 29, 31 and 32 were classified in the initial survey as Seslerio-Helictotrichetum caricetosum pulicariae, and though they are not delimited in the ordination (Figure 32), their relationships as a group are elucidated when the habitat factors are superimposed on the ordination. For example, the pH/%Co_3 ordination in

FIGURE 33. Distribution of pH and total carbonates within the ordination at Thrislington Plantation (Figure 32).



pH
%CO3
6.8
22/24.5
7.2
29-45
7.2
25.5-42.5
7.0
25-40.5
7.4
29-47
7.6 +
49-56.5
6.6
14
35
0
52

FIGURE 34. Distribution of Calcium and Magnesium within the ordination at Thrislington Plantation (Figure 32).



.37—.45 / .19
Ca / Mg
.5 — .68 / .34
1.0 — 2.0 / .39
2.5 — 3.68 / .74

Figure 33 delimits those stands with a pH value of 7.4+ and with a higher mean percentage total carbonates than other groups. The calcium/magnesium ordination in Figure 34 again delimits these stands from others of Nodum 3 which comprise Seslerio-Helictotrichetum typicum.

(vii) Logical extensions of the site research. When the vegetation/soil relationships have been studied for a number of similar ecological gradients at Thrislington Plantation, the more detailed investigations of available soil nutrients for individual species can be attempted. Extrapolating this data via detailed mineral cycling analyses and pattern and production of individual species to the community structure as a whole should then give some insight into the mechanisms of community maintenance and succession.

Ideally, the procedure to be followed should be along the following lines:-

(a) Performance and reproductive capacity of the dominant Sesleria caerulea along the ecological gradients of the ordination; detailed pattern of the dominant via analyses of variance and co-variance (cf. Kershaw 1958, Austin 1968) - (i) along the ecological gradients; (ii) this data then compared with the pattern of the species in the communities along the "plagioclimax-dominant" overlap zone (see above), with similar pattern data for Bromus erectus compared with that of the North Downs in Austin (1968);

(b) Performance, reproductive capacity and pattern of the rarer species in the communities, e.g. Antennaria dioica (representing an anomalous vegetative reproduction pattern type); Primula farinosa and Epipactis atrorubens;

(c) Performance and pattern of invading species such as Rosa pimpinellifolia and Crataegus monogyna and the mechanisms involved in the process of succession where no simple edaphic trends can be detected as causal factors (cf. Lloyd & Pigott 1967).

(C) Summary and Conclusions

The discussion of the text has been used to illustrate the logical extensions of a broad phytosociological survey using Zurich-Montpellier techniques. Any discussion on the validity of this system of classification and vegetation description has been deliberately omitted because, in the author's opinion, this subject has been adequately discussed in the last twenty years, e.g. Poore (1955 a,b,c), Moore (1962) etc. Vindication of the use of the system is seen in the text and tables themselves and further discussion seems unnecessary.

The use of the Z-M descriptive methods to give a classification scheme which serves as a basis for conservation proposals, has been shown to be invaluable, and the relationships of several aspects of the system to ordination techniques are clearly illustrated in the foregoing discussion. Both techniques of vegetation description have great value in the formulation of conservation proposals and ordination is shown to be of immense value for the correlation of vegetation and habitat variation.

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Appendix A.

Explanation of Climate Diagrams

Reference Figure A.

A. Location of meteorological station.

B. Altitude of station in metres.

C. Average annual temperature in degrees Centigrade.

D. Humidity.

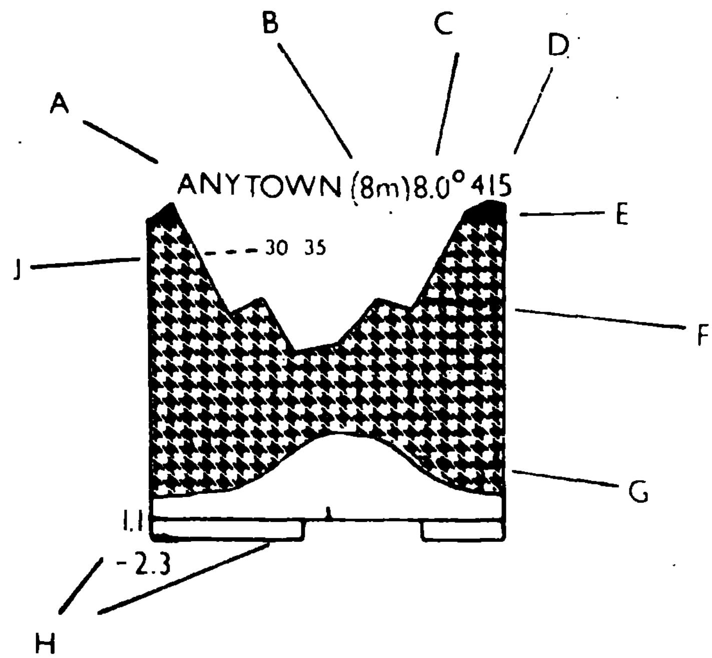
E. Period with precipitation over 100 mm.

F. Precipitation graph (mean monthly figures).

G. Temperature graph (" " ") °Centigrade.

H. Absolute minimum temperatures and period where abs. minimum temp. is below 0°C.

J. Duration of observation period in years.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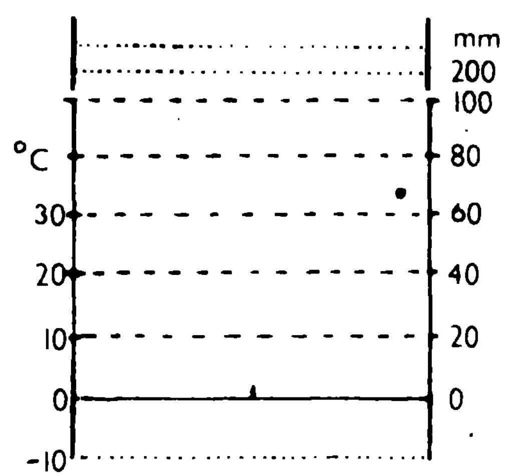
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Appendix B.

SOIL ANALYSIS

Methods

Samples of soil were collected, using a trowel, from the rooting zone of each soil profile to be studied. On arrival at the laboratory, the pH of the soils was measured by mixing about 5 gms. of soil with distilled water and testing the resultant paste using the standard laboratory procedure. A period of approximately 10 seconds was allowed to elapse between the insertion of the electrode into the paste and the reading of the value.

All the roots were then removed from the remainder of the samples and the soils were dried in an oven at 40 °C. The % humus was measured by weighing out 5 gms. of oven-dry soil and igniting overnight in an oven at 440 °C. The loss in weight of the sample was taken to equal the % humus.

For the measurement of the % of total carbonates and calcium and magnesium, a Hydrochloric Acid extract procedure as advocated by Gedroits (1964) was followed. 10% HCl extracts are usually used for the determination of "available ions", but because of the high concentrations of bases in the soil, normal (1N) HCl was used in order to obtain some idea of the total soil composition. Gedroits has shown that the normality of HCl does not affect the amount of extractable calcium, but that the amount of extractable magnesium increases by some 33% using 1N acid compared to 0.1N. This means that the results obtained for calcium are comparable with other analyses using lower normalities, but not magnesium results. Measurement of the amounts of this latter ion was attempted primarily because many of the carbonates in the Magnesian Limestone have been shown to be in the form of magnesium carbonate (McKee 1965). Another reason for the choice of 1N acid was because of Gedroits' findings that non-exchangeable calcium, (liberated only by high normality acids), differed from magnesium and other ions with regard to its availability to plants. It is not available whereas it has been shown that non-exchangeable magnesium can be used by plants.

Procedure

5 gms. of an over-dry fine earth sample were weighed out into a tall 150 ml. beaker. 100 ml. of N1 HCl were then added and then stirred several times during one hour. the contents were allowed to settle overnight and 20 mls. of the supernatant were pipetted into a small titration flask to which 15-20 drops of bromo-thymol blue were added. The solution was then titrated with standardised N1 Sodium hydroxide until the end point change of yellow to blue is reached. Blanks were run to obtain the titre of the

original HCl and pure calcium carbonate to serve as checks. The percentage of total carbonates is obtained from the expression:-

$$\% \ Co_3 = (\text{Blank titration} - \text{Actual titration}) \times 5$$

The remainder of the supernatant was then filtered off and stored in clean polythene wash bottles at a low temperature. The measurement of the amount of calcium and magnesium was completed using an Atomic Absorption Spectrophotometer with the appropriate lamp. It was found that the original solution had to be diluted considerably to obtain a reading on the instrument's scale. In the case of calcium determination, the appropriate amount of lanthanum chloride was added as recommended. Because of the high concentrations of ions, the results are expressed in grams per 100 grams dry soil, and because of the variability of the magnesium figures, the results are shown in the text, Figures 30 and 33, as an average figure rather than a range.

(1) Seslerio-Helictotrichetum - Aufnahmen Soil Analyses.

Auf. No.	pH	% humus	% CO_3	Ca	Mg
				(gms./100 gms. soil)	
UNIT 1.					
52	7.2	11.8	38.4	2.14	0.39
53	7.5	6.8	52.5	2.75	0.59
57	7.2	12.8	43.6	1.00	0.23
58	7.4	7.25	55.0	2.95	0.69
59	7.0	12.65	42.5	1.90	0.36
60	7.4	6.94	54.0	1.94	0.40
61	7.6	8.7	58.5	4.2	0.62
62	7.2	7.05	48.65	1.80	0.44
63	7.6	7.63	53.05	1.54	0.47
65	7.1	13.25	37.65	1.26	0.36
69	7.2	11.7	40.4	0.68	0.23
70	6.9	10.4	39.8	1.02	0.19
71	7.3	11.3	39.8	3.36	0.70
72	7.2	7.4	46.5	2.25	0.39
73	6.9	13.7	38.4	0.62	0.24
74	7.6	9.6	43.8	1.85	0.38
UNIT 2.					
1	6.8	18.4	27.5	0.84	0.24;
2	7.0	17.6	20.68	0.76	0.19
3	6.8	16.2	24.0	0.89	0.23
5	6.8	19.0	23.65	0.85	0.22
6	7.0	14.0	19.3	0.62	0.23
7	7.2	14.8	15.5	1.04	0.19
8	7.2	12.6	23.0	0.63	0.17
9	6.8	19.2	32.0	0.93	0.20
11	6.9	13.9	31.8	0.89	0.20
12	6.8	14.6	26.9	0.64	0.26
17	6.8	17.4	20.2	0.75	0.25
18	6.7	16.4	14.3	1.12	0.26
21	6.8	18.3	23.9	1.02	0.20
UNIT 3.					
31	7.4	8.0	46.5	2.20	0.43
32	7.3	9.6	43.6	2.60	0.50
33	7.5	7.4	53.5	3.25	0.64
34	7.3	9.7	42.0	2.75	0.48
48	7.6	6.9	55.0	3.5	0.67
54	7.7	5.8	56.5	3.45	0.65
55	7.7	6.4	54.0	3.05	0.65
56	7.6	8.0	49.5	2.8	0.69
58	7.6	8.4	48.0	2.9	0.71

UNIT 4.					
16	7.4	3.5	42.0	1.04	0.23
19	7.6	4.8	42.0	1.02	0.26
UNIT 5.					
C1	7.6	6.9	48.5	2.75	0.69
C2	7.5	7.4	52.5	2.40	0.64
UNIT 6.					
BO	7.8	9.1	56.5	3.6	0.64
B1	7.6	8.0	59.0	3.8	0.63
B2	7.4	8.4	58.5	3.4	0.65

(2) Thrislington Plantation - Site Analyses.

Auf. No.	pH	% humus	% CO_3	Ca	Mg
				(gms./100 gms. dry soil)	
NODUM 1.					
5	7.2	19.0	34.5	0.38	0.18
6	6.8	24.5	22.0	0.45	0.17
7	7.2	13.5	44.5	0.40	0.23
8	6.8	12.0	24.5	0.39	0.20
9	7.2	14.5	29.0	0.43	0.19
12	7.2	14.0	37.5	0.44	0.24
NODUM 2.					
3	7.2	24.0	38.5	0.68	0.30
4	7.2	20.5	42.5	0.58	0.35
10	7.2	28.5	35.0	0.63	0.33
13	6.6	34.0	14.0	0.50	0.29
NODUM 3.					
1	7.2	18.0	40.5	1.0	0.38
2	7.6	9.5	55.5	3.6	0.73
11	7.2	22.0	25.5	1.05	0.39
14	7.2	13.5	33.5	1.9	0.40
15	7.2	18.5	33.0	1.1	0.43
16	7.2	17.5	26.5	1.25	0.39
17	7.2	12.5	29.5	2.05	0.39
18	7.2	14.5	28.0	1.4	0.41
19	7.0	25.5	37.5	1.4	0.42
20	7.0	22.5	40.0	1.6	0.37
21	7.2	20.0	41.5	2.0	0.42
22	7.0	22.0	25.0	1.5	0.35
23	7.4	15.0	47.0	2.8	0.74
24	7.6	10.5	49.0	2.5	0.82
25	7.7	11.5	56.5	3.05	0.68
26	7.0	13.5	40.5	1.9	0.32
27	7.4	12.0	42.5	2.5	0.84
28	7.2	17.5	32.0	1.4	0.37
29	7.4	16.0	47.0	3.68	0.75
30	7.2	19.5	36.0	1.4	0.38
31	7.4	14.0	29.0	2.5	0.68
32	7.4	13.5	44.5	3.40	0.70