THE STUDY OF THE DISTRIBUTION OF BRITISH PLANTS

THE STUDY OF THE DISTRIBUTION OF BRITISH PLANTS

BEING THE REPORT OF THE

CONFERENCE

HELD IN 1950 BY

THE BOTANICAL SOCIETY OF THE BRITISH ISLES

EDITED BY

J. E. LOUSLEY

May 14th, 1951

Printed by T. BUNCLE & CO. LTD., Market Place, Arbroath,
for the
BOTANICAL SOCIETY OF THE BRITISH ISLES AND
OBTAINABLE FROM THE SOCIETY, c/o DEPARTMENT
OF BOTANY, THE UNIVERSITY, OXFORD.

CONTENTS

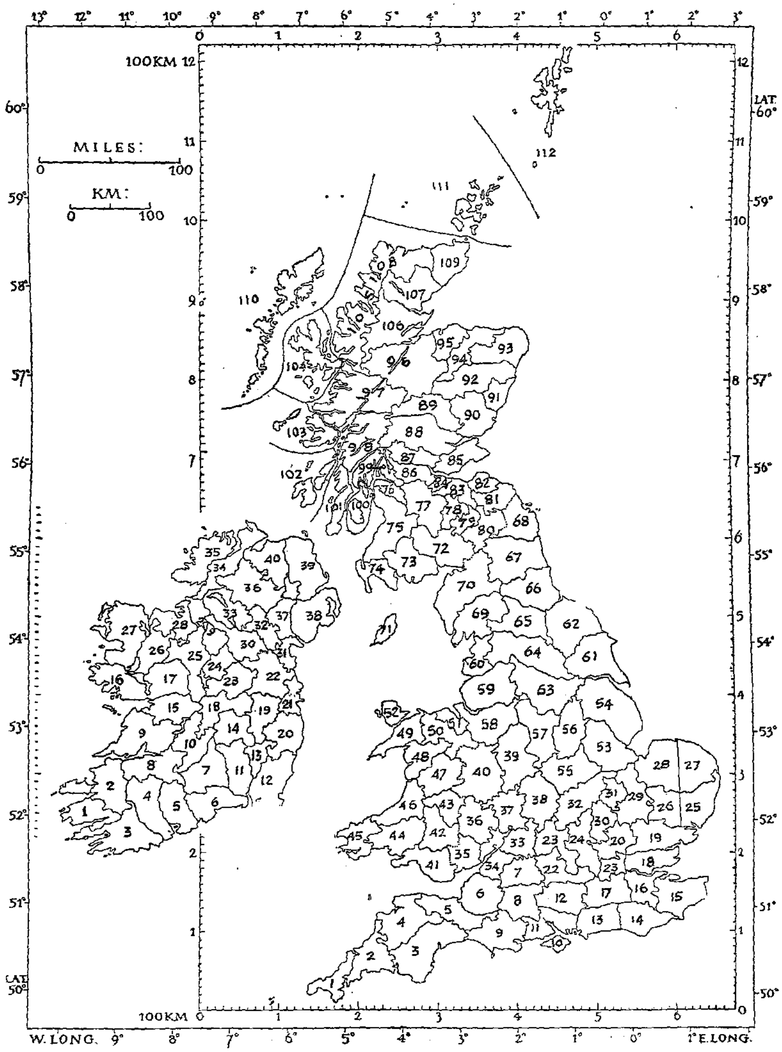


Fig. 1.

The Watsonian Vice-Counties of England, Wales and Scotland (numbered 1 to 112) and the Irish County-Divisions (numbered 1 to 40 and prefixed with "H" when cited) as in use to-day.
With acknowledgment to "The New Naturalist."

EDITORIAL NOTE

The purpose of this volume is to make available to a wider public the papers read during the two crowded days of the second Conference arranged by the Botanical Society of the British Isles. Its contents deal with a subject of growing importance in connection with recent developments in the study of the taxonomy, ecology, recent palaeobotany and even the cyto-genetics of the British flora. They appear at a time when it is appropriate to review past work and to consider future requirements. Much of the information in the papers is not easily available elsewhere and some of it is new. These collected contributions should thus provide a useful account of the various approaches to the study of plant distribution in Britain and opportunities for comparison with the methods used in neighbouring European countries.

No more suitable subject could have been chosen for a Conference arranged by the Botanical Society of the British Isles. It provides ideal opportunities for collaboration between amateur and professional botanists, since the bulk of the records are provided by the former and much of their interpretation is undertaken by the latter. Moreover the subject is one in which the Society has long played a leading part by collecting and publishing records.

In 1839, in the first publication of the Botanical Society of London, from which we claim descent, the Council in inviting communications from members asked particularly for those on botanical geography. Later a leading part in the affairs of our forerunners was played by H. C. Watson whose name is mentioned repeatedly in the following pages. After the issue of his *Cybele* in 1847-49, records in our publications were often given as additions to that work. Later his *Topographical Botany* became the standard and records extending the known distribution of British plants became regarded as of increasing importance in the Society. For the last forty years "New County and other Records", now known as "Plant Records", have appeared regularly in our annual *Report* and *Watsonia*: they provide the most important single source of recorded additions to British "geographical botany".

The papers and descriptions of exhibits as published in this book have been rearranged in a sequence more suitable for reading and reference. The order in which they were given can be seen from the Conference Programme as printed on the next two pages.

The success of the Conference was due to the energy and enthusiasm of Dr. J. G. Dony, Honorary Field Secretary, and Mr. W. R. Price, Honorary Assistant Secretary of the Society, and to the other officers and members who assisted in the organisation. We are indebted to Miss M. S. Campbell for approaching the British Council for the grant which made it possible to invite Dr. A. W. Kloos. Thanks are also due to all the other people and bodies who assisted.

I should also like to take this opportunity of acknowledging the assistance of all those who kindly gave permission for reproduction of maps or base maps used in connection with the illustrations.

J. E. LOUSLEY.

CONFERENCE PROGRAMME
1950

AIMS AND METHODS IN THE STUDY OF THE DISTRIBUTION OF BRITISH PLANTS

FRIDAY, March 31st

10.30 a.m.	Introductory Talk The President: Mr. J. S. L. GILMOUR
10.45	The Study of Plant Distribution Mr. S. M. WALTERS
11.45	Geographical Distribution and Isolation in some British Ecospecies Dr. D. H. VALENTINE
12.45 p.m.	Interval for Luncheon
2.15	The Watsonian Vice-county System Mr. J. E. DANDY.
2.45	The Watsonian Vice-county System in practice Mr. J. E. LOUSLEY
3.35	Problems of Distribution raised in the compilation of a County Flora Dr. J. G. DONY
4.15	Interval for Tea
5.00	EXHIBITION MEETING

Maps of the Watsonian Vice-counties	Mr. J. E. Dandy.
The Distribution of *Bunium Bulbocastanum*	Dr. J. G. Dony.
The Distribution of the *Digitalis purpurea* complex	Mr. V. H. Heywood
Distributional Studies and generic segregation in *Lepturus* sensu Bentham	Mr. C. E. Hubbard
Maps showing Plant Distribution in Britain and abroad.	Mr. J. E. Lousley
The topocline in *Ulmus coritana*	Dr. R. Melville
Primula elatior	Miss D. and Mr. H. Meyer

The Antarctic origin of some British *Carices*	Mr. E. Nelmes
The Ecological and Geographical Distribution of the British species of *Thymus*	Mr. C. D. Pigott
Distribution Maps of Kent Plants	Mr. F. Rose
The History and Distribution of some Brambles of S.E. England	Mr. W. C. R. Watson

SATURDAY, April 1st

10.00 a.m. *The Importance of Mapping in Ecology
Capt. C. DIVER

10.30 Some Late Glacial Species from the Lower Tees Area and their present Distribution
Dr. K. B. BLACKBURN

11.30 Some Notes on Mapping the Distribution of Species
Mr. W. T. STEARN

12.30 p.m. Interval for Luncheon

1.45 The Study of Plant Distribution in Holland
Dr. Ir. A. W. KLOOS, Jr.

2.45 A Review of the Work of the Conference
Prof. A. R. CLAPHAM
followed by a General Discussion

4.15 Interval for Tea

5.00 BRAINS TRUST
Question Master—Mr. J. S. L. GILMOUR

Mr. J. P. M. BRENAN	Dr. J. M. LAMBERT
Dr. R. C. L. BURGES	Dr. W. B. TURRILL
Mr. R. A. GRAHAM	Prof. T. G. TUTIN

6.30 Closing Remarks by the President.

SUNDAY, April 2nd

FIELD MEETING TO QUENDON WOODS, ESSEX
TO STUDY THE OXLIP (*Primula elatior*)

Leaders: Dr. D. H. Valentine, assisted by Miss D. & Mr. H. Meyer

* As Capt. Diver was prevented from attending the Conference, Mr. C. D. Pigott read the paper printed on pp. 91-95, which was prepared at very short notice. With this exception the Programme was carried out as printed.

LIST OF MEMBERS AND GUESTS ATTENDING THE CONFERENCE

March 31 and April 1, 1950

D. E. Allen
A. H. G. Alston
G K. L. Alvin
G B. W. Anderson
G. M. Ash
G O. E. Balme
E. B. Bangerter
G Miss G. Barkley
Miss F. M. Barton
P. R. Bell
F. J. Bingley
Dr. K. B. Blackburn
G B. J. Bows
R. A. Boyd
J. P. M. Brenan
Dr. M. G. Calder
Miss M. S. Campbell
G T. H. Catchpool
Miss B. M. Chalk
G J. E. W. Chalkley
G V. H. Chambers
Dr. S. E. Chandler
Prof. A. R. Clapham
Dr. W. A. Clark
G I. Clifford
G A. J. Coel
C. L. Collenette
G M. W. Cornish
Miss W. J. Cornwell
G G. F. Creber
G A. J. Crosby-Browne
J. E. Dandy
Miss E. W. Davies
G P. R. Day
G D. Dent
G Miss C. I. Dickinson
Dr. J. G. Dony
Miss E. J. Drew
G R. B. Drummond
G Prof. K. Faegri
Mrs. P. R. Farquharson
G M. E. Fox
G D. H. Friend
Miss L. W. Frost
G A. Garrard
G A. R. Gemmell
Miss E. J. Gibbons
Mrs. A. N. Gibby
G D. G. Gill
J. S. L. Gilmour
G M. A. Graham
R. Graham
R. D. Graham
P. S. Green
J. D. Grose
Mrs. B. Hassall
F. N. Hepper
G V. H. Heywood
G J. Holroyd
G P. B. Hort
C. E. Hubbard
G R. M. Hughes
Miss M. M. Hyde
S. T. Jermyn
G C. J. Kelsall
D. H. Kent
G J. Kerslake
G G. C. King
G Dr. Ir. A. W. Kloos, Jr.
Dr. J. M. Lambert
Miss C. E. Longfield
J. E. Lousley
Prof. R. C. McLean
Miss M. M. Marriott
Rev. W. Keble Martin
Dr. R. Melville
G Miss D. Meyer
H. Meyer
E. Milne-Redhead
G B. Molesworth
Miss B. M. C. Morgan
J. K. Morton
Miss C. W. Muirhead
E. Nelmes
G Miss S. Nelmes
P. M. Newey
G J. D. Ovington
G M. M. Parker
C. D. Pigott
G J. V. Poore
M. E. D. Poore
W. R. Price
C. T. Prime
W. Ramsden

	Miss E. Rawlins		P. F. Vernon
	R. C. Readett		Mrs. W. Verschoyle
	B. W. Ribbons	G	B. C. Vincent
	Mrs. M. Richards		A. E. Wade
	Miss C. M. Rob		E. C. Wallace
G	D. H. Robertson		S. M. Walters
	F. Rose		Dr. E. F. Warburg
	Miss E. M. Rosser		B. T. Ward
	N. Y. Sandwith		W. E. Warren
G	Miss R. G. Shove		Mrs. W. Boyd Watt
	N. D. Simpson		Dr. E. V. Watson
G	R. C. Sinfield		W. C. R. Watson
G	D. C. Smith		Mrs. B. Welch
G	J. D. Spink		A. W. Westrup
G	W. T. Stearn	G	D. S. White
G	D. G. Stygall		F. N. Whitehead
	V. S. Summerhayes		Miss M. M. Whiting
G	H. M. Swallow		Miss C. Wickham
	E. L. Swann	G	Prof. R. van der Wijk
G	A. C. Tallantive	G	J. Wilkinson
	P. Taylor		Miss A. F. Wood
G	M. Tindale		J. E. Woodhead
	Dr. W. B. Turrill	G	D. A. Wright
	Prof. T. G. Tutin	G	P. L. Wright
	Dr. D. H. Valentine		Dr. D. P. Young

G = Guest

INTRODUCTORY REMARKS BY THE PRESIDENT

The President, Mr. J. S. L. Gilmour, opening the Conference, referred to the great loss suffered by the Society and by Botany in general through the recent death of Mr. A. J. Wilmott, who was to have given the opening paper. He asked those present to stand as a tribute to his memory.

Mr. Gilmour then extended a warm welcome to the guests from overseas—Dr. Ir. A. W. Kloos, Jr. (Holland), Professor R. van der Wijk (Groningen), and Professor Knut Faegri (Bergen). He read a letter from Capt. C. Diver, Director-General of the Nature Conservancy, regretting that he could not be present and expressing the hope that close co-operation would be established in the future between the Conservancy and the Society. This suggestion was warmly welcomed by the Conference, and the President said it would be referred to the Council for action.

The President then outlined briefly the scope of the Conference, saying he would leave a more detailed treatment of the subject to Mr. S. M. Walters in his opening paper on the "Study of Plant Distribution."

THE STUDY OF PLANT DISTRIBUTION

S. M. Walters.

In this paper I intend to survey in a general way the study of the distribution of higher plants, with particular reference to the British Flora; and will content myself with a mere mention of those specialised fields which are to be elaborated by later speakers at this Conference. It would be best, I think, to begin with a consideration of the concept of distribution. Every species of plant or animal—indeed every higher taxonomic unit also—occupies only a limited proportion of the Earth's surface. It is common for biologists to speak of the range or area of a species; and the simplest way by which such a range may be indicated is by an outline on a map enclosing all the known occurrences of that species. Any species, genus, or family having two or more clearly separated areas is said to exhibit a discontinuous or disjunct distribution; any group completely confined to a relatively small area is said to be endemic to that area. Clearly no species can be continuously distributed over the whole of its range in the sense that the individuals occupy all the available space; even in those types of vegetation where a single species is dominant over a very considerable area—as in parts of the northern coniferous forest in, for example, Scandinavia, where *Pinus sylvestris* may be the only dominant—local physiographic features (steep rocks, rivers, lakes, etc.) must interrupt the uniformity. In practice, of course the term discontinuous is restricted to those extreme types of disjunction where the species is completely absent from a considerable area of territory between any two areas in which it occurs. As we shall see later, the phenomena of discontinuous distributions are of the utmost interest and significance to plant and animal geographers.

The study of plant distribution—indeed, of plant geography in general—is commonly assumed to date from the end of the 18th century, and more precisely, perhaps, from the publication in 1792 of Willdenow's *Grundriss der Kräuterkunde,* followed in the early 19th century by the works of Wahlenberg, von Humboldt, De Candolle, and others. In these early works the general features of the distribution of species emerged, and the correlation of distribution with climatic factors was recognised. A period of considerable activity followed, in which the study of distribution went hand in hand with that of systematics. In Britain the scientific study undoubtedly begins with Watson, whose first work, *Outlines of the Geographical Distribution of British Plants,* appeared in 1832. Before Watson's time, British botanists had been content with vague and often inaccurate generalisations on the occurrence of species in Britain, and no serious attempt had been made to systematise the rapidly growing knowledge on the distribution of the British flora. Although Watson was clearly familiar with the work of the Continental plant geographers—thus he refers to Wahlenberg, De Candolle, and others—he did not attempt to base his distribution types of the British flora on the general European range of the species, but only on their ranges within the British Isles. Before the publication of Watson's main work (the first volume of the *Cybele Britannica* appeared in 1847), Forbes had published his soon famous paper, based upon an address to the British Association in 1845, " On the connexion between the distribution of the existing fauna and flora of the British Isles and the geological changes which have affected their area ". In this paper Forbes classified British plants into five so-called " Floras " according to their general European distribution; and further set forth clearly the historical interpretation of the facts of geographical distribution. It is important to realise the nature of this hypothesis, advanced by Forbes some years before the publication of Darwin's *Origin of Species,* as it is still generally accepted and lies at the basis of all interpretative comparative plant geography. Forbes postulated the existence of what he called "specific centres "—that is, that every species has had one single centre of origin from which it has spread to occupy its present area, and that cases of discontinuous distribution are due to historical causes which have brought about the separation of originally more or less continuous populations, by destruction of parts of those populations. To quote his own words:—" The specific identity, to any extent, of the flora and fauna of one area with that of another, depends on both areas forming, or having formed, part of the same specific centre, or on their having derived their population by transmission, through migration over continuous or closely contiguous land, aided in the case of alpine floras by transportation on floating masses of ice". He considered another possible interpretation of discontinuous distributions, namely that these were to be attributed to accidental long-range dispersal, but decided that this hypothesis was quite inadequate to explain the peculiar features of such discontinuous ranges. Darwin of course was to incorporate a considerable amount of data on plant and animal distribution of this type in his *Origin of Species*, using the facts to support his hypothesis of evolution through Natural Selection.

To return to Watson. Perhaps the clearest indication of the soundness of Watson's work is to be seen in the titles of papers before this Conference, over a century after the publication of the first volume of the *Cybele*. British Botany has in fact used virtually unchanged as a basis for the recording of plant distribution within the British Isles the system invented by Watson; and although it will be argued—and in my opinion rightly argued —that for many purposes the vice-county system [see p. 23] is inadequate, there can be no doubt that by means of it a firm foundation of fact was built and the study of comparative plant distribution made possible in Britain. I do not propose to discuss the system any further here—we are to consider it in detail this afternoon—but may conveniently use it to illustrate a general principle which I must now discuss.

This concerns the relation between the *aims* of our study of plant distribution and the *methods* which we adopt—the two halves of our subject, in fact, as expressed in the Conference title. By *methods* I mean here not only the making and collection of records of the occurrence of species—the basic field work—but also their representation by means of mapping and in other ways. By *aims* I understand the use of the collected data for the testing or establishment of theories to explain the distribution of plants in terms of the environment in its widest sense, past and present, and in terms of the genetic capacity of the plants themselves. In one way the method may be independent of any aim—thus there is always a place for simple accurate observation and record of any phenomena of natural history, and the constant recording of the occurrence of species in Britain has been and still is a most important work, largely done by the amateur naturalist through such societies as our own, providing the essential basis of fact. In another sense, however, the method adopted depends, or should depend, on the aim; thus, if one wishes to study the relation between soil factors and the distribution of a species, it is immediately obvious that some more accurate measure of distribution than the vice-county system is required. This dependence is even more obvious when the representation of distribution on maps is undertaken—in the choice of a suitable projection, or the conventions to be adopted, etc. As several speakers realised at a recent symposium on mapping of biological distributions organised by the Systematics Association and the Royal Geographical Society, there is a distinct danger involved here in this dependence of methods on aims—namely that the methods of mapping, etc., used may well be chosen, perhaps more or less subconsciously, to bring out with false clarity the particular point necessary to support a theory. I do not wish to pursue this—it will probably arise in our discussion of methods; it is of course simply a particular case of a danger to which every scientist is exposed—the danger of selecting facts to suit a preconceived idea; and Darwin's remedy, which was roughly to be aware of this weakness of the human mind and to make a special note of any inconvenient fact before the mind conveniently forgets it, is probably as good as any.

Let us turn back now to the *interpretation* of the facts of distribution, and this can perhaps most easily be done by continuing the history of the study of British distributions. As I said earlier, the first workers in this field were soon impressed by the broad correlation of distribution with climatic factors. Watson himself, for example, wrote (1835, *Remarks* . . . .): "It might be expected that the countries nearest to Britain, in geographical position and climate, would exhibit the closest resemblance in their floras, and this accordingly is found to be the case". There was soon, however, a tendency by Continental workers to oversimplify the relations between climate and distribution, and to think, for example, that, if a range of mean January temperatures could be found to be closely correlated with the distribution of a species, then the range of that species could be explained in terms of that one factor only. Further reference will be made to this. The realisation by Forbes and De Candolle of the historical factors in distribution was of course a step of very great importance, and such interpretations received great impetus from the publication of the *Origin of Species* and the general acceptance of the evolutionary theory. In Britain, however, we find that the second half of the 19th century produced little in the way of comparative study of distribution; and we are well into the present century before interpretations of the distributional phenomena are debated and discussed. The main interest has tended to centre particularly round two or three groups of British plants which exhibit highly discontinuous distributions over their whole range, particularly the so-called Lusitanian element in the Irish flora, and the rather loosely termed Arctic-alpine element mostly in the mountains of Britain. These two groups are roughly two of Forbes' five Floras; he suggested that the Lusitanian species were our oldest ones, having survived the Ice Age which had destroyed them elsewhere in N.W. Europe, whilst the Arctic-alpines he interpreted as having had a widespread distribution in Europe at the time of the Ice Age, and to have become restricted to their present habitats as the climate improved. Problems such as these were considered from a new angle as a result of the researches of Clement Reid into the sub-fossil floras of various ages before and during the Glacial period; and Reid's paper to the British Association in 1911, "The relations of the present plant population of the British Isles to the Glacial period", put forward the general thesis that the flora of Britain was virtually completely exterminated during the Ice Age, and that our present flora represents the results of re-immigration from the Continent. Since that date a good deal of discussion, which many would think to have been based on too little fact to have been of great value, has gone on as to what proportion, if any, of the British flora can be supposed to have survived the various glaciations which are now distinguished within the Glacial Period. The hypothesis of per-glacial survival on ice-free so-called "nunatak" areas was introduced into this country by Woodhead in 1929, and has been used by several workers to explain the remarkable assemblages of species such as are found in Upper Teesdale. It is only very recently that, with the extremely rapid and fruitful development of the methods of peat stratigraphy and pollen-analysis throughout N. Europe, we can feel we have much more solid evidence by which to test hypotheses of this type. This kind of evidence as to the constitution of the British flora at more or less accurately defined dates since the Glacial period will be presented by Dr. Blackburn in her paper to-morrow. I should like however to put forward briefly towards the end of this paper some of the revised and extended interpretations of distributional phenomena which seem clearly to arise out of this work.

In considering modern studies in Britain, those of Salisbury, Matthews and Good should be mentioned—work with which I am sure many of you will be familiar. In 1932 appeared Salisbury's *East Anglian Flora*, a most valuable analysis of the flora of East Anglia from the point of view of the European distribution of the component species; and this was followed by a very full review of the whole subject of the "Geographical Relationships of the British Flora" in the Presidential Address given by Matthews to the British Ecological Society in 1937. In this, Matthews, acknowledging his debt to Salisbury's work, classified the British flora into 15 elements, and discussed each of these in turn, giving a comprehensive species list for all types of distribution except those of wide range (that is about half the British flora). The contributions of Good have been in two directions, which are well represented by his recent books;—one is a general account of plant geography based on the whole world flora, whilst the other is a most valuable detailed study of distribution of plants within a single British county—namely, Dorset. In this latter type of work, as in Salisbury's studies, we see the modern approach to problems of distribution which has gained much from the development of plant ecology as a special division of Botany. It is, however, more particularly with Good's attempts to state general principles of plant geography that I wish to concern myself in a little more detail now; these principles, embodying the so-called Theory of Tolerance, were set out by Good in **1931**, and there is an interesting discussion of a modified form of them in the book by the American plant geographer, Cain, *Foundations of Plant Geography,* published in 1944. Briefly, there seems to be general agreement among plant geographers on the following points:

1. That the climate, in its widest sense, is the primary factor controlling the distribution of plants.
2. That soil factors are important, but in a subsidiary manner—i.e. within the general climatic limitation.
3. That great climatic and physiographic changes have occurred in the past, and have left their mark on the present-day distribution of organisms.
4. (In a sense modifying the first three) That the relation between environmental factors and plant distribution can never be reduced to a simple cause-and-effect relation—I mentioned this earlier when discussing the early work showing correlations of distribution with meteorological data—although of course the demonstration of such correlations can be of great interest and significance.
5. That every species has a definite tolerance which limits its range and which has a genetic basis in a manner analogous to the genetic basis of the morphological characters used to define the species.
6. That the range of a species is subject to continuous variation, which may in certain cases—e.g. the Lizard Orchid in this country—be obvious, or may be so slow as to be imperceptible by the normal direct methods. Three factors are involved in this: firstly, the continuous changes in the environment; secondly, "migration" of the species in response to these changes, through new colonisation in some areas and extinction in others; and thirdly, the slow, more fundamental genetic changes within the species.

These principles seem to be well supported by observation, and offer together a reasonably satisfactory explanation of the facts of plant distribution; though detailed experiment on the tolerance of species is sadly lacking. I want to go on to discuss a further principle which is rather more difficult to formulate, and is in a sense included in the environmental factor, namely that concerning the inter-relations of different species. We have not so far mentioned the existence of more or less clearly defined plant communities. In two ways, however, the ecologist's study of plant communities concerns us: firstly, because an entirely proper study of distribution would be that of the plant community as opposed to the single species; and secondly, because it becomes increasingly obvious that the complex interrelations between species which we recognise when we speak of competition factors are of the greatest significance in the interpretation of distributional phenomena. We must, I think, omit any further consideration of plant sociology or the study of floristically-defined plant communities, as this would take us into too wide a field; but I must enlarge a little on the interrelations of species, and particularly the competition factor.

Salisbury, in *The East Anglian Flora,* draws attention to the importance for many species of the "open" habitat where competition with other plants is slight or absent, suggesting, for example, that a number of our common weeds appear to be native plants of naturally open communities such as sand dunes, alluvial washes, steep rocky slopes, etc. The studies of the Late Glacial flora, a preliminary account of which has been published recently by Godwin in the *Journal of Ecology* and of which we are to hear to-morrow, are abundantly confirming the view that a considerable proportion of our flora, including many species exhibiting marked discontinuities of range, is to be interpreted as having been widespread in the Late Glacial, and suffered enormous restriction of range through the spread, firstly of closed forest, and then, especially in the west and north, of blanket peat. This view reconciles opposing positions earlier taken up with regard to the Teesdale and other locally rich areas—such floras *are* relict, not by per-glacial survival, but by post-glacial survival in permanently open habitats. A great field of investigation is opened up by this view. One curious feature which is satisfactorily explained, I think, is the association of elements of different distribution types in these same areas—e.g. the Teesdale arctic-alpine *Juncus alpinus,* the continental *Viola rupestris,* and the "alpine" *Gentiana verna,* or the Irish (Co. Clare) Mediterranean *Neotinea intacta,* with arctic-alpine *Dryas octopetala* and continental *Viola stagnina.* To a surprising extent, indeed, species which would be called without hesitation "continental" by a central European or Scandinavian botanist—i.e. those which have their main area of distribution in the steppe regions of E. Europe and Russia and become more and more local and discontinuous in W. Europe —are found to exhibit remarkably varied patterns of distribution in the British Isles and many are by no means confined to East Anglia, which climatically is our "continental" area. One of the most striking examples is *Astragalus danicus* (cf. distribution maps, figs. 2, 3 and 4); but there are others equally impressive—the familiar example of *Potentilla fruticosa,* which is so obviously a steppe plant in Scandinavia and E. Europe that it is difficult to persuade many Scandinavian botanists that it can possibly be native in W. Ireland!—and rather less well-known ones such as *Aster Linosyris* (a steppe species which, on the basis of its British distribution only, would be called Atlantic by Watson), and *Inula salicina,* with a solitary locality in Ireland and absent from Britain, yet a widespread steppe species with a striking disjunct distribution in W. Europe. A group of continental

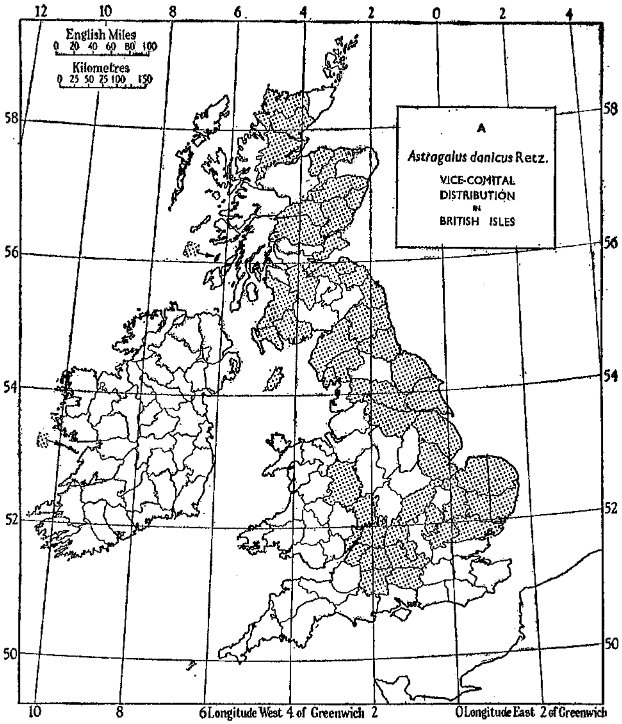


Fig. 2.

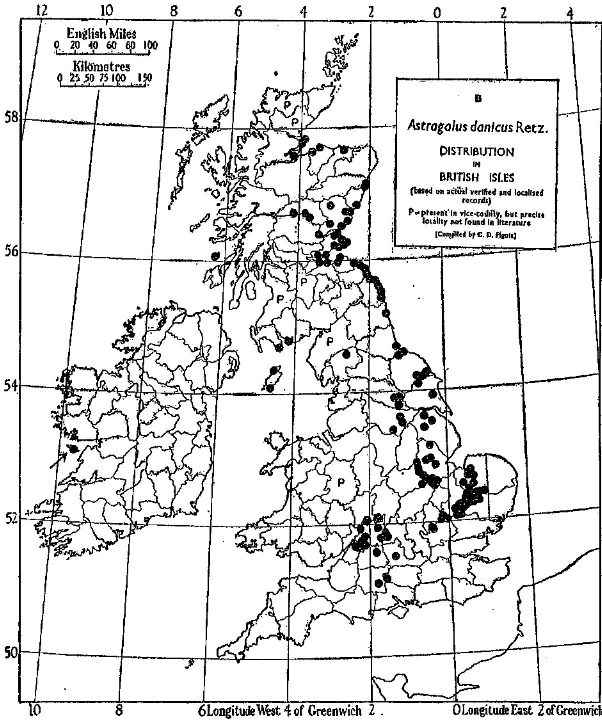


Fig. 3.

Astragalus danicus Retz. Comparison of the two maps shows that the very largely coastal distribution in the north is obscured by plotting by vice-counties as in Fig. 3.

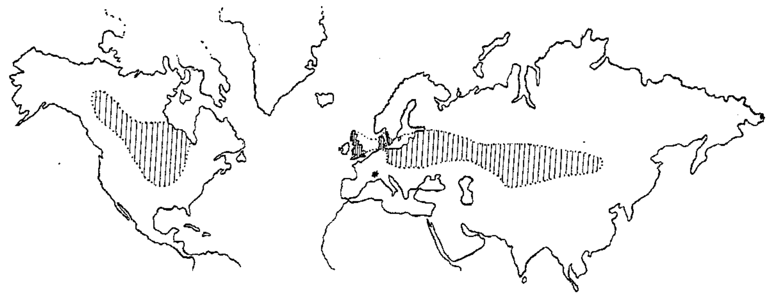


Fig. 4. *Astragalus danicus* Retz.—world distribution (partly after Meusel, H., *Vergleichende Arealkunde*, K3c).

N.B.—The N. American plant is *A. goniatus* Nutt., of which Fernald (Gray's *Manual of Botany*, Ed. X, 1950, p. 912) says " Related to and perhaps referable to the Eurasian *A. danicus* Retz."

species shows marked discontinuity in the British Isles between south-eastern habitats (usually fen or dry chalk) and western ones; these include *Teucrium Scordium, Viola stagnina, Liparis Loeselii.* In the case of *Liparis* there is varietal differentiation between the eastern fen and the western dune slack populations; and this is even more evident in the case of *Veronica spicata.* This species, which is usually quoted as an example of the steppe element in the East Anglian flora, is represented in scattered limestone cliff localities up the west coast of England by the so-called *V. hybrida.* Salisbury and others have argued that here is an example of a species pair, one eastern and continental, the other western and oceanic. In fact, however, outside Britain there is no evidence that *"V. hybrida"* is anything more than an ecotype of the widespread variable Eurasiatic *V. spicata* (Fig. 5), which in East Anglia is represented by a smaller ecotype of chalk grassland, more nearly resembling the commonest European plant. A number of commoner British species show a similar restriction to habitats of reduced competition, but have apparently been able to take advantage of the extension of such habitats through human activity. Such are many calcareous grassland species, e.g. *Filipendula hexapetala*; some of these, to judge from the range of habitats in which they occur, are almost certainly ecotypically differentiated—e.g. *Serratula tinctoria,* which occurs on dry chalk and limestone grassland, in fen, and in open borders of woods. Good's comments on this and other species which show a rather wide range of types of habitat in Dorset are very interesting.

Clearly the only factors common to all the habitats of these continental species in Britain are the high base status of the soil and the reduced competition factor: these are apparently the conditions of much of the widespread Late Glacial flora, which included a great mixture of elements of different origin—arctic-alpine, steppe, S. European.

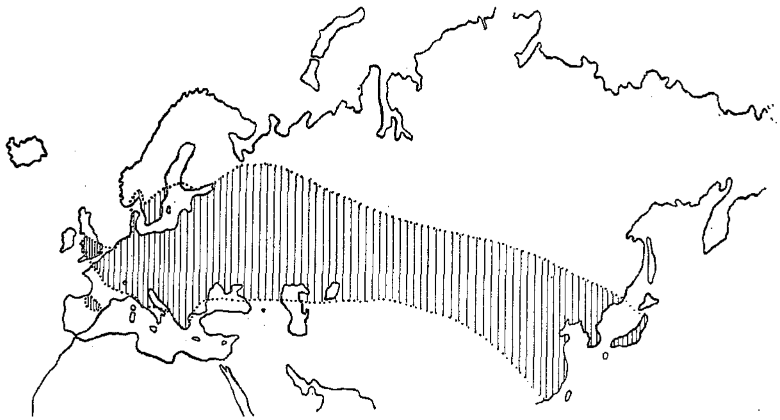


Fig. 5. *Veronica spicata* L.—world distribution (Eurasiatic) (partly after Huber, A., in *Die Pflanzenareale*, *2*, *4*, K34).

N.B.—*Veronica hybrida* L. is included.

This interpretation assumes, as Forbes assumed, that recent "accidental" long-range dispersal is not an important factor in creating these marked discontinuities. Our knowledge of the introduction and spread of many species within very recent years should, however, make us a little cautious of ruling out the possibility of long-range dispersal. It is clear that for a variety of reasons a species cannot be occupying the whole of its theoretical tolerance range; and the establishment of a chance seed introduction in an open habitat is likely to be very much easier than in a closed one. To take one or two examples: there is considerable suspicion that *Arenaria gothica* is a 19th century introduction on Ingleborough, whether accidentally or deliberately; there is reasonable doubt whether *Veronica praecox* could have been missed in the Breck had it been there throughout the 19th century; whilst in the case of *Scutellaria hastifolia,* recently found in a Breckland wood and apparently spreading very rapidly by vegetative means, the evidence in favour of its very recent arrival is very strong. The stability of many of the discontinuous populations is certainly an argument in favour of a relict rather than a recent status; and cultivation experiments to see how far such plants are represented by specialised ecotypes, distinguishable from other populations of the same species, would be extremely useful. Of course there is no reason to suppose that any such ecotypic differentiation has taken place since the isolation of the relict; a much more likely hypothesis is that these formerly widely-distributed species had already at the time of their wide extension produced ecotypes, and that there has been selective survival and elimination of these, until we are left with odd remnants in scattered localities.

The acceptance of this hypothesis does not mean, of course, that we can interpret all the cases of discontinuous distribution in terms of post-glacial vegetation changes. The distribution of such plants as *Arenaria norvegica,* and, more strikingly, the various species in the so-called N. American element of the Irish flora, seem to require some type of per-glacial refuge theory. A recent paper by J. Heslop Harrison (1947) is of considerable interest in connexion with this problem.

I should like to conclude by suggesting ways in which useful investigations might be made in the light of our present knowledge. There is a tremendous field here for the keen naturalist, much of which requires no special technique or apparatus. Firstly, there is our lamentable ignorance of the autecology of species—do they set good seed regularly in nature? what is the life of the individual plant? etc. Any species, common or rare, studied from this point of view would provide the kind of data which we need to explain its distribution, particularly its small scale distribution. Secondly, cultivation experiments on variable species, and especially on these local populations, to find the amount of ecotypic or subspecific differentiation, would be very revealing. [Cf. pp. 82-90]. Thirdly, careful recording of the spread of alien species (e.g. *Senecio squalidus*) can yield much valuable data on the relation of distribution to dispersal methods, climate, soil and other factors. Fourthly, though I am aware that this is not everyone's taste, the study of critical groups and the ranges of the segregates, many of which are as yet very far from being fully worked out. In all these ways we can contribute useful observations, and help to correct that tendency to speculate on the significance of the facts of distribution with a minimum of factual basis.

References.

Cain, S., 1944, *Foundations of Plant Geography*. New York.

Forbes, E., 1846, *Mem. Geol. Surv. U.K., 1,* 336-432.

Godwin, H., 1949, The spreading of the British flora considered in relation to conditions of the Late Glacial period, *J. Ecol., 37, 1,* 140-7.

Good, R., 1931, A theory of plant geography, *New Phyt., 30,* 149-171.

——, 1947, *The Geography of the Flowering Plants*. London.

Harrison, J. Heslop, 1947, Recent Researches on Flora and Fauna of the W. Isles of Scotland and their Biogeographical Significance, *Proc. Belfast Nat. Hist. & Phil. Soc., Ser. 2, 3, 2,* 87-96.

Matthews, J., 1937, Geographical Relationships of the British flora, *J. Ecol., 35, 1,* 1-90.

Meusel, H., 1943, *Vergleichende Arealkunde.* Berlin.

Salisbury, E., 1932, The East Anglian flora, *Trans. Norf. Norw. Nat. Soc., 13,* 191-263.

Watson, H. C., 1832, *Outline of the Geographical Distribution of British plants.* Edinburgh.
——, 1835, *Remarks on the Geographical Distribution of British plants.* London.
——, 1847, *Cybele Britannica, 1.*
——, 1873-4, *Topographical Botany, 1 & 2.*
Woodhead, T., 1929, History of Vegetation of S. Pennines, *J. Ecol., 17,* 1-34.

During the discussion on this paper Mr. Rose drew attention to the absence of various widespread calcicoles from the chalk of S.E. England and instanced *Astragalus danicus.* Mr. Walters replied that this was also true of *Anemone Pulsatilla,* and Miss Gibbons added that in Lincolnshire this species was not found on chalk but only on (older) limestone.

THE WATSONIAN VICE-COUNTY SYSTEM

J. E. Dandy.

Introductory.

The Watsonian Vice-county System, for the recording of the horizontal distribution of plants in Britain, may be said to date from 1852 when Hewett Cottrell Watson, at the end of the third volume of his *Cybele Britannica,* gave a list of 38 sub-provinces and 112 vice-counties into which he proposed to divide the country. This list was illustrated by a map. In the main body of the *Cybele* he had not used the Vice-county System but had analysed the distribution of the British flora on the basis of a division into eighteen provinces and 82 counties. As he explained in the fourth volume of the *Cybele* (1859), the object of the Vice-county System was to provide a set of unit areas more even in size than the counties, whose extreme inequality of size was "most inconvenient and objectionable". In this fourth volume Watson elaborated the scheme and provided definitions of the Vice-counties. (It may be mentioned here that Watson at first usually restricted the term "vice-counties" to the portions of divided counties, retaining the term "county" for the undivided ones; but this inconvenient distinction has long since disappeared.) The principle of his scheme was to divide the larger counties into two or more vice-counties, and to merge the smallest counties into larger neighbours. Thus Yorkshire was divided into five; Argyll into four; Hampshire and Perth into three; and numerous counties like Cornwall, Norfolk, Northumberland and Sutherland were divided into two. Of the smallest counties, Rutland was merged with Leicestershire, Kinross with Fife, Clackmannan with Perth, and Nairn with Inverness. The result was a system of 112 vice-counties, numbered consecutively from 1 (West Cornwall) in the south-west to 112 (Zetland) in the extreme north.

The system was actually brought into use by Watson in the closing chapters of the fourth volume of the *Cybele,* for example in the "Summary of Distribution" and the "Census of Species". But it was in his classic *Topographical Botany* (1873-74) that the system was first really used on a full scale. With the publication of this work, and its later edition (1883) and supplements, the Vice-county System secured general adoption by British botanists. The forerunners of this Society, together with the Botanical Record Club and the Watson Botanical Exchange Club (both now defunct), early adopted the system and played a great part in developing its use, which culminated in the production of the *Comital Flora* in 1932 by the late George Claridge Druce while Honorary Secretary of this Society. Some British zoologists, notably the conchologists, also adopted the system; and other groups, including the ornithologists, have lately shown an interest in it.

In view of the increased interest in the system, and of the fact that there were some discrepancies in the vice-county boundaries as used by different workers and shown in different maps, a joint committee was set up just before the recent war by this Society and the Association for the Study of Systematics, to examine the question of vice-county boundaries. The war unfortunately intervened when the committee had met only once. But during the war investigations were carried out by the late Mr. A. J. Wilmott and myself, and reached such an advanced stage that when the war was over a sub-committee of the Systematics Association was formed to complete the work. This sub-committee has now made its decisions and practically completed its investigations, with the result that the Ray Society has undertaken to publish a guide to the vice-counties illustrated with maps on the scale of ten miles to one inch and incorporating the decisions of the sub-committee. The guide is now in course of preparation.

Advantages of the Vice-county System.

By dividing Britain into unit areas of suitable size we can conveniently record, or index, our information about the horizontal distribution of plants and animals within the country; and we are provided with a simple means of portraying the distribution either by maps or formulae. The unit areas must, of necessity, have arbitrary boundaries, as have the vice-counties, and the question arises whether some other system, such as a system of grid-squares, would better meet the requirements. This question was anticipated, and in large measure answered, by Watson himself, who in discussing his system in the *Cybele* (vol. iv, 129-130) made the following remarks.

"These old political divisions of Britain (i.e. the counties) were found to be little suitable for the objects of phyto-geography. As a first step downward, in subdividing the three ancient kingdoms of England, Wales, Scotland, they were found to be inconveniently numerous. Their extreme inequality of size was also most inconvenient and objectionable; the largest of them being more than a hundred fold the size of the smallest. Other divisions or sections of the surface were required instead, more equal in their dimensions, and bearing some better relation to the physical geography of the surface. By utterly disregarding the old comital divisions, and tracing out an entirely independent series of districts, the required objects might have been met very completely. But the advantages thereby gained would have been attended with disadvantages so great as to become practically insuperable. An entirely new set of boundary lines would have been necessary, not in accordance with those laid down in existing maps; and which would thus have necessitated new maps, on a large scale, for tracing them out satisfactorily. Most of the local Floras and other lists of species, with arrangements and specifications of localities, have been made in reference to county limits; so that a large portion of our printed records would have been rendered much less available, by the adoption of other divisions which disregarded the old comital boundaries.

"These and other considerations made a general adherence to the long-established county limits practically unavoidable, when fixing upon other sections to be used instead of the counties themselves, or jointly with them. Larger and fewer districts could be formed by uniting counties into provinces. Smaller and more numerous sections could be formed by dividing the great counties into vice-counties . . . ."

One of Watson's points—about the necessity for an entirely new set of boundary lines if counties were disregarded—has of course now been met by the introduction of the grid; but even so it must be remembered that only some of the most modern maps bear the grid, whereas all maps of Britain show the county boundaries and the other features, such as rivers and highroads, used by Watson in delimiting his vice-counties.

Watson's other point, about the relation of his system to the counties, is of paramount importance. British botany and zoology have traditionally been worked out to a very great extent on a county basis, as is shown by the long array of county floras and county lists, many of them prepared by county natural history societies whose members take great pride in recording the plants or animals of their native county. The Vice-county System, with its county basis, links up admirably with this work and its attendant literature.

Connected with this point there are two others in favour of the Vice-county System as opposed to some purely arbitrary system such as a grid. Firstly, county boundaries are commonly discernible in the field, very often being related to some physical feature such as a stream, a footpath or even a hedgerow; whereas grid lines, as we used to be told of the Equator, are imaginary and cannot be seen in the field. Secondly, every Briton has some idea of the counties and their arrangement on the map; and those who as botanists or zoologists are capable of remembering hundreds or thousands of generic and specific names should have little difficulty in memorizing a sequence of 112 vice-counties. Who, however, could be expected to memorize the positions and references of grid-squares?

Finally there is another most important point in favour of the Vice-county System. Whatever its merits or demerits, the fact is that for nearly eighty years, ever since the publication of *Topographical Botany,* British plants have been recorded on the Vice-county System. A large proportion of the records, especially those in *Topographical Botany* itself, cannot be translated into any other system because precise localization within the vice-counties was not given. Unless we are to jettison these records, the valuable results of so much painstaking work, the Vice-county System must remain.

Difficulties of the Vice-county System.

It must not be supposed from the foregoing that there are no difficulties attached to the use of the Vice-county System. There are in fact two sources of difficulty: changing county boundaries and lack of precision in some of Watson's definitions.

Changes in County Boundaries. The county boundaries accepted by Watson were of course those of his time; in fact, as indicated in the *Cybele* (vol. *5,* 139), his boundary lines were adapted to the maps of England and Scotland in an atlas published in 1844 by the Society for the Diffusion of Useful Knowledge. Copies of these maps are still available, so that we know just what he meant. Watson, however, appears to have taken no account of the fact that county boundaries are subject to occasional modification, and certainly he did not visualize the considerable changes which were to come about as the result of the industrial revolution with its attendant increases and shiftings of human population. Before the end of last century Local Government Acts made many boundary changes (among other things the County of London and the first of the County Boroughs were formed), and the process has steadily been going on especially in the neighbourhood of expanding cities like Birmingham, Bristol, Manchester and Sheffield which are situated near the edge of their original counties and gradually absorb territory from adjoining ones. It seems certain, too, that more and far-reaching changes will be made in the not too distant future. Obviously the Vice-county System cannot be worked on a basis of changing boundaries. The system must have stability by means of fixed boundaries, and if the great accumulation of records built up under it by Watson and his successors is to have permanent value these fixed boundaries must be the same as those used by him. This was the first decision made by the Joint Committee which met before the war, and it was endorsed by the Systematics Association Sub-committee set up after the war. Difficulties existed, however, because the scale of the maps used by Watson was not large enough for his county boundaries to be worked out in detail. During the war Mr. Wilmott, in order to overcome these difficulties, consulted the Ordnance Survey who readily agreed to help; the result was the preparation of a set of modern parish diagram maps on which the Survey marked the changes since Watson's time so far as they could be ascertained. These maps, which are deposited at the British Museum (Natural History), have been compared with the maps used by Watson and found to show close agreement. The Sub-committee has accordingly agreed that this set of marked maps should be accepted as the standard by which to interpret Watson's county boundaries.

While on the subject of county boundaries it is important to consider the question of enclaves, i.e. detached minor portions of counties separated by land and surrounded by the territory of other counties. To-day only five such enclaves remain, but in Watson's time they were very numerous and ranged in size from large areas like the Dunbarton enclave to tiny plots of land too small to be marked in detail on a half-inch map. Watson made no general statement about enclaves, but it is clear from his occasional references to them in his text, and from his maps, that he took the commonsense course of merging them all into the territory of the counties surrounding them; for example, the Worcestershire (Dudley) enclave is merged with Staffordshire. Thus the only enclaves which presented any difficulty in interpretation were those which were sandwiched between two or more counties, like the Dunbarton enclave which lies between Stirling and Lanark. Fortunately it has been found possible, from a study of Watson's maps and other considerations, to decide the position of all the "sandwich" enclaves. The Dunbarton enclave, for example, is merged with Stirling, as Kidston and Stirling long ago decided.

UNPRECISE DIVIDING LINES. Where Watson divided a county to form two or more vice-counties he usually chose and stated a dividing line which is not in doubt. These definite lines included rivers (as in Lancashire, Yorkshire, Perth); canals (Wiltshire, Yorkshire, Argyll); highroads (Cornwall, Hampshire, Sussex); arms of the sea (Hampshire, Argyll, Inverness); watersheds (Inverness, Ross, Sutherland); administrative boundaries (Yorkshire Ridings); and a meridian of longitude (Suffolk, Norfolk). All these lines are readily discernible on a map, and most of them are obvious in the field. In some cases, however, Watson's definition of a dividing line is not precise enough for clarity, for example in Devon, where he cites not the actual watershed over Dartmoor but "an imaginary line, adapted to the water-shed"; in Somerset, where he describes a line simply as "curving round" from Ilchester to the northern extremity of Dorset; and in Yorkshire, where he divides the county by the rivers Humber, Ouse and

Wiske but omits to complete the line northwards to the Durham border. The Sub-committee has decided each of these cases on its merits. If an unprecise line (as in Devon and Northumberland) has been satisfactorily defined in print by local workers the definition has been accepted. If no such definition has been published the Sub-committee has, where possible in consultation with local workers, decided on a line. In conclusion, I may mention some particular cases where confusion has arisen in the past.

The Great Ormes Head is in Caernarvonshire and was so in Watson's time; yet his vice-county maps in the *Cybele Britannica* and in *Topographical Botany* show it as in v.-c. 50 (Denbigh). This was an accident due to a misprint in the map published by the Society for the Diffusion of Useful Knowledge (the basis of his own maps), which correctly showed a dotted boundary across the Great Ormes peninsula but failed to mark it in red like the rest of the county boundaries. The Great Ormes Head is in v.-c. 49 (Caernarvon), as made clear in *Topographical Botanu* under *Cotoneaster*.

Watson divided v.-c. 88 (Mid Perth) from v.-c. 87 (West Perth) by the watershed dividing the tributaries of the Tay from those of the Forth; but he failed to mention the small area in the south-west of the county drained by tributaries of the Clyde. Druce's map in the *Comital Flora* places this area in Mid Perth, but it is clear from Watson's maps that its correct place is in West Perth.

The line dividing Cornwall was defined by Watson as traced along the highroad from Truro through St. Columb to the inland extremity of Padstow Creek. But there are two highroads from Truro to St. Columb, one through St. Erme, the other through Ladock. Watson's maps suggest the former, but Davey's *Flora of Cornwall* takes the latter. The question is settled by reference to the map published by the Society for the Diffusion of Useful Knowledge, which shows only the western (St. Erme) road. This is therefore the line to be accepted.

This was discussed by Miss Longfield, Mr. Brenan, Mr. Nelmes, Mr. Rose and Mr. Whitehead.

Mr. Nelmes stated that a recent work had treated part of Somerset round Brislington and south of the Avon as belonging to Gloucestershire and he enquired whether this area should be regarded as part of v.-c. 6 or v.-c. 34 following Mr. Dandy's researches.

Mr. Dandy replied that the boundary between v.-c. 6 and v.-c. 34 should be as shown in the map accompanying the recently published *Flora of Gloucestershire*. A small area of the city of Bristol, south of the Avon and of Floating Harbour, is to be included in v.-c. 34. The larger area referred to by Mr Nelmes, which includes Brislington and has been added to Bristol in recent times, is to be treated as part of v.-c. 6, i.e. North Somerset.

Miss Longfield asked how boundaries were traced where they ran out to sea and hence how islands were allocated to the appropriate vice-counties.

Mr. Dandy answered that administrative boundaries rarely run out to sea, but where they do so they are followed. In general, islands are allocated to the counties to which they belong for administrative purposes (e.g. Steep Holme to Somerset and Skokholm to Pembroke); but in some cases, as in the Hebrides, islands are specially grouped by Watson and he is of course to be followed. Such insular vice-counties are not separated by definite boundaries like the county boundaries on land, but are separated by imaginary lines following, say, the middle of a main channel.

Mr. Rose enquired how the line of longitude one degree east employed by Watson as the boundary between East and West Suffolk (v.-cc. 25 and 26) and between East and West Norfolk (v.-cc. 27 and 28) could be fixed on one-inch and other maps used by botanists in the field.

Mr. Dandy replied that this is one of the least satisfactory boundaries chosen by Watson and serves to show the difficulties that would arise if a system entirely based on such lines (e.g. a grid system) were adopted in place of the Vice-county System. Botanists working in Norfolk and Suffolk should, if near the line of longitude one degree east, use extra care in localizing and, if in any doubt about the vice-county, consult maps on a bigger scale such as the six-inch.

Mr. Whitehead suggested that much of the difficulty in using a grid for plotting distribution depended on the choice of scales of maps used for work in the field.

Mr. Brenan asked whether there would be inset maps on larger scales included in the Ray Society publication and pointed out that these would be extremely useful in certain areas which included special difficulties.

Mr. Dandy replied that this depended on limitations imposed by the selection of a convenient size for the book. If it proved impossible to include such inset maps the description of detailed boundaries would be expanded in the text.

Finally Mr. Dandy expressed his willingness to help with problems arising over the interpretation of vice-county boundaries and reminded members that this is one of the subjects covered by the Society's Panel of Specialists.

MAPS OF THE WATSONIAN VICE-COUNTIES (Exhibit)

J. E. Dandy.

The following were exhibited throughout the Conference to illustrate the above paper:

(1) H. C. Watson. *Cybele Britannica.* Vol. 3. 1852.

(2) *Atlas* issued by the Society for the Diffusion of Useful Knowledge in 1844.

(3) Two manuscript maps prepared for the projected Ray Society publication.

(4) Map of the *Biological Subdivisions of Ireland,* Ed. *2,* on the scale of 50 miles to the inch showing the Hibernian vice-counties and recently published by the Ordnance Survey Office, Dublin.

(5) One of the maps prepared by the Ordnance Survey to show changes in boundaries since Watson's time and deposited at the British Museum (Natural History). The map exhibited showed Worcestershire with modern boundaries shown by red lines and the boundaries in Watson's day where different by green.

THE WATSONIAN VICE-COUNTY SYSTEM IN PRACTICE

J. E. Lousley.

The state of British geographical botany when Watson first became interested was, as he pointed out (1847, p. 20), chaos rather than science. The best handbook was Turner and Dillwyn's *Botanist's Guide,* which was little more than a guide-book for collectors arranged in alphabetical sequence of counties. "Arrangement is the first effort of science," and Watson soon found the need for a framework, or grid, for the purpose of marshalling and arranging the available records. In his first work (1832) he divided England and Wales into four districts and Scotland into two. In 1843 he divided England and Wales into 12 districts and Scotland into 6. In 1847 and onwards he re-named these as 18 Provinces, and divided them into 38 Sub-provinces and eventually into 112 vice-counties. It was not until the first edition of *Topographical Botany* in 1873-74 that he recorded the actual distribution of species under these vice-counties, which he introduced into his studies incidentally, and for the purpose of arranging the detailed records supporting his more generalised statements. Watson thus found a need for smaller and smaller units for his framework—first Districts, then Provinces, then Sub-provinces, and finally Vice-counties (Fig. 6).

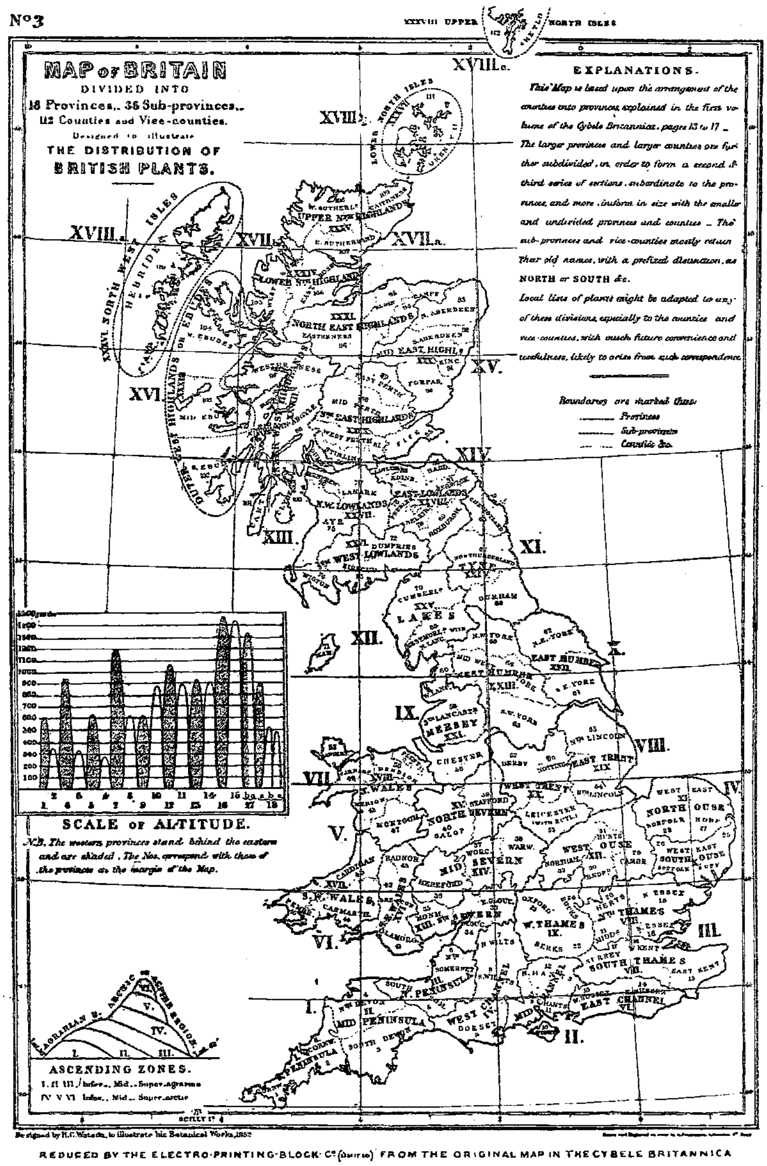


Fig. 6.

H. C. Watson's map, showing his 18 provinces, 38 sub-provinces, and 112 vice-counties, as reproduced in *Topographical Botany*, Edition 1, and reduced from the original map in *Cybele Britannica*.

He died in 1881, and at the request of Bernard Quaritch, the publisher, a second edition of *Topographical Botany* was hurriedly prepared by J. G. Baker and W. W. Newbould and published in 1883. This was based on Watson's interleaved copy of the first edition, and has served as the basis for our records ever since. The work was continued in the quinquennial summaries of the *Botanical Record Club,* and in the supplements to *Topographical Botany* issued by Arthur Bennett in 1905, and by Bennett, Salmon and Matthews in 1929-30.

Watson's work did not include Ireland. Records of flowering plants and ferns in that island were first arranged under Districts corresponding to and continuing Watson's 18 Provinces (Moore & More, 1866), and later under County-divisions corresponding to Watson's vice-counties. The records as given in Praeger's *Irish Topographical Botany* (1901) and supplements (1906, 1929, 1934a, 1939) arranged under these County-divisions are the basis of our present knowledge of the distribution of the Irish flora. It should be added that there have been several minor alternative schemes (see Praeger, 1934b, p. 77) and that Dr. Praeger has this year (1950) handed over the responsibility for future supplements to Professor D. A. Webb.

The records, both for Britain and Ireland, were summarised by Druce in his *Comital Flora of the British Isles,* which was published for our Society in 1932. For quick reference, when a general idea of the British distribution of a species is required, this work is extremely useful. It is the one on which are based indications of New County Records in the Plant Records section of *Watsonia,* and the Society has a heavily corrected official copy kept up to date for this purpose. I have also an annotated copy of my own which was first corrected from the late P. M. Hall's copy (which became the official one) and has since been altered independently. It must, however, always be remembered that the printed text of *Comital Flora* gives no authorities for the records it includes and, to this extent, it is not part of the system of scientific recording of plant distribution in Great Britain. It is essential that summaries of vice-county records should be based on references which can be followed up and checked, and it is desirable that further supplements to *Topographical Botany* and *Irish Topographical Botany* should precede a fresh edition of *Comital Flora.* In practice it has proved impossible to discover the source of some of the entries in Dr Druce's work and in such cases they cannot be accepted until proper evidence is forthcoming.

For Ireland there is a summary on rather similar lines in the *Census List* towards the end of Dr. Praeger's *The Botanist in Ireland* (1934b), but in this case supporting evidence for entries can be found in his other works already mentioned. A useful summary of records for the Principality appears in Hyde and Wade's *Welsh Flowering Plants* (1934) where many of the supporting records are cited and the evidence for others can be obtained by writing to the National Museum of Wales.

The Accuracy of the Records.

The value of the results obtained from any system of recording plant distribution is obviously dependent on the accuracy of the facts on which it is based. Both Watson and Praeger were very well aware of this, and showed careful discrimination in the records they accepted.

Watson's standards were explained at great length in the second edition of *Topographical Botany,* and may be summarised as giving priority to personal evidence of which he rated his own observations highest of all. For our purpose the records he gives fall under the following five headings:—

1. *Herbarium material.* This included specimens in his own collection which is now at the Royal Botanic Gardens, Kew, and in addition gatherings which had at various times passed through his hands. Most of this material is still available for examination.

2. *Local catalogues marked by his correspondents.* Many of these may still be seen at Kew and usually consist of copies of the *London Catalogue of British Plants* of various editions in which the species supposed to have been seen are marked. It is notoriously easy for even the best botanists to make errors in work of this kind, and without independent confirmation such records are of little value.

3. *Personal observations by Watson.* In spite of the very high standard of accuracy which he set himself, it is on record (*loc. cit.,* p. 587) that he knew that some of these were errors as printed, and in addition corrections will have become necessary owing to advancing knowledge since his time. Confirmation is desirable.

4. *Manuscript notes sent by correspondents.* To these the same objections apply with additional risk of error.

5. *Published literature.* Watson professed that he placed little reliance on printed records but nevertheless he included a very large number of records without authority, which indicates that he accepted published records for the counties concerned. Unfortunately he refused to include the appropriate references owing to foolish and short-sighted contemporary insistence on book references being given *in extenso*—which for practical reasons was impossible. It is still possible to trace most of the book references he had in mind, and in many cases they supply further evidence which can be followed up.

The supplements to *Topographical Botany* give authorities, or references, for all the records included. These provide a similar assortment of evidence of varying value but lack the advantage of having been subject to the refining influence of Watson's ruthless pruning.

Praeger's work appeared nearly 30 years later and attained a much higher standard than Watson's. For most county-divisions he gives more than one authority; often he paired a personal or manuscript record with a printed one. Dates were added and also statements of frequency. I should like to take this opportunity of expressing my admiration of this fine book which the veteran Irish botanist completed nearly half a century ago.

The imperfections which exist in our accounts of vice-comital distribution based on the sources just given may be summarised as follows:—

a. *Errors in identification.* Some of these determinations were wrong at the time they were made, as in the case of *Chenopodium urbicum* L., for which variations of *C. rubrum* L. have often done duty. Similarly *Rumex maritimus* L. and *R. palustris* Sm. have been frequently confused. Other determinations have been correct, as far as they went, at the time they were made, but have become inaccurate or misleading owing to advances in the knowledge of taxonomy or nomenclature—or both. For example, it would now be almost impossible to disentangle all the records of *Orchis latifolia* L. which has been used in wide and also restricted senses and for different plants. Investigations such as those by Walters (1949) on *Aphanes,* and by Howard and Manton (1946) on *Nasturtium,* which substitute two species for one in the British list, necessitate re-examination of all the records of the plant replaced. Such cases emphasise that an ideal system of recording would be based on herbarium material, properly cited, and always available. It would be a practical proposition to indicate with appropriate signs the vice-counties for which supporting specimens could be seen at say the Natural History Museum, Kew, Edinburgh, Oxford, Cambridge, Dublin and Cardiff and thus account for the majority of the records. In Denmark, localities vouched for by specimens in the Botanical Museum of Copenhagen are indicated with a special sign on their distribution maps.

b. *Errors in status.* A very large proportion of our plant records include no assessment of the status of the species at the locality concerned. In the case of plants which are regarded as native anywhere in the British Isles it is too commonly assumed that additional stations must also be native, and the results are extremely misleading. A good example is *Iberis amara* L. This may well be native in chalk districts in central England, and particularly in the Chilterns, where it is found in fields and woods and on chalky banks with a continuous distribution over a limited area. In other parts of Britain it is found under varying conditions which often give clear indication that it is adventive. Sometimes the garden plant, *Iberis umbellata* L., is likely to be the species actually found. Nevertheless, in at least one instance, all this hotch-potch of records has been used for the preparation of a map purporting to show the distribution of the species in Britain, and totally obscuring the true position.

Similar errors arise in the case of far more species than is generally supposed. For example, *Rumex Hydrolapathum* Huds.

and *R. maritimus* L. are probably, or even certainly, introduced in some of the vice-counties for which they are claimed. *Clematis Vitalba* L. is a plant for which it is not at all easy to work out the exact distribution towards the margin of its area in the north. It is likely that many undisputed natives get carried by accident or design by human agency to places where they do not naturally grow. Assessment of status is a difficult exercise in judgment for which long experience is desirable, but if recorders would make a regular practice of noting their impressions we should eventually amass data which might lead, in the case of some species, to surprising conclusions.

c. *Lack of veracity on the part of recorders.* This, fortunately, is responsible for only a very small fraction of the misleading records but some of these are of exceptional importance. When such falsehoods are detected or suspected it still remains necessary to repeat them in each new publication with reasons why they should not be accepted. The detection of a single deliberate mis-statement in a botanist's work very properly throws doubt on all his other publications, and it cannot be overemphasised that the few people who have behaved in this way are not only a nuisance to science, but also their own worst enemies.

d. *Incorrect assignment to vice-counties.* Difficulty in this connection arises in two ways. First, there is the fact that some records are not localised with sufficient accuracy for it to be possible to ascertain with certainty the vice-county to which they should be assigned. Second, there has been much difficulty in the past in determining the precise boundaries of Watson's vice-counties. The book which Mr. Dandy has in preparation for the Ray Society will make it very much easier in the future to allocate records correctly, and doubtful cases already published should be re-examined.

e. *Neglect of the time factor.* The inclusion of this as a source of imperfection in our records may perhaps be a little controversial and may be illustrated by a straight-forward example. *Diotis maritima* Cass. has been recorded from 11 English, 2 Welsh, and 2 Irish vice-counties and also from Jersey, and at present it is only certainly to be seen in Ireland. Yet these records (two of which may be errors) were collected over a period of some 350 years and it is unlikely that it was ever possible to see the plant in more than three or four vice-counties at any one time. It may well be a case of a Mediterranean species making repeated attempts to establish itself at the northern limit of its range and each fresh colony may have only a limited life until destroyed by extreme climatic conditions which only occur at intervals. However that may be, it is extremely misleading to telescope all the recorded occurrences without differentiation into one map. The time of the records should be indicated as well as their distribution.

The importance of time is obvious in the case of aliens—the spread of *Senecio squalidus* L., *Cardaria Draba* (L.) Desv., and *Veronica persica* Poir., are well-known examples where it must be indicated on maps showing the extension of their range. But it is to supposed native rather than alien species that I wish to draw attention in this connection.

It is not unlikely that there is an ebb and flow in numbers and area of many of our native plants. There is evidence of this in the case of *Himantoglossum hircinum* (L.) Spreng. (Good, 1936) which on account of certainty of identification, rarity, and public interest, offers exceptionally good opportunities for studies of this kind. More detailed studies are likely to reveal that the distributions of many native species are less static than is often supposed.

f. *Failure to incorporate records in the general works.* Both Watson and Praeger cast their nets widely and overlooked surprisingly few records but the compilers of the supplements to *Topographical Botany* were less thorough in their work. Many records scattered through the literature of the last half-century or so have still to be incorporated although we have made an attempt in this Society in recent years to include those noticed in Plant Records, or in special papers listing additions to be made from particular local floras.

The total number of errors and imperfections arising from these six sources is large—perhaps very large—but I should like to make it clear that they affect only a small percentage of the enormous number of county records which have been accumulated. Their incidence is heavy only in the case of certain species, and our published studies are in general sufficiently accurate to give a reasonably true picture of the distribution of most of the plants concerned. In spite of its shortcomings in detail, the work done in Britain must be regarded as a very creditable performance by comparison with most of that done abroad.

Having considered the reliability of the facts (i.e. the records) it is necessary to discuss the framework by which they are arranged.

The Framework of Vice-counties.

Systems for the arrangement of plant records fall broadly into two classes—irregular *frameworks* based on political boundaries and arbitrary and regular *grids*.

The Watsonian system is an example of the first-named class, for Watson accepted political county boundaries as laid down at the time and introduced certain subdivisions in order to obtain vice-counties of very approximately equal area (average 850 square miles). The main disadvantage of the system in practice is that considerable research has proved necessary to determine the precise political boundaries he had in mind and these are no longer those used on the maps in the hands of recorders. Also the vice-counties vary in size too much for accurate comparison on a statistical basis.

On the other hand the system has great practical advantages. Political boundaries are those selected for most works on floristics, and this is particularly true in Britain where most local floras are on a county basis. Even with the changed boundaries to-day there is not the slightest difficulty in allocating the great majority of the records. Once the average educated user knows that Surrey is v.-c. 17, he can allocate nearly all the appropriate records to v.-c. 17 without difficulty, and often without reference to maps and books. Similarly it has been customary in neighbouring countries to base most botanical work on political boundaries and their publications can usually be correlated easily with our own. An example is Good's comparison of the floras of Kent and the Pas de Calais (1928).

The alternative is a grid by which horizontal and vertical parallel lines on the map produce arbitrary squares. The best examples are the kilometre grids used in Holland and Belgium. In this country we could adopt the 5 kilometre grid marked on our One-inch Ordnance Survey maps, much as has been done in the German system on exhibition. The great advantage of such an arrangement is that all squares are of exactly the same size and they can all be compared statistically. Moreover, it is possible to make indefinite subdivisions of each square and equally to collate the system to larger squares. Thus the varying demands of the ecologist, who often works on a metre square, and the world plant geographer, who is likely to require say 100-kilometre squares, can be served. There is no doubt that this is a much more scientific method. Nevertheless, the grid-system suffers from the great practical disadvantage that much labour and care must be expended on assignment of records to the correct squares, and the results can only be read back by reference to maps. It does not lend itself to setting out distribution in simple formulas like those in *Comital Flora*.

Single Records for Each Vice-county.

Watson, as a pioneer, accepted a single record for each vice-county. Provided the record was accepted as reliable his system called for no further attention to that particular vice-county and, incidentally, led to keen competition among amateur botanists for "N.C.R.'s" (New County Records). While the study of distribution in Britain was in its infancy this was adequate, but it is insufficient for modern research.

Distribution maps showing whole counties blacked-in or shaded from the lists in *Topographical Botany* and its supplements or, worse still, from *Comital Flora*, are reproduced even to-day. If intended to show general distribution in relation to that elsewhere, and if the scale used is not larger than about 1:15,000,000 (i.e. John o' Groats to Land's End about $2\frac{1}{2}$ inches) they are not seriously misleading. On larger scales they cannot be condemned too strongly. Such maps fail to show:—

A. *Dependence on special habitats.* The most obvious example of this is to be seen in maritime plants. Many of these are restricted to the coast and it is absurd to show them as growing far from the sea in counties which include large inland areas as well as a stretch of coast. To do so obscures the very special conditions which some require (e.g. *Obione pedunculata* (L.) Moq. and *Eleocharis parvula* (Roem. & Schult.) Link), and also the fact that some also grow inland (e.g. *Glaucium flavum* Crantz, *Spergularia salina* J. & C. Presl, *Spartina Townsendii* H. & J. Groves, *Puccinellia distans* (L.) Parl.) under very different conditions.

Similarly plants growing by or in rivers or estuaries (*Scirpus triqueter* L.—see maps, p. 44), or ponds (e.g. *Cyperus fuscus* L.), or restricted to high altitudes (e.g. *Luzula arcuata* (Wahlenb.) Wahlenb., *Lactuca alpina* (L.) Hook. f.) or to bogs (e.g. *Eriophorum gracile* Roth) should certainly not be shown over areas which include habitats where they would be unlikely to occur. Much the same applies to species confined to certain soil types like *Anemone Pulsatilla* L. and *Cirsium tuberosum* (L.) All. which are restricted to calcareous soils.

Much greater detail than is provided by marking in whole vice-counties on the basis of single records is required to show the relationship of species to topography, soil and other factors.

B. *Frequency.* For the study of plant distribution it is almost as important to be able to compare frequencies as it is to have a record of the mere fact that species occur in certain areas. When the southern botanist goes north he is likely to be impressed by the much rarer occurrences, as well as absences, of some of the species he regards as common at home, and conversely by the abundance of plants he seldom sees in the south. As an example of this I am exhibiting a map of the distribution of *Antennaria dioica* (L.) Gaertn. which is plentiful in many northern counties, but only found in some of the southern ones in tiny patches of uncertain appearance. To mark in all vice-counties in which it has been found without differentiation fails to give a true picture of the distribution.

There are similar contrasts in frequency within the range of very many British plants. Watson's system made no provision for its study. Praeger in his *Irish Topographical Botany* gave brief and most useful statements on frequency for many of his county-divisions.

The Dot Method.

It is evident that the Watsonian Vice-county System in its essential form does not provide sufficient detail and that maps should show actual occurrences. The signs used for the latter I will refer to as "dots" for want of a better term, although in practice they may take many forms other than simple specks on the map. Whatever form they take, frequency is automatically indicated. Where they coalesce or are very close together the area may be shaded to show continuous distribution.

Such a system can be grafted on to the Watsonian plan. We already have a very large number of local floras covering one or more vice-counties which will provide information about detailed localities. They also include notes on status and other matters. The localities they provide can be plotted without difficulty on outline maps showing the vice-counties on which the irregular boundary lines serve to pin-point almost any localities. In practice the chances of error are less than those likely in plotting on a mechanical grid.

Some of the maps issued in the *Biological Flora* have been based on information collected in this way to show plants restricted to the coast or by different shading of the vice-counties to indicate the dates of the first records, or changes in frequency (cf. maps on pp. 85 and 116). They are a great improvement on maps shaded in without differentiation but would gain in accuracy in some cases by the plotting of actual localities.

It should be noted that " dots " have the advantage that they can be varied to give much information in addition to frequency. Such important facts as dates of occurrence, the whereabouts of herbarium material and supposed extinctions can be shown without difficulty. In this connection the Danish scheme in which " dots " of various kinds are skilfully combined with shading, is worth very careful examination.

Sub-division of Vice-counties.

In spite of the ease with which localities can be plotted in the present vice-county outlines, there is still need for smaller divisions in some connexions. One such need arises in the compilation of county floras and the difficulties which Dr. Dony will describe in his paper are representative. They arise chiefly from the fact that vice-county boundaries are political rather than botanical. Even the boundaries invented by Watson, such as the lines dividing v.-cc. 25 and 26 and v.-cc. 27 and 28, are arbitrary and form no natural areas. In these circumstances it is not surprising that writers of the floras of the larger counties are sometimes tempted to carry their divisions across the vice-county lines. This practice makes it difficult for their publications to be used to check the distribution for Britain as a whole, and I would thoroughly endorse the late Mr. Wilmott's protest against it. In his paper (1944) he shows clearly how a more satisfactory subdivision of the particular Scottish vice-counties concerned could be made.

This question of the sub-division of vice-counties arises whenever it is necessary to create smaller areas for individual workers. The high standard to which Watson in his lifetime raised our recording on the " single record for a vice-county " arrangement shows how much can be achieved by having people interested in particular areas. Now that further detail is required we might follow the example of the Danes and sub-divide our political areas, though our parishes are less suitable (Lousley, 1942) for the purpose than their *Herreder*. But some sort of sub-division is essential for the organisation of any investigation of the flora calculated to ensure that all parts of the country eventually receive examination on a more or less uniform standard. One of the advantages of the grid as used in Holland and Belgium is that an attempt can be made to list all the plants of any given square kilometre and maps can be prepared showing which squares still require attention. The Watsonian system has not only failed to provide sufficient detail but in late years it has also suffered from haphazard attention to some of its divisions and neglect of others. The efforts of our field workers could be more effective if proper organisation were provided.

Conclusion.

In the early part of this paper I reviewed the compilation of records under the "single record" system inaugurated by Watson and indicated sources of inaccuracy in those records. I then tried to show that the standards of Watson's time are inadequate for modern purposes and that botanists are already obliged to supplement the records accumulated by the strict Watsonian system by more detailed information from local floras. Some of my comments have been controversial, and I should like to conclude by suggesting some possible developments as headings for discussion.

First I would suggest that we should set up a permanent committee charged with the organisation, revision and extension of the work of collecting records. In this we should follow the example already set in Denmark, Holland and Belgium. The committee should seek reasonable publicity and collaboration from local botanists.

They should undertake a revision of the existing records to produce a new Topographical Botany in which the whereabouts of herbarium material supporting vice-county records should be indicated wherever possible. They should appoint local observers in each vice-county—our own Society's local Recorders might be the basis of this list—and charge them with the energetic revision of records. As a further step the sub-division of vice-counties into smaller areas might be considered. As an interim measure the divisions already in use in many county floras might be added to the vice-county numbers as a suffix separated by an oblique line. Thus v.-c. 4/1, North Devon: Barnstaple; v.-c. 4/2, North Devon: Okehampton, etc. Even in the counties where such divisions are available they sometimes include parts of more than one vice-county (e.g. *Flora of Gloucestershire*), and are of very unequal size. A better and uniform method might be devised with the co-operation of local botanists.

The procedure by which our method of keeping records might be improved is a matter for discussion but there can hardly be doubt about the necessity for greater energy and enthusiasm than has been apparent in the last few decades. I hope that this will be one of the results of the present Conference.

References.

BAKER, J. G., 1883, On the Present State of our Knowledge of the Geography of British Plants, *Naturalist* for *1883*.

BENNETT, ARTHUR, 1905, Supplement to Topographical Botany, Ed. 2, *J. Bot., 43,* Suppl. (and issued separately, 1906).

BENNETT, A., SALMON, C. E., & MATTHEWS, J. R., 1929-30, Second Supplement to Watson's Topographical Botany, *J. Bot., 67, 68,* Suppl. (and issued separately, 1930).

BOTANICAL RECORD CLUB (otherwise the BOTANICAL LOCALITY RECORD CLUB), *Reports,* 1873-1886.

DRUCE, G. C., 1932, *The Comital Flora of the British Isles.* Arbroath.

GOOD, R. D'O., 1928, Notes on a Comparison of the Angiosperm Floras of Kent and the Pas de Calais, *J. Bot., 66,* 253-264.

——, 1936, On the Distribution of the Lizard Orchid (Himantoglossum hircinum Koch), *New Phyt., 35,* 142-170.

HOWARD, H. W., & LYON, A. G., 1950, The Identification and Distribution of the British Watercress Species, *Watsonia, 1,* 228-233.

HOWARD, H. W., & MANTON, I., 1946, Autopolyploid and Allopolyploid Watercress with the description of a new species, *Ann. Bot., N.S. 10,* 1-13.

HYDE, H. A., & WADE, A. E., 1934, *Welsh Flowering Plants.* Cardiff.

LOUSLEY, J. E., 1942, Flora of Devon (Review), *B.E.C. 1939-40 Rep.,* 385-390.

MOORE, D., & MORE, A. G., 1866, *Contributions towards a Cybele Hibernica.* London.

MORE, A. G., COLGAN, N., & SCULLY, R. W., 1898, *Contributions towards a Cybele Hibernica, Ed. 2.* Dublin.

OSTENFELD, C. H., 1931, The Distribution within Denmark of the Higher Plants . . . ., *Kgl. Danske Vidensk. Selsk. Skrift., Ser. 9, 3,* 1-15.

PRAEGER, R. L., 1901, *Irish Topographical Botany.* Dublin.

——, 1906, Supplement to I.T.B., 1901-1905, *Proc. Roy. Irish Acad., 26 B*, 13-45.

——, 1929, (Second) Supplement to I.T.B., 1906-1928, *Proc. Roy. Irish Acad., 39 B,* 57-78.

——, 1934a, Third Supplement to I.T.B., 1929-1934, *Proc. Roy. Irish Acad., 42 B,* 5, 55-86.

——, 1934b, *The Botanist in Ireland.* Dublin.

——, 1939, A Further Contribution to the Flora of Ireland, *Proc. Roy. Irish Acad., 45 B,* 10, 231-254.

——, 1946, Additions to the Knowledge of the Irish Flora, 1939-1945, *Proc. Roy. Irish Acad., 51 B,* 3, 27-51.

TURNER, D., & DILLWYN, L. W., 1805, *The Botanist's Guide . . . .* London.

WALTERS, S. M., 1949, Aphanes microcarpa (Boiss. & Reut.) Rothm. in Britain, *Watsonia, 1,* 163-169.

WATSON, H. C., 1832, *Outlines of the Geographical Distribution of British Plants.* Edinburgh.

——, 1835a, *Remarks on the Geographical Distribution of British Plants.* London.

——, 1835b, *The New Botanist's Guide . . . ., Vol. 1.* London.

——, 1837, *The New Botanist's Guide . . . ., Vol. 2.* London.

——, 1843, *The Geographical Distribution of British Plants, Vol. 1* (all published). London.

——, 1847-1859, *Cybele Britannica or British Plants and their Geographical Relations, Vol. 1* (1847), *Vol. 2* (1849), *Vol. 3* (1852), *Vol. 4* (1859). London.

——, 1860, *Supplement to the Cybele Britannica.* London.

——, 1870, *Compendium of the Cybele Britannica.* London. (Parts published privately in 1868, 1869 and 1870 and reissued.)

——, 1872, *Supplement to the Compendium of Cybele Britannica . . . .* Thames Ditton (published privately).

——, 1873, *Topographical Botany, Part 1.* Thames Ditton (privately printed).

——, 1874, *Topographical Botany, Part 2.* Thames Ditton (privately printed).

——, 1883, (Edited Baker, J. G., & Newbould, W. W.), *Topographical Botany, Ed. 2.* London.

WILMOTT, A. J., 1944, Vice-counties, *B.E.C. 1941-42 Rep.,* 524-526.

There was no discussion on this paper.

MAPS SHOWING PLANT DISTRIBUTION IN BRITAIN AND EUROPEAN COUNTRIES
(Exhibit)

J. E. Lousley.

This exhibit was arranged to illustrate the preceding paper by demonstrating maps, prepared to show distribution in the British Isles, which were misleading in various respects, and maps illustrating various schemes initiated in other European countries with commendable features.

(1) British Isles.

(a) *Scirpus triqueter* L. A map was exhibited on which the distribution had been marked strictly according to *Comital Flora* as published, and another for comparison marked with " dots " showing individual localities on a modification of the Danish scheme (see below). The first map was faulty in showing:—(a) A species restricted to estaurine mud as occurring over whole vice-counties. (b) A vice-county marked for which it has since been shown that the record was an error and two other vice-counties marked as doubtful for which the records are now discredited. (c) No distinction between extant stations and those where the plant is believed to be extinct. The second map was based on herbarium material but is subject to the criticism that the " dots " cover much larger areas than the species occupies. (See Figs. 7 and 8.)

(b) *Antennaria dioica* (L.) Gaertn. A map with the whole of each vice-county from which the plant is recorded blacked in. This failed to show the great contrast in frequency between southern vice-counties where the species is extremely rare and certain northern vice-counties where it is common.

(c) *Anemone Pulsatilla* L. A map showing whole vice-counties from which the species has been recorded was shown for comparison with one plotted with actual localities and indicating at which of these the plant was believed still to exist. The first map exaggerated the distribution and failed to indicate the association of the species with calcareous soils which was very evident on the second.

(d) *Various Base Maps.* Of particular interest was one prepared by Dr. Otto Stapf just prior to 1914 in connection with his work on the relationship of the British and European floras, of excellent design and well printed on good quality paper.

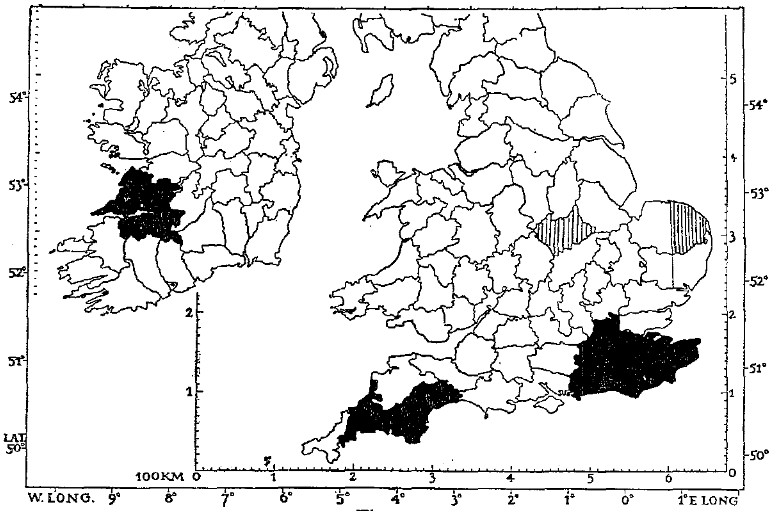


Fig. 7.

Scirpus triqueter L. Distribution plotted by vice-counties as printed in *Comital Flora*. The whole of the vice-counties for which it is there given as recorded with certainty are shown in black; those given there in square brackets as doubtful are hatched.

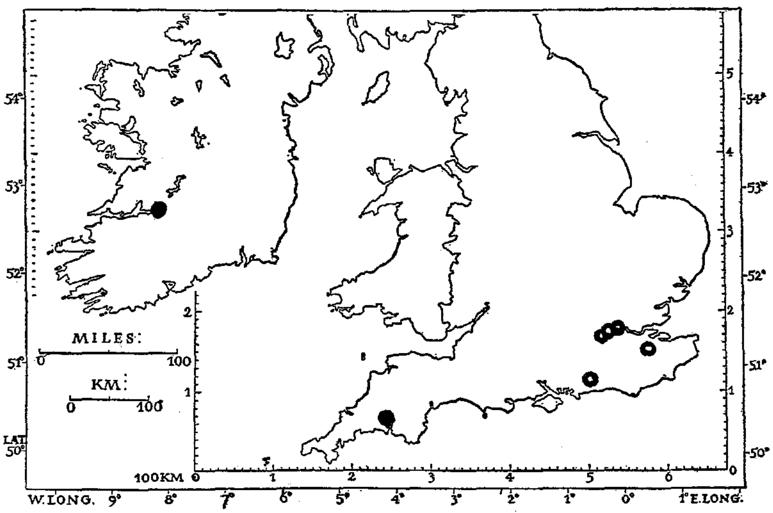


Fig. 8.

Scirpus triqueter L. Distribution plotted from localities checked against specimens and recent information. Full circles indicate places where the species still grows; rings where it is believed to be extinct. The principal inaccuracy of this method arises from the necessity of making the rings and circles extend over a greater area than the plant occupies in order to make them prominent in the reproduced map.

With acknowledgment to "The New Naturalist."

(2) Belgium and Holland.

In Belgium, maps showing the distribution of the higher plants are prepared by the Institut pour la floristique de la Belgique (I.F.B.) which was founded in 1942. The base map is covered by a grid with 16-kilometre squares (each called a *carré*) which are subdivided into 16 1-kilometre squares (each known as a *case*). There are 2072 carrés.

The method of investigation is to make a list as complete as circumstances permit of the species to be found in each kilometre square. A master map shows which of these have been examined. The map exhibited showed the distribution of *Himantoglossum hircinum* (L.) Spreng.

The Dutch system of the Instituut voor het Vegetatieonderzoek van Nederland (I.V.O.N.) is being described fully by Dr. Kloos, but examples of the maps as published in *Nederlandsch Kruidkundig Archief* were exhibited for comparison with the Belgian map. It was evident that the two-colour printing of the Dutch maps showed up much better than the monochrome of those of Belgium. The Dutch example, showing the distribution of *Galinsoga parviflora,* employs different markings for records before and after 1920. It is a matter for regret that in the later Belgian scheme it was not possible to adopt the 1 : 2,500,000 scale used for the Dutch maps.

(3) Denmark.

The maps exhibited were from one of the publications of the Danmarks Topografisk-Botaniske Undersøgelse of the Dansk Botanisk Forening. The detailed investigation of the distribution of the higher plants was initiated in 1904 and the country was divided into 53 Districts, of which those numbered 13, 22, 39 and (an added) 54 were later subdivided into two for convenience. The boundaries chosen were those regarded as "most accessible to the local investigators" and were mainly based on *Herreder* (administrative areas comprising several parishes). In this respect the scheme closely resembles our own Watsonian vice-county system.

The records are incorporated in a Card Catalogue and there is careful distinction between localities based on material in the collection of the Botanical Museum (Copenhagen), manuscript lists from the local investigators, and those based on published information.

Most of the maps published have been in accounts of taxonomic groups which have appeared in *Botanisk Tidsskrift* and the letterpress has included valuable details of the distribution of the plants. The following signs are used:—

Solid dot = a locality from which the plant is represented in the herbarium of the Botanical Museum of Copenhagen.

Circle with small dot in centre = a locality not represented in the herbarium but published in the literature or included in a manuscript list.

Circle = a locality from which the species is said to have disappeared.

Shading with continuous lines = indicates that the frequency of the species is characterised as " fairly common " or " common ".

Shading with broken lines = indicates that the frequency of the species in the particular area is characterised as " here and there ".

(4) GERMANY.

The exhibit illustrated the method of plotting at present in use in west Germany. The German maps equivalent to our Ordnance Survey are marked with a kilometre grid, each square having sides 2 cm. long. Further accuracy in marking is obtained by superimposing grids of 16 squares marked on transparent paper. The position of the locality within the appropriate square of the 16 on these smaller grids is recorded. Thus the localities are plotted with great accuracy.

The observations are transferred to a printed *Katalogblatt* of which one is prepared for each species for every map-sheet investigated. Each *Katalogblatt* has an outline grid corresponding to the kilometre grid of the maps, with the sub-divisions printed in thinner lines, and on this the occurrences are plotted as dots. On the second leaf of the *Katalogblatt* the observer is asked to give precise map references and habitat notes for each station, and general observations.

The sheets exhibited were provided by the Naturhistorischer Verein der Rheinlande und Westfalens which is carrying on the scheme initiated by Prof. Dr. Mattfeld and Dr. Fritz Mattick in 1922 for the whole of Germany. Unfortunately the great amount of work carried out before the War was lost when the relevant *Katalogblätter* were destroyed at Dahlem when the Botanical Museum there was burned out. Some idea of the immense size of the undertaking may be gathered from the facts that in 1936 about 850 botanists were assisting in the scheme and that 3,179,000 reports of the type exhibited would be required to cover all the 3179 species listed for Germany by Mansfeld. As a first target Mattfeld and Mattick aimed to cover about 600-800 species only but even so the undertaking is a remarkable example of German thoroughness and capacity for organisation.

(5) POLAND.

The maps exhibited were part of a world-wide scheme organised by Dr. Tad. Wisniewski for the Archives of Plant Cartography (Archiwum Kartografii Botanicznej). An important feature of the scheme was insistence on all maps being on scales which could easily be related to one another. Reproduction was inexpensive.

The signs used in marking maps were as follows:—

Solid dot = isolated and boundary localities.
Circle = uncertain localities.
Vertical cross = extinct localities.
Solid dot crowned with a " T " = Type specimen locality.

Continuous distribution was shown by vertical hatching. Boundary lines of distribution areas known with certainty were shown by continuous lines and boundaries approximately known by dotted lines.

REFERENCES.

BROCKHAUS, W., 1949, Die pflanzengeographische Kartierung Westdeutschlands, *Natur & Heimat, 9,* 12-15.

DE LANGHE, J. E., 1944, Sur la Dispersion Géographique du Loroglossum hircinum (L.) L. C. Rich. en Belgique, *Bull. Soc. Bot. Belg., 26,* 20-30.

GRØNTVED, J., 1939, Polygonaceernes Udbredelse i Danmark, *Bot. Tidsskr., 45,* 10 58.

STAPF, O., 1916, A Cartographic Study of the Southern Element of the British Flora, *Proc. Linn. Soc., 129,* 81-92.

VAN SOEST, J. L., 1941, De Verspreiding van Galinsoga in Nederland, *Ned. Kruidk. Arch., 51,* 288-301.

I should like to express my gratitude to Herr Wilhelm Brockhaus (Luedenscheid) and to the Secretary of the Dansk Botanisk Förening for assistance in connection with the preparation of this exhibit.

MAPS OF THE DISTRIBUTION OF VASCULAR PLANTS IN N.W. EUROPE
(Exhibit)

E. HULTEN.

The exhibit consisted of specimen maps and proof of the English summary of Professor Hultén's magnificent atlas of maps showing the distribution of vascular plants in North-West Europe which has since been published under the title *Atlas över Kärlväxterna i Norden* (Stockholm, 1950).

The work of collecting together the vast number of records of Scandinavian plants was commenced about 1935 and three years later the task of transferring these to base maps was started. Arrangements for publication were made in 1945 and since then the manuscript maps have been checked, revised and prepared for the printers.

Critical groups receive special treatment but apart from these there are separate maps for all wild and many naturalised species occurring within the area. The maps are reproduced on the scale of 1 : 20,000,000, four to the page. The topographical features are printed as a blue-grey base-map with the distribution overprinted with reddish dots for isolated localities and reddish hatching of two intensities to indicate areas where the plants are more frequent. The lines of the hatching are broken in districts where records are fewer than usual. In addition there are maps showing altitude, geology, meteorological statistics, phenological data, phytogeographical groups, etc.

MAPPING THE DISTRIBUTION OF SPECIES

WILLIAM T. STEARN.

The object of these notes is not to summarize the results of research into the distribution of plants but to discuss briefly the means by which these results can be expressed visually. Ascertaining and mapping the ranges of species and infraspecific taxa are essential procedures in modern phytography. The distribution of a genus (Fig. 9) being the sum of the areas occupied by its constituent species, a knowledge of these thus forms the basis of any discussion of the wider problems of plant geography. The area occupied by an organism and its abundance within that area indicate how successfully it has met the challenge of its environment. Its past history, its inherited potentialities, the opportunities for colonization presented by changes in the environment, the impact of adverse factors, all these affect the range of an organism and any investigation of them necessarily involves an investigation of its range as well. This needs no further discussion here. For working purposes species and subspecies must be

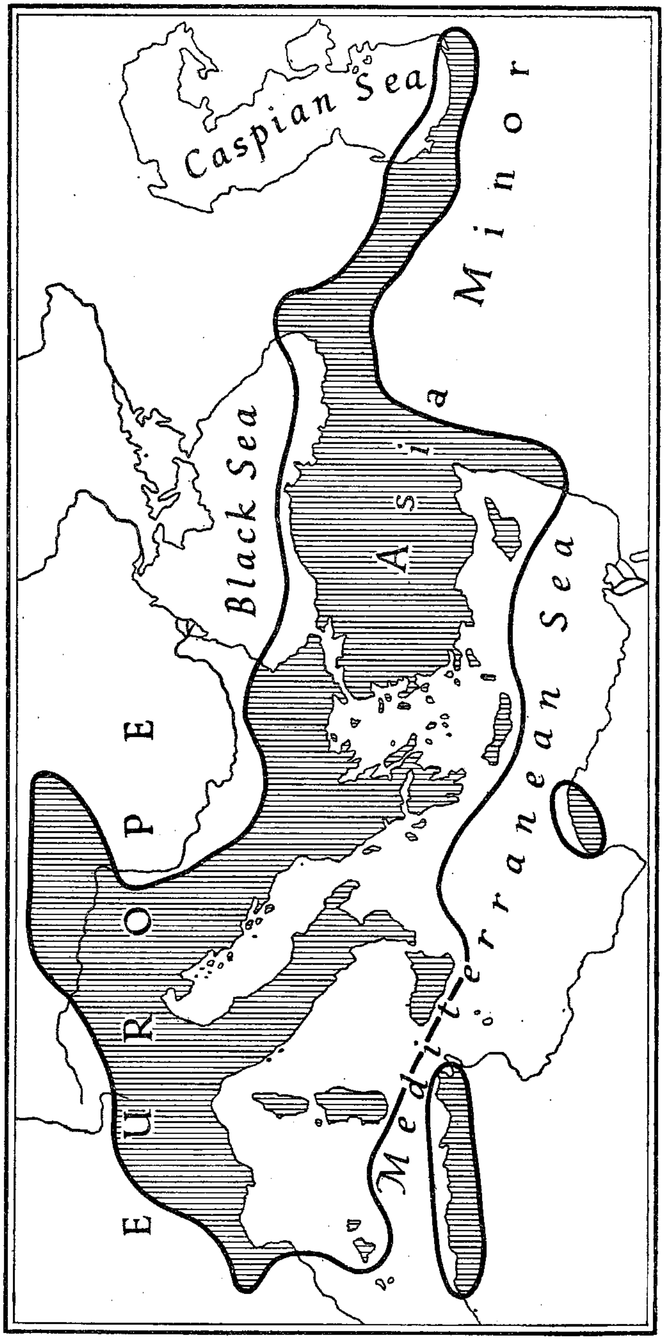


Fig. 9. Distribution of the genus *Cyclamen*. Map with hatching over combined areas of species (based on maps by O. Schwarz in *Gartenflora*, N.F., 1938).

defined by their morphological characteristics, i.e. the differences between populations which the taxonomist finds easiest to observe and describe, but the genetical differences they express are usually also reflected in differences of distribution. In other words, although the differences, which best suit the convenience of taxonomists drawing up keys and descriptions are not necessarily those which matter most to the organisms as living creatures and hence regulate their distribution, all seem to be so intimately linked that they postulate one another. Much taxonomic procedure rests upon the probability of such correlation. Thus a systematic botanist often begins his study of a difficult group by sorting the available herbarium material on a geographical basis and noting how closely the incidence of certain morphological characters is associated with this. The pattern becomes clearer if he charts the provenance of his specimens. The work completed, he can make the results more easily available through the use of maps showing the general or detailed distribution of the members of the group. Such maps form an essential part of a good modern monograph.

A map is, of course, an attempt to do what cannot be done precisely, as it aims to express three dimensions in two and to give information simply about what is really complex and large. It succeeds in being useful only because its conventions and limitations are generally understood and accepted. Much can be learned quickly from a sketch-map illustrating plant-distribution, provided that it has been based on reliable data and has been drawn with care, but too much should not be expected of it.

In dealing with the flora of so self-contained an area as the British Isles, it should be constantly remembered that the British distribution of a plant often constitutes only a small part of the total range (cf. Figs. 10, 11 and 13); to a monographer, its interest often lies primarily in its relation to the total range. The following notes give a few suggestions arising out of monographic work on genera such as *Epimedium, Vancouveria, Paeonia, Tofieldia* and *Narthecium,* of which few or no species grow wild in Britain. The author is accordingly unable to deal from personal experience with the range-mapping of more than a few British plants. Moreover, some of the best as well as the worst examples of botanical cartography occur in publications only slightly if at all concerned with the British flora. They are mentioned here because the best techniques can be usefully applied to the flora of any area.

The distribution of an organism, like its morphological features, can be expressed verbally and pictorially in a variety of ways. All depends on how much is known and how much needs to be put on paper. Thus gardeners are as a rule content with the information that a plant grows wild somewhere in China but, if it inhabits a more accessible region, e.g. the Alps, they often desire more precise localities. One botanist may be interested primarily in the distribution of a species as compared with that of related species. Another may wish to know the distribution of certain characters over an area. For others, the interest of the distribution of a plant may lie in its being, say, the host of certain pests or diseases or in its relation to climatic and other environal factors; plants with a limited tolerance may serve as indicators of special conditions. Obviously such diverse needs call for different degrees of precision in mapping; the extent to which they can be satisfied depends largely upon the herbarium material available.

The tendency, as in all science, is, of course, towards greater precision and more and more detail. Thus Linnaeus (1707-78) in his *Species Plantarum* of 1753 described the distribution of *Epimedium alpinum* in two lines, recording it from three localities, of which one has proved erroneous! However, for his time that was good enough. Augustin Pyramus de Candolle (1778-1841) in his *Regni vegetabilis Systema naturale* of 1821 took nine lines to enumerate localities for the same species. In the present author's monograph of *Epimedium* published in 1938 (*J. Linn. Soc. London, Bot., 51,* 409-535) the account of the distribution of *E. alpinum,* as ascertained from the study of material in forty-two herbaria, supplementary data obtained from seven other herbaria and statements in the literature, occupies 145 lines. In such an account the distribution has to be treated analytically, the range being broken into parts and the localities listed under convenient geographical headings, just as a description, though concerned with the plant as a whole, has nevertheless to deal with it analytically organ by organ. However good the description, the characters of the plant can be grasped more easily and swiftly if they are portrayed in a good illustration. Distributional maps bear the same relation to lists of localities; whenever possible both should be provided, as in the monograph mentioned. The lists show the evidence on which the maps are based. If a choice has to be made, good maps are preferable, as observed by E. N. Munns (The Distribution of important Forest Trees of the United States, *U.S. Dept. Agr. Misc. Publ. 287*: 1938), "because of the greater accuracy, simplicity and detail possible in this form of presentation. Even the most detailed published descriptions of species distribution are found to be too broadly generalized when an attempt is made to plot the ranges on maps."

Alphonse de Candolle (1806-1893) seems to have been the first to use maps to illustrate the distribution of plants. The two maps in his *Géographie botanique* (1855) are marked with the northern limits in Europe of a number of unrelated species. The emphasis of this work being climatological rather than taxonomic, it does not attempt to use maps as a tool for the study of related species; indeed the extensive herbarium collections necessary as a base for good maps of the ranges of species did not then exist. Another pioneer contribution to botanical cartography was made a few years later by the Austrian botanist and geologist, Dionys

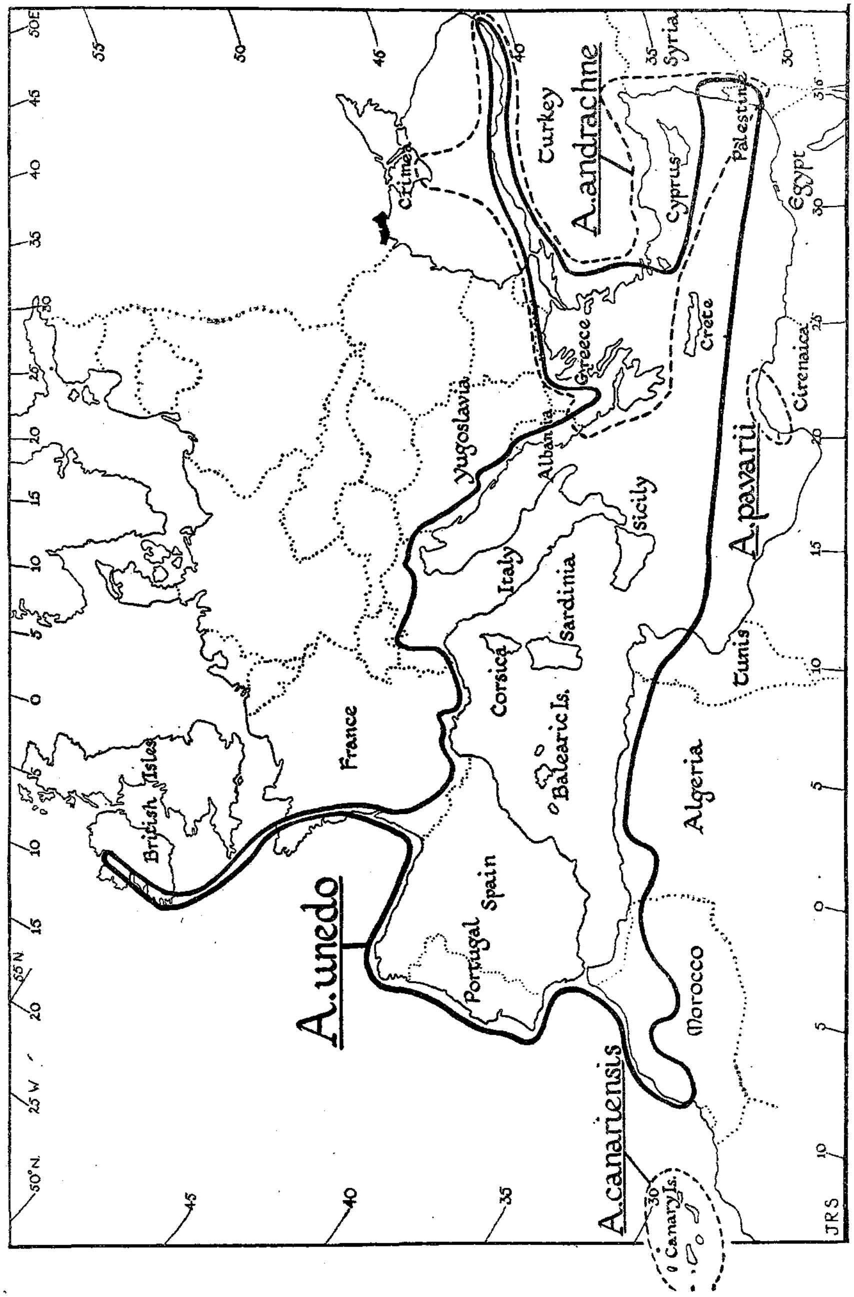


Fig. 10. Distribution of Old World species of the genus *Arbutus*. Map with boundaries of species areas outlined. (By courtesy of J. R. Sealy, from *J. Ecol.*, *37*: 379; 1949.)

Rudolf Josef Stur (1827-1893), in his "Beiträge zu einer Monographie der Gattung Astrantia" (*Sitzungsb. Math.-Nat. Akad. Wiss. Wien, 40,* 469-524; 1860); here coloured areas on a map represent the areas of related species. Stur's method of coloured shading—an elaboration of A. de Candolle's simple outlining of the boundaries—was adopted by another Austrian, Anton Kerner von Marilaun (1831-1898), later the author of the perennially interesting *Pflanzenleben* (1887-91) or *Natural History of Plants* (1894). Kerner was an outstanding many-sided biologist keenly interested in the inter-relations of plants with their environment. He was also a critical taxonomist who attempted to define microspecies geographically as well as morphologically. It is thus significant that he illustrated with maps his paper of 1869 (*Festschr. zur 43. Versamml. Deutsch. Naturf. und Aerzte zu Innsbruck,* 1-48) on the correlation of plant-form, climate and soil and that he took as a basis the geographical distribution, etc., of *Cytisus* sec. *Tubocytisus.* The maps themselves are drab, the areas being coloured dull yellow and green, but serve their purpose. Kerner's star-pupil and son-in-law, Richard Wettstein von Westersheim (1863-1931), followed him as professor of botany at the University of Vienna and developed his ideas further by taking up the study of critical genera like *Euphrasia, Gentianella* (*Gentiana* sect. *Endotricha*), etc. Wettstein promoted the geographical-morphological method, which is now so thoroughly part of modern taxonomy as to be taken for granted, and he likewise illustrated his works with maps employing either coloured outlines as in his *Monographie der Gattung Euphrasia* (1896) or coloured specific areas as in his "Die europäischen Arten der Gattung Gentiana aus der section Endotricha Froel." in *Denkschr. Math.-Nat. Akad. Wiss. Wien 64*: 309-382 (1896) and his *Grundzüge der geographisch-morphologischen Methode der Pflanzensystematik* (1898). Maps of the latter kind illustrate other Austrian monographic works, e.g. A. Jakowatz's "Die Arten der Gattung Gentiana sect. Thylacites" in *Sitzungsb. Math.-Nat. Akad. Wiss. Wien, 108,* 305-356 (1899), J. von Sterneck's "Monographie der Gattung Alectorolophus" in *Abh. Zool.-Bot. Ges. Wien, 1* H. 1 (1901) and A. von Hayek's "Monographische Studien über die Gattung Saxifraga: Die Sektion Porphyrion" in *Denkschr. Math.-Nat. Akad. Wiss. Wien, 77,* 611-709 (1905). Such maps are pleasing and clear provided they represent few species and the ranges of these overlap but little. When numerous species with overlapping ranges are involved, then coloured boundaries will be found more satisfactory; as in F. von Schwerin's "Monographie der Gattung Sambucus" in *Mitt. Deutschen Dendrol. Ges., 18,* 1-56 (1909) when red, blue and green lines are used. The high cost of colour printing restricts the use of such methods of overprinting in colour; if maps are to illustrate every revision of a genus, cheaper methods must be used.

Plain black and white maps have the great advantage that they can be printed as text-figures and their cost is little higher than that of the equivalent space of text. They can represent distribution in five ways:—(1) by outlining the area, a boundary line running through or around the outermost points; (2) by shading, hatching or blacking in the area; (3) by dots indicating the stations; (4) by a combination of hatching and dots; (5) by a combination of boundary lines and dots. Each method has its advantages; choice depends on the information available and the aspect to be emphasized. All have been used to express the distribution of plants in Britain.

Hitherto the shading, etc., of vice-counties has found most favour with British botanists, because so much of the results of floristic work in Britain for the past hundred years has been recorded under these and by means of them can be easily utilized. Mapping by vice-counties provides a quick and convenient method for getting an impression of the general distribution of a species within the British Isles. You look up the species in G. C. Druce's *Comital Flora of the British Isles* (1932) and shade every vice-county listed; those from which the species is not recorded are left blank. The chief objection to this rather crude method is that it exaggerates the area. Thus a species which just manages to cross the vice-county border or which occupies a limited area and has a specialized habitat is represented as if it grew all over the whole vice-county. Most British counties and vice-counties display considerable diversity in geology and topography and it is probably true that in almost every one, as R. Good has observed after mapping the distribution of plants within the county of Dorset (vice-county 9), no species "is completely and evenly distributed. Even the commonest plants are absent from some small areas and are of more or less than usual frequency in many others, while at the other end of the scale there are certain rare species known only from a single spot and in very small quantity." This geographical segregation is well illustrated by the dot maps in Good's *Geographical Handbook of the Dorset Flora* (1948). Under the vice-county system all have to be treated as if they extended evenly over the whole vice-county. Another objection is that some vice-county records accepted by Druce are erroneous. An improvement of this method is to black in the vice-counties where the species is common and hatch variously the vice-counties where it is less frequent. Even so the distribution of uncommon species may be grossly misrepresented. Many examples of the mapping of distribution by vice-counties are to be found in the "Biological Flora of the British Isles" now being published in *J. Ecology,* and in E. J. Salisbury's "The East Anglian Flora" (*Trans. Norfolk & Norwich Nat. Soc., 13,* 191-263; 1932). Mapping by the blacking in or marking of grid squares can be considered a variant of the vice-county method and has been used by a number of Continental botanists dealing with local distribution. Its degree of precision depends, of course, on the size of the areas represented by the grid squares on the map.

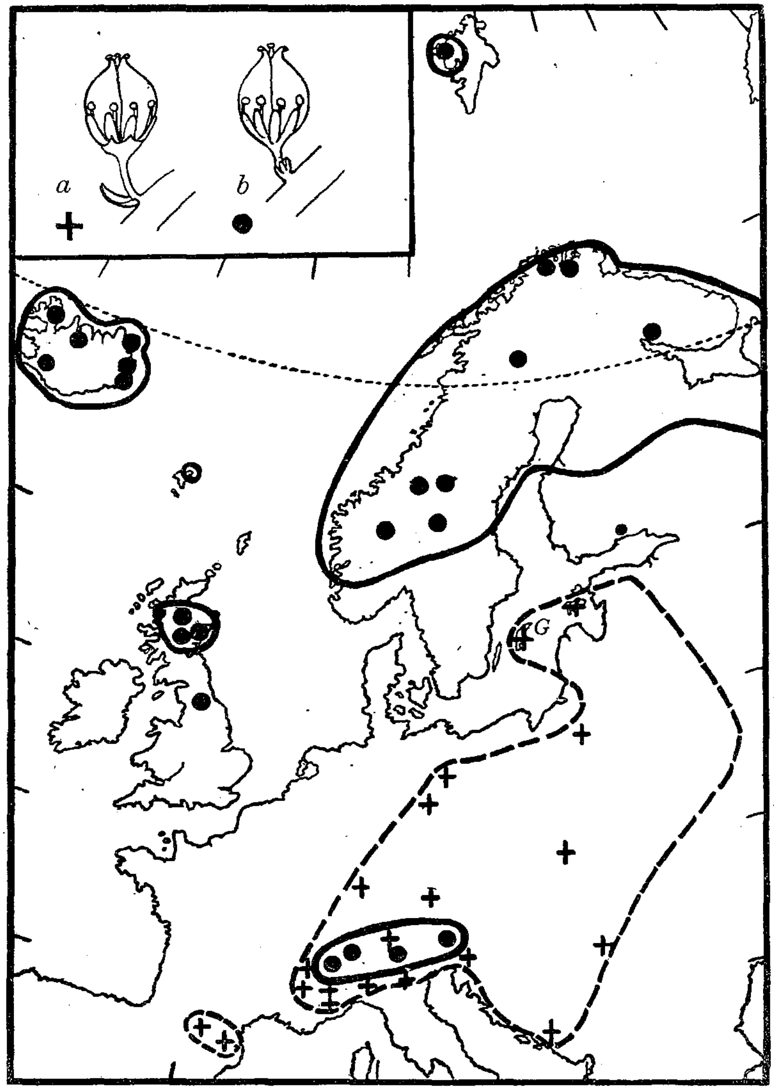


Fig. 11. European distribution of *Tofieldia pusilla* (—— general boundary; ● localities represented in British herbaria). General distribution of *Tofieldia calyculata* (— — general boundary; + localities represented in British herbaria). Map combining outlines and dots (from *J. Linnean Soc. Bot.*, *53*: 196; 1947).

The dot method goes to the other extreme. In this method each station or group of adjacent stations, according to the scale of the map, is indicated by a dot, cross or other distinctive mark. As the author, unless dealing very thoroughly with a very small area, cannot know every station, such a map is necessarily incomplete and likely to under-state the distribution. The appeal of a dot map lies in its honesty. It makes clear how much the author knows; it may also indicate how much remains to be learned. When the species is fairly common over a well-investigated region the dots will tend to touch and coalesce and the result will then be a more or less solid black area marking out the range. Maps of this type will be found in many publications, notably in E. N. Munns' "Distribution of important Forest Trees of the United States" (1938) which summarizes the results of over thirty years' intensive work by the United States Forest service. The information available about such economically important, easily observed and identified plants as forest trees is naturally very detailed and is reflected in maps like those of *Salix nigra* where the thick black sinuous lines recording the occurrence of this species chart the main river system of the eastern United States. After looking at such a map one is not surprised to learn that the species inhabits "banks of streams, shores and rich low woods". The distribution of many other species is indicated by a simple unrelieved large black area, implying a more even occurrence. If more than one species had to be represented as growing in the same region, obviously this method could not be used, but boundary lines would serve the same purpose.

For a species with limited occurrences the dot method of mapping (Fig. 11) is the best; for species which occur abundantly and fairly evenly over an area, hatching may be preferable. A species may be common in some areas, rare in others, e.g. *Narthecium ossifragum,* which is widespread and abundant over some areas in the Highlands of Scotland but rare in East Anglia. For such plants a combination of the two methods, with hatching over the areas of abundance but dots elsewhere, would seem the best procedure. It has been effectively employed in K. Jessen's "Distribution of the Liliales within Denmark" in *Bot. Tidsskr., 43,* 71-113 (1935) and E. Hultén's *Atlas of the Distribution of Vascular Plants in N.W. Europe* (1950). Good dot maps are to be found in numerous monographs and revisions. E. Anderson and R. E. Woodson's "The Species of Tradescantia indigenous to the United States" (*Contrib. Arnold Arb. 9*; 1935), M. L. Fernald's "The Linear-leaved North American Species of Potamogeton, Section Axillares" in *Mem. Amer. Acad. Arts. & Sci., 17,* pt. I (1932), R. Nordhagen's "Om Arenaria humifusa" in *Bergens Mus. Arbok Naturvid. 1935,* Nr. 1 (1935), E. Hultén's "Flora of Kamtchatka" in *Kungl. Svensk. Vet. Akad. Handl. III. 7, 8* (1927-30), the memoirs in *Acta Phytogeographica Suecica* such as R. Sterner's "Flora der Insel Oeland" (*op. cit. 9*;

1938), G. Samuelsson's "Die Verbreitung der Alchemilla-Arten aus der vulgaris-Gruppe in Nordeuropa" (*op. cit. 16,* 1943) and S. Ahlner's "Utbredningstyper bland nordiska Barrträdslavar" (*op. cit. 22,* 1948) are but a few of the many excellent American and Scandinavian works employing dot maps. Various refinements can be introduced into such maps, e.g. a special mark or letter to indicate the type-locality; when dealing with distribution over a small area places where the species once occurred but is now extinct can be marked differently, e.g. by rings or crosses. In maps intended to illustrate differences of range between cytologically distinct plants, large dots may be used to mark the localities from which the plants have been cytologically examined and the smaller dots the localities for plants presumed on morphological grounds to be the same; see for example Baldwin and Speese's map illustrating the cytogeography of *Saururus cernuus* (*Bull. Torrey Bot. Club 76,* 213-216, 1949).

In many monographs the range is indicated by boundary lines; these lines enclose the area in which the species occurs. This method (Fig. 10) is especially useful when the overlapping ranges of several or many species have to be represented on the same map and when the region is a very large one and the scale consequently small. The range of one species may be distinguished from that of another by the employment of different kinds of boundary lines; a thick unbroken line can serve for one, a broken line for another, and so on, according to the number of species and the ingenuity of the author. A few examples are:

— • — • — • — • — • —

└┘ └┘ └┘ └┘ └┘ └┘ └┘ └┘ └┘ └┘

ooooooooooooooooooooo

+ + + + + + + + + +

• • • • • • • • • • • • • • • • • • •

o—o—o—o—o—o—o—

In the text of a monograph all species should be numbered and infraspecific taxa given letters α, β, γ, δ, etc., A, B, C, D, etc. The same numbers and letters should be placed against the boundary lines of the species, etc. This system, which is employed in the present writer's monograph of *Epimedium,* is a convenience to the reader who can turn straight from the description to the map itself without having first to study an elaborate explanatory caption. If these numbers are used, such diversely fashioned boundary lines as those indicated above may prove unnecessary. Even better, when space permits, is the addition of the names of the species (Fig. 10). Good examples of the use of the boundary method are to be found in the German periodical *Pflanzenareale* (1926 et seq.), which is devoted entirely to maps of the general ranges of plants. The base maps are blue, with the plant boundaries printed black. The disadvantage of this method is that it gives no information about the occurrence of the species within the area enclosed. It tells the systematist what species are to be expected among the material from a certain area but it does not tell him from which localities they are known; it gives no indication as to whether a species is evenly spread over the area or occurs only at isolated localities. Moreover, the drawing of the boundary line itself is essentially subjective. A great variety of patterns can be made by drawing a line through or round the outermost of a number of scattered dots representing the localities from which a species is known (Fig. 12). The smoother the curves and the more regular the outlines become, the more they please the eye by simplifying the map; unfortunately so much the more do they depart from the facts. A consideration of the topography may help to indicate how the boundary should be drawn. Thus if a montane or alpine species

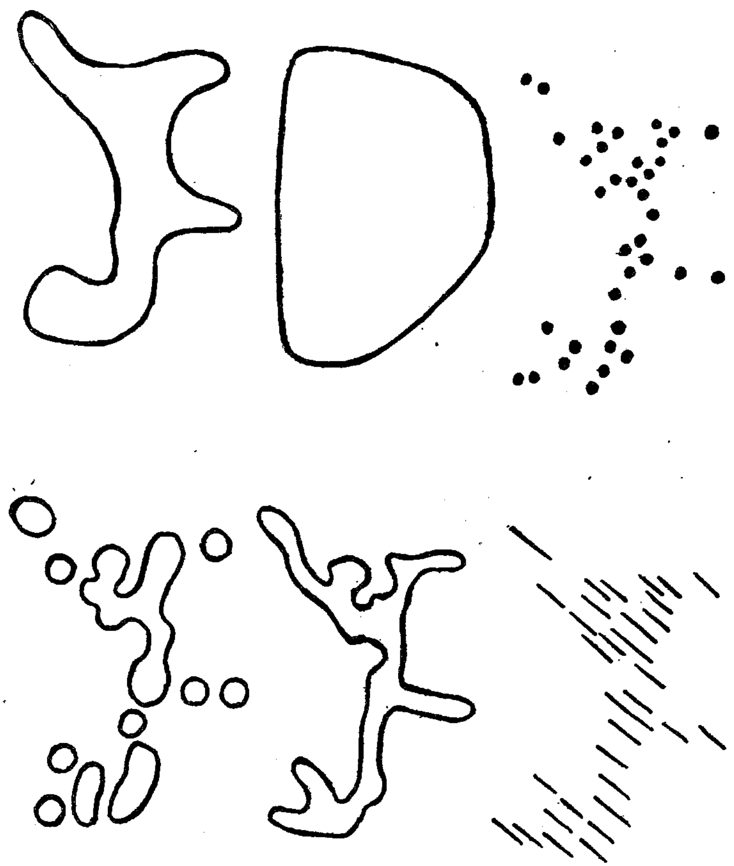


Fig. 12. Distribution of a species of lichen expressed by dots, hatching and outlines. all based on the same data.

occupies a series of mountains separated by wide lowland regions in which it does not occur, the boundary connecting the dots might well follow the general outline of the mountainous areas instead of cutting across the lowlands.

Some maps compiled by the author of this paper and published in *J. Linn. Soc. London, Bot., 51,* 430, 433 (1938; *53,* 196 (1947) and in F. C. Stern's *Study of the Genus Paeonia* 18, 20, 22, 30 (1946) combine dots and boundary lines, the localities known to the author through herbarium material being marked by dots, crosses and small circles while a line outside these gives the general range as indicated by apparently trustworthy literature (Fig. 13). This method has many advantages. Scattered dots and crosses, especially if many occur on the same map, tend to distract the attention; an enclosing line focuses attention on the range as the whole.

Boundary lines are probably of more scientific use for the study of generic than of specific distribution. This subject lies outside the field of the present paper, since no genus of flowering plants is endemic to the British Isles, but it may be of interest to call attention to a method devised by W. Rothmaler and used in his papers on *Alchemilla* sect. *Calycanthum* (Fedde, *Repert., Beih. 100,* 89-91, 1938) and *Ulex* (Engler, *Bot. Jahrb. 72,* 78, 1941). It provides monographers with a means of comparing the morphological diversity of a genus in different parts of its area. A grid is superimposed upon a map of the generic area, thus dividing it into a large number of squares, on each of which the number of species of the genus occurring within the square is marked. It thus calls for very detailed and precise information as a working basis. Lines are then drawn to connect the squares with the same number of species. They thus form boundary lines, called by Rothmaler isopores (*Isoporien*) and analogous with isotherms, enclosing areas with the same number of species: within a wide area with few species will probably lie smaller and smaller areas with more and more species. The map will then emphasize the areas where the greatest number of species occur. In one the species may be numerous but closely allied, manifesting many combinations of a few characters; such an area is probably one where conditions in the past favoured a few variable populations which mingled and then broke up into smaller units. In another the species may be morphologically very distinct, probably representing very old types for which the area has been a refuge. To distinguish the two kinds of areas Rothmaler's method evaluates the degree of morphological diversity by drawing boundary lines termed isopsepheres (*Isopsepheren*) enclosing areas wherein the species exhibit the same number of diagnostic characters though not necessarily the same characters. This too calls for very detailed and precise information. The method is thus one which only a monographer can apply. Investigation of the genus as a whole may show that, say, twenty characters can be utilized for the distinction of species. If only one species occurs in the area, 20 can be taken as the number of morphological characters represented in that area. If two species agreeing in fifteen of these but differing in five occur within the area, then the number will be 25. The same grid as mentioned above is then superimposed upon the map of the generic area, thus dividing this into squares, on each of which the number of characters represented within the square is recorded. Lines are then drawn to connect the squares having the same number. Within the area enclosed by a low-number isopsephere will probably lie areas of greater and greater morphological diversity with higher and higher numbers. The map will thus emphasize the areas where the most diverse species occur and may enable distinctions to be drawn between areas of refuge (characterized by high numbers) with very heterogeneous relict species and primary and secondary centres of specific differentiation (with lesser numbers). Such a method cannot be fruitfully applied to all genera; indeed to a genus like *Narthecium* with no overlapping species it cannot be applied at all while in some genera it would merely confirm what was already obvious. Critical genera like *Euphrasia* and *Thymus* and probably *Crepis* might yield information of considerable phytogeographical interest tackled from this aspect.

Constructing a map of distribution, whatever the aim and method, is rarely a simple task. Apparently the first thing to ascertain is where the species occurs, but this necessitates being quite clear as to its morphological limits and may call for monographic study of the whole group of species. First-hand information derived from the correct identification of the specimens in as many herbaria as possible is thus of prime importance; without such a backing the value of literature records cannot be assessed; indeed, unless the species lacks any close ally within the area, with which it might be confused, unsupported records are best ignored when making maps of distribution. The basic procedure is first to sort all the specimens available into morphologically defined groups and then to sort the specimens of each morphological group into geographical groups, i.e. by countries, provinces, counties and vice-counties. The specimens should next be listed under these geographical headings and each record numbered. Each locality represented can now be marked in pencil on a suitable base-map by a dot and the reference numbers of the specimens. If later investigation reveals that some material has been misidentified, these reference numbers will enable the erroneous records to be quickly found on the map. Care should, of course, be taken to place the dots correctly. A map inaccurately drawn or based on inaccurate records and misidentifications may easily become a source of long-standing error and confusion, in addition to being the target for such criticism and advice as M. L. Fernald gave in *Science, 68,* 145-149 (1928) to the editors of *Pflanzenareale,* namely, " they must make sure that the distinguished authors of the maps have at least an elementary knowledge of geography and, passing this test, that they take a real interest in presenting the facts without distortion"! It is surprising how many different places possess the same name; moreover the data and handwriting on herbarium labels are not always as clear and precise as they should be. If only collectors stated on their labels the latitude and longitude of the places named or gave their distance and direction from a well-known place, how much time-consuming and tedious poring over maps they would save the conscientious student of their material! The

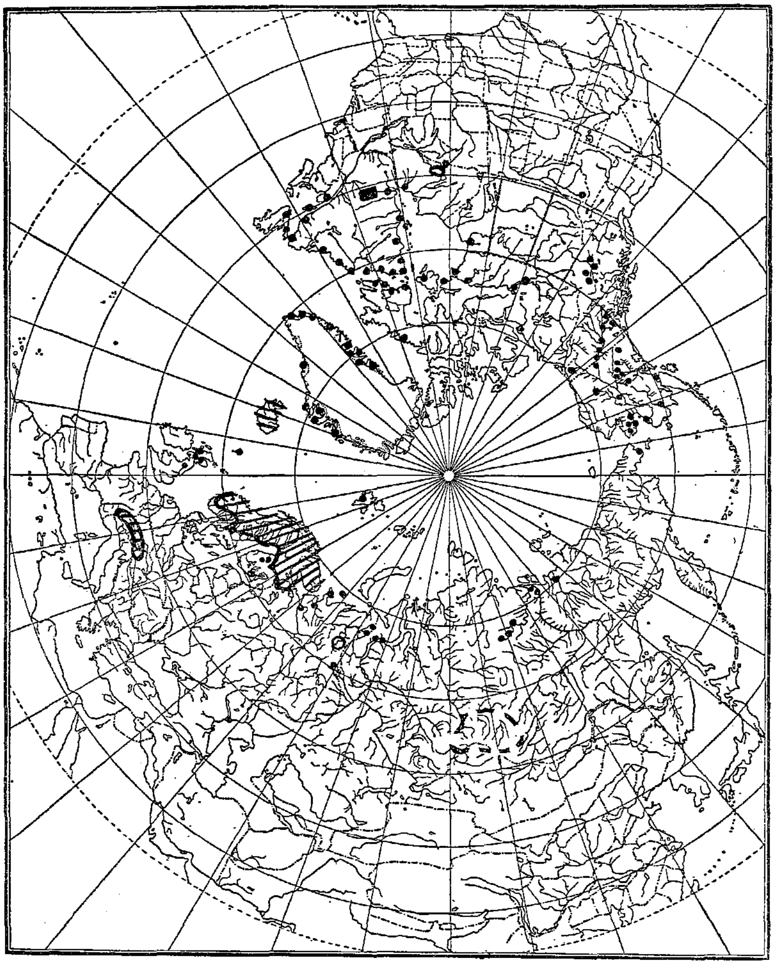


Fig. 13. Distribution of *Tofieldia pusilla.* Circumpolar map with dots for localities; ▬ type-region: //// area of abundance; — — unverified (from *J. Linnean Soc. Bot., 53*: 195; 1947).

monographer of a genus almost invariably comes across specimens which he can identify but nevertheless cannot chart on his maps because their provenance is ambiguously or vaguely stated. If the specimens are dated it may be possible to localize them by reference to the collector's diary or an account of his travels. Thus for collections made in China last century, E. Bretschneider's *History of European botanical Discoveries in China* (1898) provides invaluable help. The enterprise of A. and D. Löve in distributing their specimens of Icelandic plants with labels having the provenance of the specimen clearly marked on an outline map is much to be commended.

The choice of a suitable base map raises problems. It should be simple enough not to obscure the botanical information but at the same time adequate to give this precision. The courses of rivers and lines of latitude and longitude supply the best indicators of position. As a rule the outline maps published by commercial map-makers for school exercises are not good enough for botanical purposes. In the United States, the University of Chicago publishes Goode's copyrighted outline maps which are used by many American botanists, and excellent base maps of Scandinavia and the Northern Hemisphere, centred on the North Pole (Fig. 13), have been printed for the use of Scandinavian botanists. Unfortunately comparable British maps seem not to be available at the present time. The author of a paper is thus driven to tracing the outline from a suitable atlas map of the right scale, which is not always easy to find, or to employing a professional cartographer. The first procedure is tedious and the second may be costly. Avoid maps on cylindrical projections (e.g. Mercator's and Gall's) when charting the ranges of northern plants especially if they are circumpolar; for these plants a circular map centred on the North Pole (cf. Fig. 13) is the best. Cylindrical projections may, however, be convenient when dealing with more southern plants of a wide Mediterranean or Eurasian distribution; the map of the Old World range of *Paeonia* in F. C. Stern's *Study of the Genus Paeonia,* 32 (1946) provides an example. Most maps of specific distribution cover too small an area for the projection to matter much. Murdoch's Third Conical Projection, enthusiastically sponsored by A. R. Hinks, is used in that masterpiece of beautiful cartography, *British Council Map No. 1, Europe and the Middle East* (Royal Geographical Society, 1941). As regards the British flora the Botanical Society of the British Isles might well give support to the publication of a set of outline maps of the British Isles for the use of botanists and zoologists. The coast-line should be boldly shown, with the vice-counties and chief rivers lightly indicated on one set and contours of, say, 500 ft., 1000 ft. and 1500 ft. on another set. In this way there could be two maps of the British Isles as a whole on, say, the same scale as the map (which measures roughly 20 in. by 11 in.) in Druce's *Comital Flora,* two maps of Ireland, two of Britain south of, say, Edinburgh, two of Britain north of, say, Middlesbrough, making eight base-maps in all. It would also be useful to have a smaller outline map of the British Isles, say 6 in. by 9 in., with only the vice-counties shown.

If no cheap and suitable base maps are available, it is economical to work first with squared paper, the lines being taken to represent meridians and parallels and the coast-lines and political or administrative boundaries being temporarily ignored. Make a chart for each species, giving a reference number to each dot corresponding to a locality mentioned on a herbarium specimen or in trustworthy literature. Comparison of the charts will then make it simpler to decide upon the best method of presentation. Thus, if the species are found nowhere to overlap in range, an outline around the outermost stations of each species may tell all that is necessary. If, however, their ranges overlap and especially if they hybridize, these simple outlines will probably not suffice and a system of dots, stars, crosses, triangles, small squares and circles may more effectively portray the facts. The grids of the squared paper will help to ensure accuracy when transferring the data to the final map intended for printing. Avoid trying to put too much on one map. Such a confusing tangle of overlapping and imperfectly differentiated lines as occurs on the maps in R. Schulz's *Monographische Bearbeitung der Gattung Phyteuma* (1904) and B. Stefanoff's "Monografiya na Roda Colchicum" in *Sbornik na B'lg. Akad. Nauk* (Sofiya), *22* (1926) detracts greatly from the value of the work. R. E. Woodson's monograph of *Apocynum in Ann. Missouri Bot. Gdn. 17,* 17-136 (1930) ingeniously succeeds in charting the ranges of 22 species and varieties on one small-scale map by employing a great variety of bold outlines, but they could have been more clearly and pleasingly represented on several maps.

To ensure maximum accuracy, maps intended for reproduction should be drawn larger than they will be when published. Indian ink should be used. To counteract the effect of reduction the dots and boundary lines should be drawn boldly. Imperfectly aware of this I once drew a large map of the distribution of *Epimedium alpinum* but made the dots too small; reduced to about a twentieth of their original size they appear like pin-pricks in *J. Linn. Soc. London, Bot., 51,* 474 (1938). A reducing lens will be found a help in avoiding such an error of judgment. The lay-out of the map deserves consideration. Thus if the latitude and longitude is given, the map will look best if one meridian runs vertically through the centre; the parallels and the meridians east and west of the one chosen will then balance symmetrically. After the outlines or dots, etc., have been inserted, a few place-names may be added. Small capitals can be used for the whole of the names of seas, countries, states and provinces, upper and lower case letters for the names of towns, mountains, lakes and rivers. Italic lettering pleasantly distinguishes water (seas, lakes and rivers) from land features. Good penmanship adds much to the general appearance of a map but not all of us possess the gift or the time to cultivate it. If need be, an obliging printer will set up the names required and print them off; they can then be pasted on to the map before the block is made.

Botanical cartography, like botanical illustration, must necessarily be educational and scientific, aiming as it does at the accurate presentation of verifiable data about natural phenomena, but it can also be artistic and give pleasure to the eye as well as material for thought. The *Journal of the Royal Geographical Society* abounds in beautiful black and white maps, some very simple, some very elaborate, but all of them pleasingly arranged and lettered; they thus provide models which botanists would do well to study.

[The above paper on the principles and methods of botanical cartography was illustrated by a series of maps taken from the publications mentioned and shown by means of an epidiascope. Fig. 10 is reproduced by courtesy of Mr. J. R. Sealy and the Cambridge University Press. Figs. 11 and 13 by courtesy of the Linnean Society of London.]

THE STUDY OF PLANT DISTRIBUTION IN HOLLAND

A. W. Kloos.

(Readers who heard this paper read by Dr. Kloos will remember with pleasure the charm with which it was enunciated in a language which is not his own. It is with great reluctance that I have amended the wording to make the meaning as clear in the printed form as it was at the Conference.—Editor.)

I hope to succeed in giving you an idea of the work of I.V.O.N. These initials are an abbreviation for *Instituut voor het Vegetatie-Onderzoek in Nederland*—the Institute for the Investigation of the Vegetation of Holland. I hope to show you how the work of I.V.O.N. leads to the production of maps illustrating the distribution of Dutch plants.

The method, which we owe to J. W. C. Goethart and W. J. Jongmans, is based on the Military Geographical Map on the scale 1:50,000. This is published in 58 sheets, all of the same size, covering an area of 40 × 25 kilometres. These sheets are the largest units of our system and each folds into 16 rectangles which in turn are divided into 3 "squares". These 48 "squares", each covering 5,000 × 4,133 metres are known as *uurhok*—"hour-squares", so called because their sides represent approximately the distance which can be comfortably walked in an hour.

Each "hour-square" is in turn divided into four "half-an-hour squares" and each of them once more into four *kwartier hokjes*—

"quarter-squares", which are the principal units and measure 1250 × 1044 metres. Whenever more detailed studies are required of a small area the divisions can be repeated and the "quarter-squares" can be subdivided into 4 or 16 smaller squares numbered in the same way:—

1	2
3	4

The basic fieldwork consists of making an inventory of the species observed in a quarter-square. For this purpose Goethart

Exc.
Quendon
(Essex)
19.

Hokje: ....,..........,..........

door: Exc. Brit. Bot. Soc.

datums April 2nd 1950

Acer,*ca*. Ach,*m*,*p*. Acon,*L*,*N*. Acor. Act. Adon,*a*,*v*. Adox. Aeg. Aeth. Agrim,*E*,*o*. Agrostem. Agrostis,*a*,*c*,*s*. Air,*c*,*d*,*f*. Aj,*ch*,*g*,*r*. Alch,*a*,*r*. Alis,*n*,*P*,*r*. Alliu,*ca*, *o*,*Sch*,*Sco*,*ur*,*vi*. Aln,*g*,*i*. Alop,*a*,*b*,*f*,*g*,*p*. Als,*t*. Alth,*o*. Aly,*cal*,*camp*. Amar,*B*,*r*,*s*. Ambr,*a*. Ammi,*m*. Ammo,*a*,*b*. Anac. Anag,*a*,*c*,*t*. Anch. Andr. Anem,*n*,*P*,*r*. Ang. Anthem,*ar*,*c*,*r*,*ti*. Antho,*o*,*P*. Anthr,*C*,*s*,*v*. Anthyl. Antir,*O*. Ape,*i*,*S*. Api,*g*. Aq,*v*. Ara,*ar*,*G*,*h*,*s*. Are,*l*,*s*. Aris,*Cl*. Arm,*e*,*m*. Arni. Arno. Arrh. Art,*Abs*,*c*,*m*,*v*. Aru,*i*,*m*. Asa. Aspara,*o*,*p*. Asperug. Asperul,*a*,*c*,*o*. Aspl,*A-n*, *R-m*,*T*. Aste,*s*,*T*. Astra,*g*. Athy,*f-f*. Atri,*d*,*ho*,*lac*,*lat*,*li*,*p*,*r*. Atro. Av,*c*,*fa*,*fl*,*prae*, *prat*,*pu*. Az.

Ball. Barb,*a*,*i*,*p*,*s*,*v*. Bark,*f*,*s*,*t*. Bat,*d*,*f*,*hed*,*het*,*o*,*s*,*tric*,*trip*. Bel. Berb. Beru. Beta,*m*. Beto. Betu,*p*,*v*. Bid,*c*,*t*. Ble. Bli,*c*,*v*. Bor. Bot. Brach,*p*,*s*. Bras,*e*,*l*, *Na*,*ni*,*o*,*R*. Bri. Bro,*ar*,*as*,*c*,*e*,*h*,*i*,*m*,*r*,*se*,*st*,*t*. Bry. Bup,*t*. But.

Cak. Calama,*E*;*H*,*la*,*li*,*n*. Calami,*A*,*o*. Cale,*a*,*o*. Calla. Calli,*a*,*h*,*s*,*v*. Callu. Calt. Came,*d*,*m*,*s*. Camp,*l*,*pa*,*pe*,*ra*--*des*,*ra*--*us*,*rot*,*T*. Caps. Carda,*a*,*h*,*p*,*s*. Cardu, *cr*,*n*. Care,*ac*--*a*,*ac*--*is*,*ar*,*br*,*Bu*,*can*,*dig*,*dio*,*dista*,*disti*,*div*,*ech*,*el*,*er*,*ex*,*fi*,*flav*, *fu*,*gl*,*hi*,*Ho*,*lepo*,*lig*,*lim*,*mu*,*pall*,*panice*,*panicu*,*par*,*pe*,*pi*,*prae*,*Ps*,*pu*,*re*,*rip*,*ro*, *Sch*,*stric*,*strig*,*sy*,*te*,*trin*,*ves*,*vulg*,*vulp*. Carl. Carp. Caru,*B*,*C*,*v*. Cas. Cata. Cau. Centa,*Ca*,*Cy*,*J*,*n*,*Sc*,*So*. Centu. Ceph,*g*. Ceras,*ar*,*glo*,*glu*,*s*,*te*,*tr*. Cerat,*d*,*s*. Chae,*t*. Chamag. Cheir. Chel. Chen,*a*,*b-h*,*f*,*g*,*h*,*m*,*o*,*p*,*r*,*u*,*v*. Chl,*p*,*s*. Chon. Chrysa,*i*,*L*,*P*,*s*. Chryso,*a*,*o*. Cicen. Cich,*I*. Cicu. Cin,*p*. Circae,*l*. Cirsi,*ac*,*an*, *ar*,*l*,*o*,*p*. Clad. Clayt. Clem,*V*. Cli. Coch,*an*,*Ar*,*d*,*o*. Colch. Colu. Com. Coni. Conva,*maj*. Convo,*a*,*se*,*So*. Coris. Corn,*s*. Coroni,*v*. Corr. Coryd,*ca*,*cl*,*l*,*s*. Coryl,*a*. Coryn,*c*. Cram. Crat,*m*,*o*. Crep,*b*,*p*,*t*,*v*. Cri. Cucub. Cus,*Epil*,*Epit*,*eu*. Cynan,*V*. Cynod,*D*. Cynog,*o*. Cynos,*c*. Cyp,*fl*,*fu*. Cys.

Dac. Daph. Dat. Dau. Del,*c*. Dian,*Arm*,*Cart*,*d*,*p*,*s*. Dig,*l*,*p*. Dipl,*m*,*t*,*v*. Dips,*p*,*s*. Dor,*P*. Dra,*m*,*v*. Dro,*i*,*l*,*r*.

Echin,*d*,*L*. Echiu. Ela,*he*,*Hy*,*t*. Elo. Ely,*a*. Emp. End. Epil,*a*,*h*,*m*,*pal*,*par*,*r*,*t*,*v* Epip,*a*,*l*,*p*. Eq,*a*,*h*,*l*,*m*,*p*,*s*,*v*. Eran. Eric,*c*,*T*. Erig,*a*,*c*. Erio,*g*,*l*,*p*,*v*. Erod,*c*,*pimp*. Eruc,*P*. Eryn,*c*,*m*. Erys,*Ch*,*h*,*or*,*r*,*v*. Eryt,*C*,*l*,*p*. Eupa. Eupho,*Cy*,*Es*,*ex*,*G*,*H*, *pal*,*Par*,*Pep*,*pla*,*seg*,*str*,*vir*. Euphr,*Od*,*of*. Ev.

Fagu. Far. Fes,*a*,*d*,*e*,*g*,*l*,*M*,*o*,*rig*,*rub*,*Sc*. Fic. Fil,*ar*,*g*,*m*,*s*. Frag,*e*,*v*. Frax. Frit,*M*. Fu,*c*,*d*,*me*,*o*.

Gag,*a*,*l*,*sp*,*st*. Gala. Galeobd. Galeops,*b*,*L*,*o*,*p*,*T*,*v*. Galins. Galiu,*ap*,*b*,*c*,*elo*,*M*,*o*,*p*,*sax*, *sylvat*,*sylves*,*t*,*u*,*v*. Geni,*a*,*g*,*p*,*t*. Gent,*a*,*ca*,*cr*,*g*,*P*. Ger,*c*,*d*,*m*,*Ph*,*pr*,*pu*,*py*,*Rob*. Geu,*i*,*r*,*u*. Glauc,*c*,*l*. Glaux. Gle. Gly,*d*,*f*,*m*,*s*. Gna,*d*,*l-a*,*s*,*u*. Good. Gra. Gym,*a*,*c*. Gyp,*m*,*p*.

Halim,*ped*,*por*. Hed. Heleo,*a*,*m*,*p*,*u*. Helia,*g*,*v*. Helich. Heli,*f*. Helm. Helo,*i*,*n*,*r*. Hera. Herm. Hern,*g*. Hiera,*aura*,*Auri*,*b*,*cae*,*m*,*Pi*,*pr*,*r*,*tr*,*u*,*vu*. Hiero. Hippo. Hippu. Holc,*l*,*m*. Holo. Honck. Hor,*ma*,*mu*,*se*. Hott. Hu. Hydroch. Hydroco. Hyo. Hype,*E*,*hi*,*hu*,*m*,*pe*,*pu*,*q*,*t*. Hypo,*g*,*r*.

Ile. Illec. Im,*n-t*,*p*. In,*b*,*C*. Ir,*ps*. Isn.

Ja,*m*. Junc,*al*,*ba*,*bu*,*ca*,*comp*,*cong*,*d*,*e*,*f*,*Ge*,*gl*,*l*,*m*,*o*,*p*,*sq*,*su*,*sy*,*Tena*,*tenu*. Juni.

Kn. Koch,*h*,*s*. Koel,*c*.

Lac,*m*,*sal*,*sc*. Lami,*al*,*am*,*inc*,*int*,*m*,*p*. Lamp. Lap,*i*,*ma*,*mi*,*t*. Lar. Lathr. Lathy, *A*,*m*,*nig*,*Nis*,*pa*,*pr*,*s*,*t*,*v*. Leer. Lem,*a*,*g*,*m*,*p*,*t*. Leont,*a*,*h*. Leonu. Lepid,*c*,*D*,*g*, *l*,*p*,*r*,*s*,*v*. Lept. Leu,*a*,*v*. Lig. Lil,*b*. Limn. Limo. Lina,*a*,*C*,*E*,*m*,*sp*,*st*,*v*. Linu,*c*. Lis,*o*. Lith,*a*,*o*. Litt. Lob,*D*. Lol,*l*,*m*,*p*,*t*. Lon,*P*. Lot,*c*,*t*,*u*. Luz,*a*,*c*,*ma*,*mu*,*p*. Lychn,*f*,*F*,*ves*. Lyci. Lycopo,*cl*,*co*,*i*,*S*. Lycops. Lycopu. Lys,*ne*,*Nu*,*t*,*v*. Lyt,*H*,*S*.

Maj. Malach. Malax. Malv,*A*,*m*,*r*,*s*,*v*. Mar,*v*. Matr,*Ch*,*d*. Med,*d*,*f*,*l*,*ma*,*me*,*mi*,*s*. Melam,*a*,*p*. Melic,*n*,*u*. Melil,*alb*,*ar*,*c*,*d*,*o*,*p*. Ment,*aq*,*ar*,*g*,*r*,*sy*. Meny. Merc,*a*,*p* Mes. Mil,*e*,*s*. Moehr. Moen. Mol. Mono. Mont,*m*,*r*. Musc,*b*,*c*. Myoso,*c*,*h*,*i*,*p*, *stric*,*strig*,*sy*,*v*. Myosu. Myric,*c*,*G*. Myrio,*a*,*s*,*v*.

Naj,*ma*,*mi*. Nardu. Narth. Nast,*am*,*o*,*p*,*s*. Neo. Nep,*C*. Nes. Nu. Ny.

Oena,*fi*,*L*,*Ph*. Oeno,*b*,*L*,*m*. Onon,*r*,*s*. Onop. Ophi. Ophr,*a*,*m*. Orch,*c*,*f*,*i*,*l*,*mac*, *mas*,*mil*,*mo*. Orig. Ornithog,*n*,*u*. Ornithop,*p*. Oroba,*a*,*c*,*G*,*m*,*pa*,*Pi*,*ram*,*Rap*,*ru*. Osm. Ox,*a*,*c*,*s*. Onobrychis viciaefolia

Pan,*C-G*,*l*,*s*. Pap,*A*,*d*,*h*,*R*. Parie,*o*,*r*. Paris. Parn. Pas. Ped,*p*,*s*. Pep. Peta,*a*,*o*. Peu,*C*. Phalar,*a*,*c*. Phe,*D*,*p*,*R*. Phl,*a*,*p*. Phr. Phyt,*n*,*s*. Pice,*e*. Picr. Pil. Pim,*m*,*S*. Ping. Pinu,*sy*. Piro,*m*,*r*,*s*. Plan,*a*,*C*,*l*,*maj*,*mar*,*me*. Platant,*l*,*m*,*v*. Poa,*an*,*b*,*co*,*n*,*pr*,*se*,*su*,*t*. Polyc. Polygal,*c*,*d*,*v*. Polygona,*m*,*o*. Polygonu,*am*,*av*, *B*,*C*,*D*,*H*,*lap*,*min*,*mit*,*n*,*Pe*,*ta*. Polypod. Polys,*a*,*c*,*F-m*,*O*,*s*,*T*. Pop,*a*,*n*,*t*. Pota,*a*, *co*,*cr*,*d*,*g*,*Ho*,*l*,*mu*,*n*,*obt*,*pec*,*per*,*po*,*pr*,*pu*,*r*,*t*. Potent,*ans*,*arg*,*c*,*f*,*i-v*,*n*,*o*,*pi*,*pr*,*rec*, *rep*,*T*,*ve*. Pri,*e*,*f*,*o*. Prune. Prunu,*Pa*,*sp*. Pt. Pule. Puli,*d*,*v*. Pulm. axe

Qu,*R*,*s*. ×

Rad. Ran,*ac*,*ar*,*au*,*b*,*Fl*,*L*,*n*,*Ph*,*po*,*r*,*sce*. Raphanu,*r*,*s*. Res,*lutea*,*luteo*. Rha,*c*,*F*. Rhina,*A*,*ma*,*mi*. Rhynch,*a*,*f*. Rib,*a*,*G*,*n*,*r*. Rob. Ros,*ar*,*ca*,*cin*,*co*,*du*,*pi*,*po*,*ru*,*s*,*t*. Rubia. Rubus,*cae*,*Id*,*sax*,*spp*. Rum,*Ac*--*sa*,*Ac*--*la*,*cong*,*cons*,*cr*,*div*,*Hip*,*Hyd*,*la*, *le*,*mar*,*max*,*o*,*p*,*sa*,*sc*. Rup,*m*,*r*.

Sagin,*a*,*c*,*n*,*p*,*str*,*su*. Sagit. Salic,*h*,*r*. Salix,*ac*,*al*,*amb*,*amy*,*au*,*b*,*ca*,*ci*,*f*,*i*,*pe*,*pu*,*re*,*Ru*, *se*,*sm*,*st*,*un*,*vim*. Sals. Salvia,*p*,*Sc*,*sy*,*ve*. Salvin. Samb,*E*,*n*,*r*. Samo. Sang,*m*,*o*. Sani. Sap,*o*. Sar. Sax,*g*,*t*. Scab. Scan. Scheu. Schoe,*n*. Scil,*b*. Scir,*cae*,*co*,*D*,*f*, *l*,*m*,*pa*,*pu*,*ru*,*se*,*sy*,*Ta*,*tr*. Sclera,*a*,*p*. Sclero,*B*,*p*. Scol. Scor,*h*. Scro,*a*,*E*,*Ne*,*no*,*v*. Scut,*g*,*m*. Sed,*ac*,*al*,*B*,*C*,*d*,*r*,*r*. Sel,*c*. Sem. Seneb,*c*,*d*. Senec,*a*,*err*,*eru*,*F*,*J*,*p*, *sa*,*sy*,*vi*,*vu*. Set,*g*,*ve*,*vi*. Sh. Silau. Sile,*A*,*c*,*d*,*g*,*i*,*no*,*nu*,*O*. Sily. Sin,*al*,*ar*,*Ch*. Sis,*A*,*C*,*I*,*L*,*o*,*p*,*S*,*T*. Siu. Sola,*D*,*n*. Soli,*v*. Son,*ar*,*as*,*o*,*p*. Sor,*a*. Sparg,*a*,*f*,*m*,*r*,*s*. Spart. Spec,*s*. Spergula,*a*,*M*. Spergularia,*ma*,*me*,*r*,*sa*,*se*. Spirae,*U*. Spiran,*ae*,*au*. Stach,*am*,*an*,*ar*,*p*,*s*. Stat,*L*. Stel,*gl*,*gr*,*H*,*m*,*n*,*u*. Stra. Stu. Suae,*f*,*m*. Sub. Suc. Sym,*o*.

Tan. Tar. Tax. Tee. Tetr. Teu,*sc*. Tha,*fla*,*fle*,*mi*. The. Thl,*alp*,*ar*,*c*. Thr. Thym. Thys. Tili,*g*,*i*,*pa*. Till. Tor,*A*,*H*,*n*. Trag,*m*,*po*,*pr*. Trie. Trif,*ar*,*di*,*fi*,*fr*,*h*,*i*,*ma*, *me*,*mi*,*pra*,*pro*,*rep*,*sc*,*st*,*su*. Trigl,*m*,*p*. Trio, Trit,*a*,*c*,*j*,*pu*,*r*. Tul. Turg. Turr. Tus. Typha,*a*,*l*.

Ule. Ulm,*c*,*s*. Ur,*d*,*u*. Utr,*B*,*i*,*m*,*n*,*v*.

Vacca,*s*. Vacci,*ma*,*My*,*O*,*u*,*V*. Valeriana,*d*,*o*. Valerianella,*A*,*ca*,*d*,*o*. Verba,*B*,*L*,*n*, *phl*,*Sch*,*th*--*forme*. Verbe. Vero,*ag*,*An*,*ar*,*Be*,*Bu*,*Ch*,*h*,*la*,*lo*,*m*,*of*,*op*,*pe*,*po*,*prae*, *pro*,*sc*,*se*,*t*,*u*,*v*. Vib,*L*,*O*. Vic,*a*,*C*,*g*,*hi*,*la*,*sa*,*se*,*t*,*v*. Vin,*mi*. Vio,*cal*,*can*,*h*,*o*,*pa*,*R*, *st*,*sy*,*t*. Vis.

Xanthium,*s*.

Zan,*pa*,*pe*. Zos,*m*,*n*.

Fig. 14. The *Hoklijstje* used by Dr. Kloos to score the plants he observed on the Quendon Field Meeting.

Each species found in Holland is represented by its scientific name in a very abbreviated form which is crossed through if the plant is observed. For example, the first three species in the list are *Acer campestris*, *Achillea Millefolium* and *Achillea Ptarmica*—only the second was crossed through as observed.

and Jongmans' prepared printed inventory lists, known as *Hoklijstjes*. These include the names of all species, likely to be found in any part of Holland, printed in a very abbreviated form. As each plant is observed in the quarter-square, the name is crossed off in the list. The work can be undertaken by a single person but it is performed more efficiently by teams of three to five botanists. One of these undertakes the reading of the map, another marks off the plants on the list while the remainder observe the plants and call out the names. The party "play leap-frog"—i.e. they go ahead in turns so that the ground is adequately covered. It is evident that the value of such work depends on the trustworthiness of those taking part and the need for accuracy is impressed on all workers. The completed lists are sent to the secretary of I.V.O.N.

The data are worked out by collaborators, appointed for each sheet of the military map and chosen as knowing its flora well and, for preference, as living in the region concerned. Each species found within the territory of the sheet is plotted on a separate distribution map. These are on the scale 1 : 200,000 and printed on more or less transparent paper. On one side there is a reversed reproduction of the main contours of the area, on the other a complete grid of the squares. The quarter-squares in which the species has been observed are marked with a red spot. By holding the map against the light the two are combined and the distribution of the species in the territory can be seen against the background of the contours.

These distribution maps are filed in loose-leaf binders and form a complete florula for each sheet of the military map. For most sheets there are three binders, for some of them four are needed. From these sheets the indefatigable secretary of I.V.O.N., Mr. Jan G. Sloff at Bergen op Zoom, plots the observations on to maps covering the whole of Holland on the scale of 1 : 1,500,000. These maps are less detailed and show only the hour-squares in which the species has been found. It will be appreciated that the presence of a plant in an hour-square may represent its occurrence in all of the 16 quarter-squares or, equally, it may occur in only one of them or in several. Although the local frequency cannot be shown on the general maps, they have nevertheless proved very useful. They show at a glance whether the plant is common over the whole country or rare, and the pattern of its distribution which can be compared with maps for other species or with the geological or meteorological maps, etc. Reference can be made back to the separate sheets for more detailed information.

The published maps were at first on the scale 1 : 1,500,000 as used by Goethart and Jongmans, 1903-1908. The distribution was shown in red overprinted on a black background. It was proved by experience that this scale was hardly large enough to indicate the quarter-squares by red dots, while failure of the over-printing to register exactly was a frequent cause of inaccuracy. Moreover publication was too expensive. It was therefore

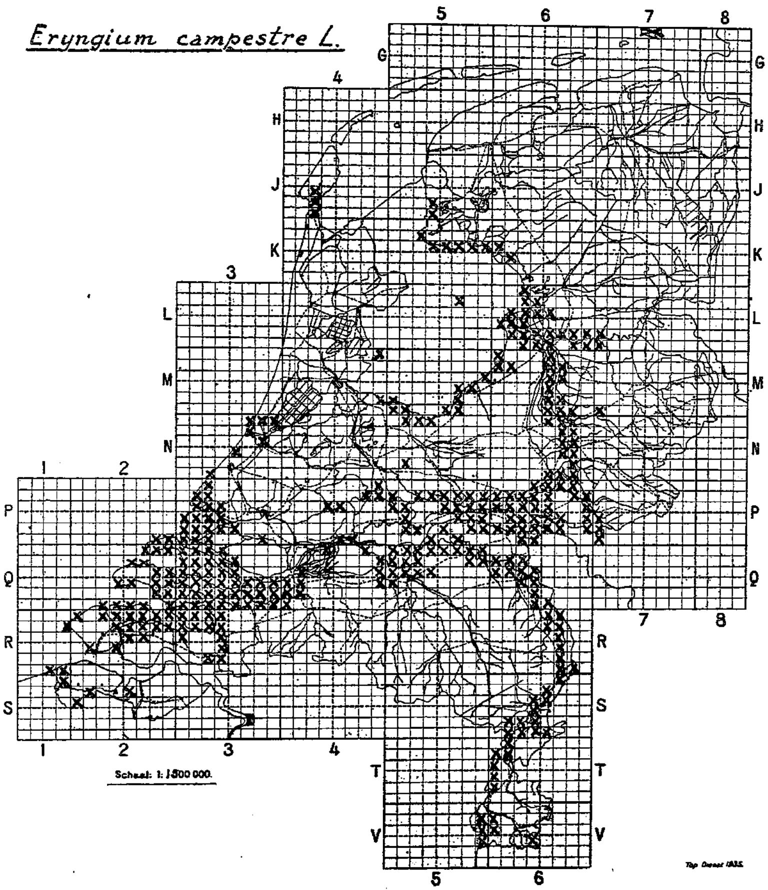


Fig. 15. The distribution of *Eryngium campestre* L. in Holland (reduced to 1 : 3,000,000).

necessary to be content with showing only the hour-squares on a scale of 1:3,000,000 (later 1:2,500,000): see Fig. 15.

The plan was at first applied only to phanerogams and pteridophytes but later extended to bryophytes, lichens and fungi. It has also been used for other groups—e.g. mollusca.

This paper was discussed as follows:—

Dr. Valentine enquired whether a soil map was available on the small scale of the published maps. Dr. Kloos replied that only a geological map printed on the military maps was available, but this was easily used in connection with the distribution maps by employing the grid.

PROF. TUTIN asked if difficulty was found in tracing the boundaries of the squares in the field. DR. KLOOS replied that in practice they found no difficulty. The scale of the military maps was sufficiently large, and the detail sufficient, in a crowded country like Holland, for lines on the map to be traced with ease for this work.

DR. TURRILL suggested that it would be an advantage to print the outline of the coast in heavier lines so that foreigners could pick it out more easily in the printed maps. DR. KLOOS agreed that this might be an advantage when the maps were consulted abroad but the Dutch were so familiar with the outline of their own coast that to them it hardly seemed necessary. Moreover, in the later publications the land of Holland was shaded so that it contrasted with the sea and land of neighbouring countries.

MR. LOUSLEY commented that he had been most impressed with the rapidity with which his Dutch friends could supply detailed information about the distribution of their plants and suggested that this was an extremely commendable feature of the scheme. DR. KLOOS replied that the files of maps were always available for consultation in Leiden.

MR. SANDWITH enquired whether microspecies were given on each card used for listing purposes. DR. KLOOS said that they were.

MR. BRENAN asked to what extent the records as plotted on the squares were backed by herbarium specimens. DR. KLOOS replied that critical species and the rarer plants were usually collected to authenticate the records but clearly this was impossible in the case of common and well-known plants. He emphasised that great care was taken to ensure that the lists used were reliable as far as possible.

(At the Field Meeting to Quendon Wood on the following day, Dr. Kloos demonstrated the use of the Hoklijstjes (Fig. 14). Once the user became accustomed to the very abbreviated plant names printed in the lists the vegetation could be scored quickly and accurately and the record was available for filing without the necessity for transcription.)

PROBLEMS OF DISTRIBUTION RAISED IN THE COMPILATION OF A COUNTY FLORA

J. G. DONY.

The urge to write a Flora of his county has long been strong in many a British botanist and is likely to continue. The county can be the basis of local patriotism at its best and even if the Watsonian vice-county system is ultimately discarded there is little doubt that county floras will continue to be published. A county Flora attempts to portray the individuality of the flora of a county and to study the distribution of plants within its boundary, especially in relationship to their distribution in neighbouring counties. This latter becomes a matter of increasing importance with an inland county.

Bedfordshire is a small inland county. It is indeed one of the smallest counties, the Watsonian vice-county *30, Bedford,* coinciding very closely with the present administrative county (see Dony (1947)). The county contains only one distributed species which does not occur in any of the neighbouring counties. This species, *Ornithogalum pyrenaicum,* is relatively abundant in a narrow strip of country about twelve miles long in the north-east of the county, just as it is in a similar stretch of country near Bath. Species which occur in one station only are not considered to have a distribution.

Two main factors appear to determine plant distribution in Bedfordshire: (a) surface geology, (b) the physical factors of altitude, rainfall and temperature. Minor factors such as man's use, or in Bedfordshire more often misuse, of the land, are usually related to these two main factors.

The Rock Geology of the county is simple as the various strata are exposed in belts of land crossing the county from the south-west to the north-east. These geological formations could be made the basis of a division of the county, as they divide it into districts which conform to the botanist's first impression of its various plant communities. The species of the Chalk and the Lower Greensand are each brought together and the large and comparatively uninteresting Oxford Clay, occupying the northern half of the county, is brought into sharp contrast with the rest. This simple picture is, however, complicated by the Drift Geology. The Ouse and Ivel, with their wide stretches of alluvium and river gravels, cut into the Oxford Clay, and extensive caps of Boulder Clay overlie large areas and have no respect for the boundaries of the rock deposits beneath. Much of the Chalk is overlain by Clay-with-Flints which has a flora peculiarly its own.

The physical factors are of less consequence in their effect on plant distribution. The rainfall varies directly with altitude and in the lower reaches of the Ouse, only 50 ft. above sea level, the rainfall is less than 20 inches, while in the south-west, where the highest part of the Chalk is above 800 ft., it increases to 30 inches. There are too few temperature records from which one could

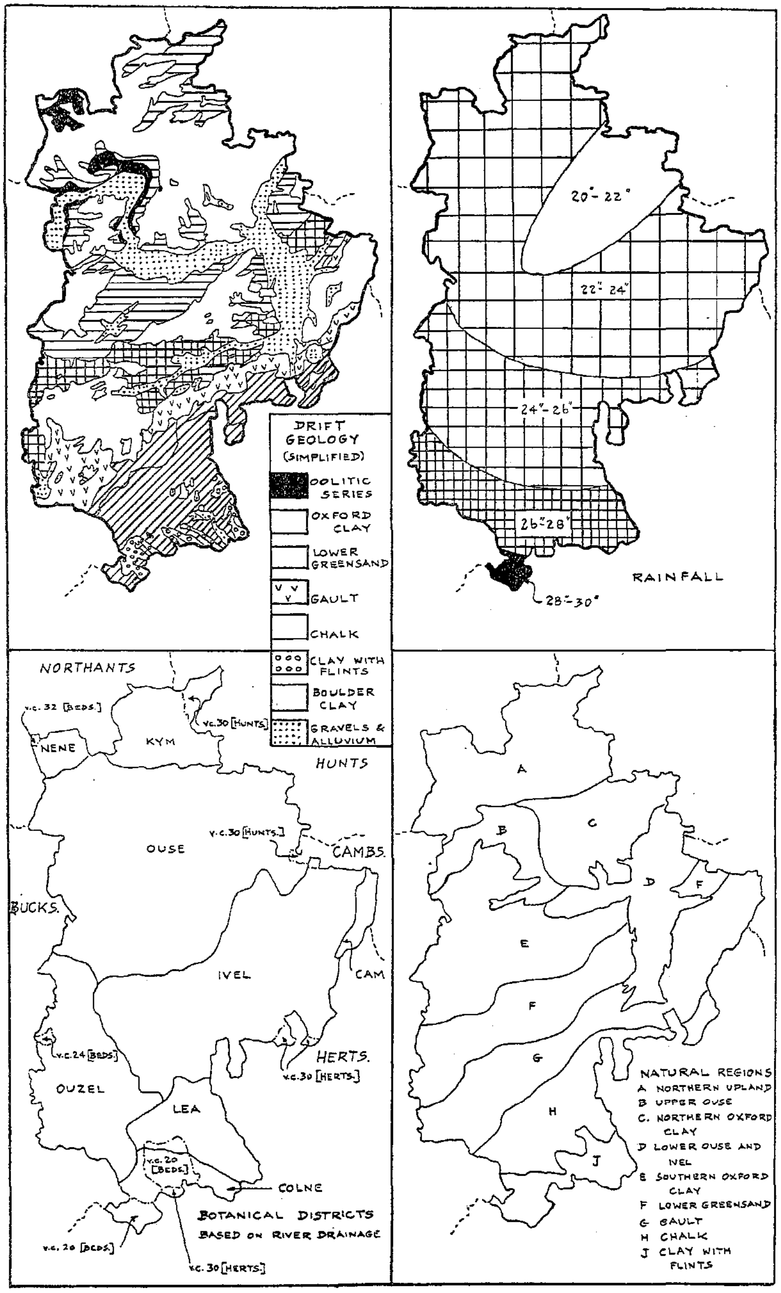


Fig. 16. Bedfordshire: Drift Geology, Rainfall, and division into Botanical Districts based on (a) River Drainage and (b) Natural Regions.

draw reliable conclusions but there is little doubt that generally speaking the eastern parts of the county have greater extremes of temperature than the western parts. The contrast of the low lying and drier eastern part of the county with the higher altitudes and more temperate and wetter conditions of the western part determines the distribution of some of the more interesting Bedfordshire species. *Trifolium ochroleucon, Primula elatior, Melampyrum cristatum, Ajuga Chamaepitys* and *Phleum phleoides* appear only in the eastern part of the county and are absent or exceedingly rare in counties to the west. *Melandrium dioicum* is abundant in the west of the county but is rare or absent in the east as it is also in Cambridgeshire. The fern flora of the western parts is more varied than that of the eastern part and Watson (1948) found the same to hold for the bramble flora.

A combination of the geological and physical features could be the basis for the division of the county into natural regions. In the earliest attempt to do this Batchelor (1808) made five regions based on soils. Hillhouse (1877), no doubt influenced by Babington, suggested seven regions, and to allow for all factors sub-divided each into seven further divisions. This was no doubt an ideal which could now be amended in the light of more exact knowledge of the drift geology, but it is too complicated and would be almost impossible to work satisfactorily. A more workable division for the field botanist could be made on a basis of twelve regions which could bring together all the more important plant communities and give a reasonably accurate picture of the flora of the county. But such a system would have serious disadvantages, as the boundaries of the regions are difficult to memorise and constant reference to maps would be necessary. The Lower Greensand is divided into two parts and some regions, especially the Gault Clay, being an awkward shape, would limit serious work in the field. To divide the regions further would bring one back to Hillhouse and his almost unworkable system.

A study of the methods adopted in neighbouring counties is necessary, for a new county flora affords a useful comparison with similar work already done in a wider field. In Hertfordshire, Webb and Coleman (1839) used a river drainage basis, being the first botanists to adopt this method. Pryor (1887) followed their lead and produced a model county flora of its kind and period and the method was retained by Hopkinson (1902). Druce used the same basis for Buckinghamshire (1905 and 1926B) and Northamptonshire (1930). There is no map in the last-named work but one may be found in an earlier account, Druce (1902). Huntingdonshire is one of the few English counties without a published county flora and it is unlikely to have one for some time. In an inadequate account of its flora Druce (1926A) considered it as a whole. For Cambridgeshire, Babington (1860) used eight natural regions and Godwin (1938) dealt with its types of flora. Evans (1939), in a disappointing account, considered it as a whole.

In the previous work done in Bedfordshire, Abbot (1798), and Saunders (1911), considered the county as a whole. Hillhouse (1877) suggested natural regions but no records had been related to them. Druce (1904), who knew little of the county, made seven districts based on river drainage. It is interesting to note that for one district, the Nene, he listed only one species, picked up from W. W. Newbould, and from another, the Cam, he recorded nothing. On the other hand, Little (1936) subsequently did some useful work on Druce's Ivel district and his field notes contained some records from the Cam district. Much of the useful work already done both in the county and in neighbouring counties has been on a river drainage basis.

The boundaries adopted by Druce were, however, badly in need of revision. His Lea district contained two catchment areas and Pryor had two districts, the Lea and the Colne, based on these. He had divided the large Ouse district somewhat artificially into East and West Ouse for which there were no corresponding districts in his treatment of Northamptonshire. It appears better to introduce a new district, the Kym, based on river drainage. This is somewhat smaller than Druce's East Ouse, but its boundary is more easily seen in the field. It could, if need be, be adopted in a division of Huntingdonshire. A study of the watershed showed the Cam district to be larger than his map indicated.

The river drainage basis has some practical virtues. The boundaries can usually be seen in the field and in most cases a road, footpath, or at least a field boundary is found to follow the watershed closely. It conforms in a crude way with some of the natural factors affecting plant distribution; the eastern and western parts of the Lower Greensand with their differing floras, for instance, are brought into separate districts. The greater part of the Clay-with-Flints is brought into one district, the Colne.

Its most serious defect is that the Chalk is brought into four districts with few corresponding differences of flora. The districts differ greatly in size, but this has proved in some respects an advantage. If a species is recorded from all districts it can almost certainly be said to be well distributed in the county. This is the case with some species comparatively rare in the county, e.g. *Ophioglossum vulgatum* and *Saxifraga tridactylites.* On the other hand some species, *Primula vulgaris, Stellaria Holostea* and *Knautia arvensis,* which one would have considered from their general abundance to be well distributed, are each, for no accountable reason, apparently absent from one district. The close search of some of the smaller districts has added some interesting species to the county flora and at least one, *Cerastium brachypetalum,* to the British flora.

There would appear to be, for Bedfordshire, no perfectly satisfactory basis for a division of the county. Natural regions are being used for all descriptive matter relating to the flora of the county as a whole and to individual species. Records, which should be related to boundaries that can be readily checked in the field, are linked to the river drainage system. Yet a third alternative, a purely artificial one based on a grid system, has been rejected. Bedfordshire is a relatively compact county yet it contains only five complete ten kilometre grid-squares and parts of seventeen others.

Each county will have its own difficulties and the divisions adopted in Bedfordshire would probably be of little use in another county. A simpler method could have been adopted by resorting to compromise, all too readily adopted by Druce. A basis, once adopted, should be worked out to its logical conclusion. If the final choice is between alternatives each with defects and virtues the basis of useful work already done, not only in the county under consideration but in neighbouring counties, may well be considered.

References.

ABBOT, C., 1798, *Flora Bedfordiensis.* Oxford.

BABINGTON, C. C., 1860, *Flora of Cambridgeshire* (Map). London.

BATCHELOR, T., 1808, *A General View of Agriculture in the County of Bedford* (Map). London.

DONY, J. G., 1947, What Bedfordshire Is, *Journ. Beds. Nat. Hist. Soc., 1,* 8-12 (Map).

DRUCE, G. C., 1902, Botany, *V.C.H. Northamptonshire, 1* (Map).

——, 1904, Botany, *V.C.H. Bedfordshire, 1,* 37-67 (Map).

——, 1905, Botany, *V.C.H. Buckinghamshire, 1.*

——, 1926A, Botany, *V.C.H. Huntingdonshire, 1.*

——, 1926B, *Flora of Buckinghamshire* (Map). Arbroath.

——, 1930, *Flora of Northamptonshire.* Arbroath.

EVANS, A. H., 1939, *Flora of Cambridgeshire* (Map). London.

GODWIN, H., 1938, Botany, *V.C.H. Cambridgeshire, 1.*

HILLHOUSE, W., 1877, On the Surface Geology and Physical Geography of Bedfordshire, *Trans. Beds. Nat. Hist. Soc., 1875-6,* 83-91 (Map).

HOPKINSON, J., 1905, Botany, *V.C.H. Hertfordshire, 1.*

LITTLE, J. E., 1936, The Ivel District of Bedfordshire, *B.E.C. 1935 Rep.,* 50-67.

PRYOR, A. R., 1887, *A Flora of Hertfordshire,* edited by B. Daydon Jackson (Map). London.

SAUNDERS, J., 1911, *The Field Flowers of Bedfordshire.* London.

WATSON, W. C. R., 1948, The Brambles of Bedfordshire, *Journ. Beds. Nat. Hist. Soc., 2,* 21-25

WEBB, R. H., & COLEMAN, W. H., 1839, *Flora Hertfordiensis* (Map). London.

This paper was discussed as follows:—

MR. ROSE suggested that in dividing counties up into drainage areas it might be desirable to treat the chalk, which had no surface drainage, separately. Dr. Dony replied that he agreed that chalk areas with few streams did provide a problem but he found that he could deal with it satisfactorily by using the Catchment Board's map as a check on his own.

Mr. Brenan remarked that if each author of a county flora adopts his own system it becomes difficult to make comparisons between neighbouring counties. Dr. Dony said that he had this point very much in mind but as the authors of three out of the four neighbouring counties of which floras had been published had adopted drainage areas, it seemed clear that to base the divisions of Bedfordshire on these would not create any difficulties in making comparisons.

Mr. Rose said that while he could agree that drainage areas provided suitable divisions for Midland counties he felt that in S.E. England physical features, which are there much more prominent, were more satisfactory.

Mr. Meyer asked whether it was not advisable to use main-roads, railways, electric grid wires, and similar features easily traced in the field as boundaries for the divisions. Dr. Dony replied that these were not sufficiently permanent for the purpose.

Mr. Wade pointed out that the division of counties into drainage areas produced divisions of very varied sizes. In Monmouthshire, for example, it resulted in very unequal divisions.

THE DISTRIBUTION OF BUNIUM BULBOCASTANUM (Exhibit)

J. G. Dony.

Bunium Bulbocastanum was first discovered in Britain by W. H. Coleman, who found it at Cherry Hinton, Cambs., v.-c. 29, in 1839. In the two following years he studied its British distribution and found it to be common on the chalk in v.-c. 30, Bedford, and v.-c. 20, Herts. In 1877, Newbould and Pryor recorded it from v.-c. 24, Bucks. Its distribution and frequency have apparently remained constant.

It is found most abundantly in arable fields and in previously disturbed soils; it is rarely found in well-established turf. It is apparently found in similar habitats on the Continent.

Maps were exhibited designed to show three alternative methods of plotting this distribution:—

(1) On a comital basis.

(2) On a grid basis.

(3) By indicating each recorded locality by a dot. (See map).

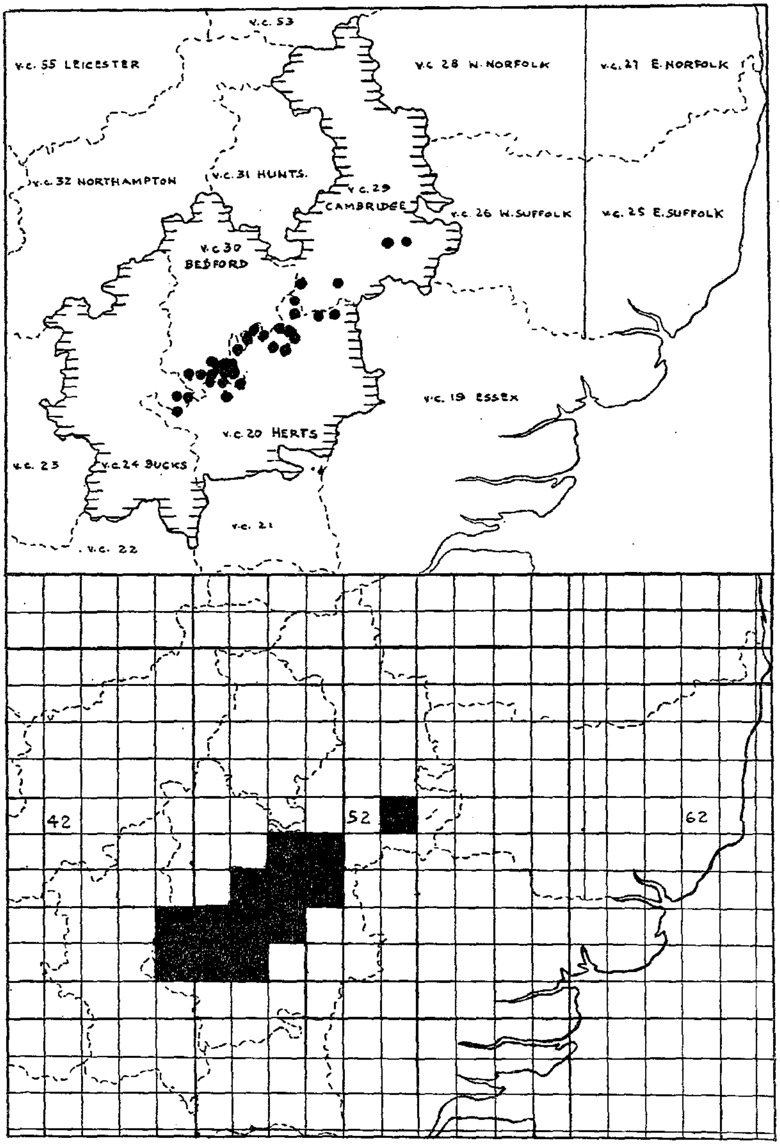


Fig. 17. The Distribution of *Bunium Bulbocastanum*.

Comparison of the three maps clearly demonstrated the relative advantages of the methods employed. In the case of the one using the grid as a base it seems likely that closer search in some of the grid squares would give the species a continuous distribution.

DISTRIBUTION MAPS OF KENT PLANTS
(Exhibit)

F. ROSE.

In connection with work on a new Flora of Kent, a number of distribution maps of species occurring in the county have been prepared and it is hoped eventually to map the majority of the species.

The distributions are plotted upon an outline map of Kent, which shows rivers, a few of the main geological boundaries, and the larger built-up areas. Copies of this have been duplicated for use as a base-map.

The records for each species are collected in the first place in a card-index, which includes:—

(a) personal field-observations.
(b) records from other sources.

These latter include records confirmed by herbarium specimens and also other records of reliable origin.

KIND OF RECORDS ACCEPTED.

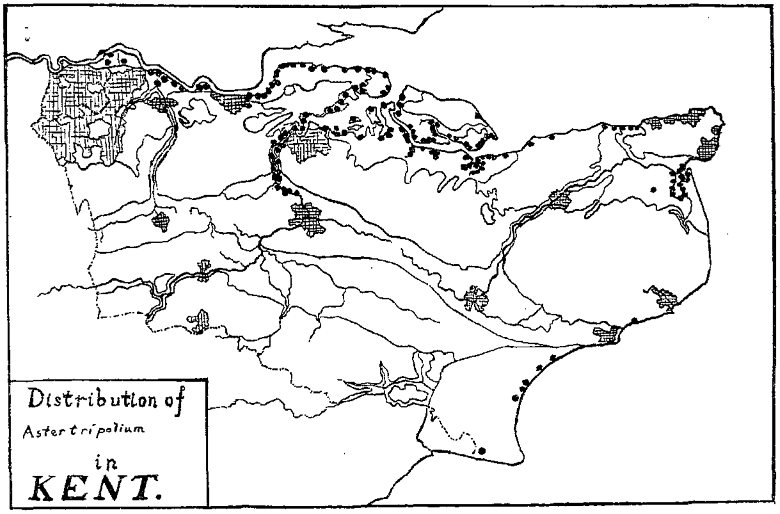
In plotting the present-day distribution of a species, the first category of records is regarded as of most value as:

(I) One can be certain of the plant's present existence.
(II) The exact locality is known.

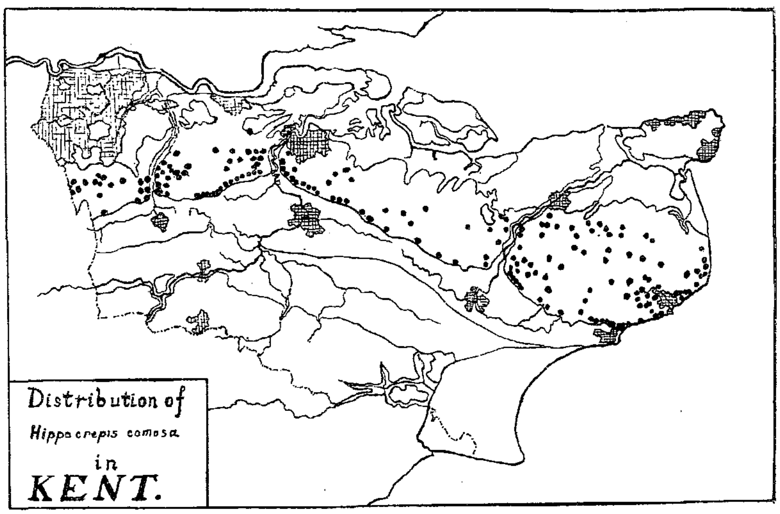
With records from other than personal sources, discretion has had to be exercised in their use, as when they are old the plant may be extinct in the given locality, and in other cases, the locality may not be defined exactly enough for accurate mapping. Unreliable records are not used in the maps.

METHOD OF PLOTTING.

For each species, each acceptable record is marked by means of a solid black dot; reliable localities now apparently extinct are marked by black circles. In some cases dots of different colours are used to show the distribution of related species on one map. To fix the position of the dots, it was decided that minute exactitude was not necessary for the purpose for which the maps were intended. They are therefore sketched as accurately as can be judged by eye from the one-inch Ordnance survey map.



A.



B.

Fig. 18. Maps to illustrate Distribution in the County of Kent (V.-cc. 15 and 16).
A. *Aster Tripolium* L.—restricted to the coast and tidal estuaries.
B. *Hippocrepis comosa* L.—confined to the chalk.

Field Methods.

In making field observations to determine the distribution of species within a county, two methods may be used.

1. The "stand" method, by which complete lists are made of all the plants seen at a very large number of different points throughout a county. This is the method so excellently employed by Prof. Good in his *Geographical Handbook of the Dorset Flora* (1949).

2. The method of searching all suitable localities for one, or a few, species at a time.

Both methods have been attempted by me, the first for determining general distribution of the commoner plants, and the second in special cases—for certain rather local plants it gives profitable results.

The Results Revealed by Plotting.

The production of a large number of detailed distribution maps reveals many points of often more than local interest. In a county like Kent with well-marked natural geological and geographical divisions, most species, apart from a few that are ubiquitous, show a definite distribution-pattern. The simplest kind of distribution-pattern is that which is determined by soil-types; for example, some species are confined to chalk, but are there widely distributed in old grassland (e.g. *Hippocrepis comosa* —Fig. 18B). Others are fully distributed on both the chalk and calcareous ragstone, but are rare or absent elsewhere (e.g. *Clematis Vitalba, Viola hirta*).

The species which are confined to certain types of habitat (e.g. littoral species, salt-marsh species) reveal this clearly on their maps (e.g. *Glaucium flavum*; *Aster Tripolium*—Fig. 18A).

There is a large group which are widespread on all soils in woodland districts, but avoid the marshland areas where woodland is absent (e.g. *Mercurialis perennis*). Besides these simple examples, there are many more complex types of distributions, where (a) historical and (b) climatic factors would appear to have an influence.

(a) In the first of these categories come such plants as *Campanula glomerata, Dentaria bulbifera, Sium latifolium,* which, though locally frequent in certain areas, are absent from other areas which are apparently quite suitable and similar ecologically. (b) In the second class some species such as *Ophrys sphegodes* and *Smyrnium Olusatrum,* although not strictly maritime, are far commoner near the coast than inland: and *Vaccinium Myrtillus,* concentrated in the west of Kent on high ground where rainfall is somewhat higher.

Then there are species with a very local distribution focus with no obvious ecological explanation, e.g. *Thesium humifusum,* only in a few spots on the chalk near Canterbury, or *Vicia sylvatica*; and some with two or more such local foci, e.g. *Lathyrus* *sylvestris, Carex helodes. Chrysosplenium oppositifolium* occurs only in those areas where permanently moist but well-drained stream banks or springs occur, and thus is widespread in the dissected, well watered Hastings Beds country of the Weald. It also occurs elsewhere along the springlines at the junction of pervious and impervious strata. Its distribution map is very complex as a result; besides the dry chalk and sand, both the low-lying Weald Clay and the alluvial marshlands of the coast are avoided, for in both there is a lack of permanently damp, well-drained, shaded habitats.

DISTRIBUTION MAPS OF LINCOLNSHIRE PLANTS (Exhibit)

MISS E. J. GIBBONS.

Maps were exhibited to illustrate the distribution of the following species in South and North Lincolnshire (v.-cc. 53 & 54):—

(1) *Tilia cordata* Mill. Although this is given only for v.-c. 53 in *Comital Flora,* it is not uncommon in v.-c. 54 where there are old woods.

(2) *Sorbus torminalis* (L.) Crantz. Given for both vice-counties in *Comital Flora* in brackets (i.e. with doubt as to nativity or identification) but herbarium specimens exist for v.-c. 53 and it is no doubt indigenous in three or four woods in v.-c. 54 where it has been found recently.

(3) *Geum rivale* L. Fairly common in suitable habitats.

(4) *Oenanthe crocata* L. Very rare in both vice-counties.

(5) *Petasites hybridus* (L.) Gaertn., Mey. & Scherb. Map to show distribution of male and female plants—the former known only from near Grantham. All colonies checked were found to be female.

(6) *Digitalis purpurea* L. Rare in both vice-counties.

Paintings of Lincolnshire flowers executed from 1895 to 1903 by Mrs Cheales (née Miss E. M. Lane-Claypon) were also exhibited.

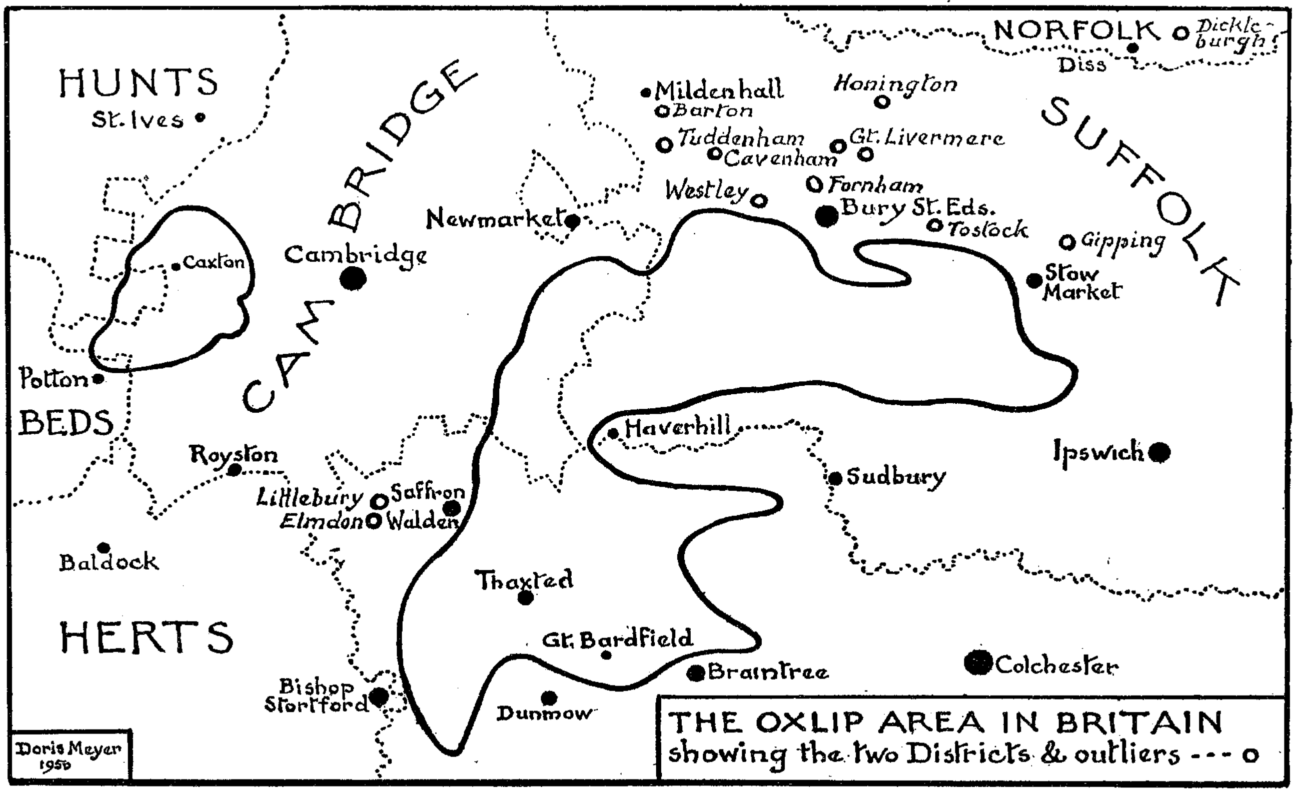
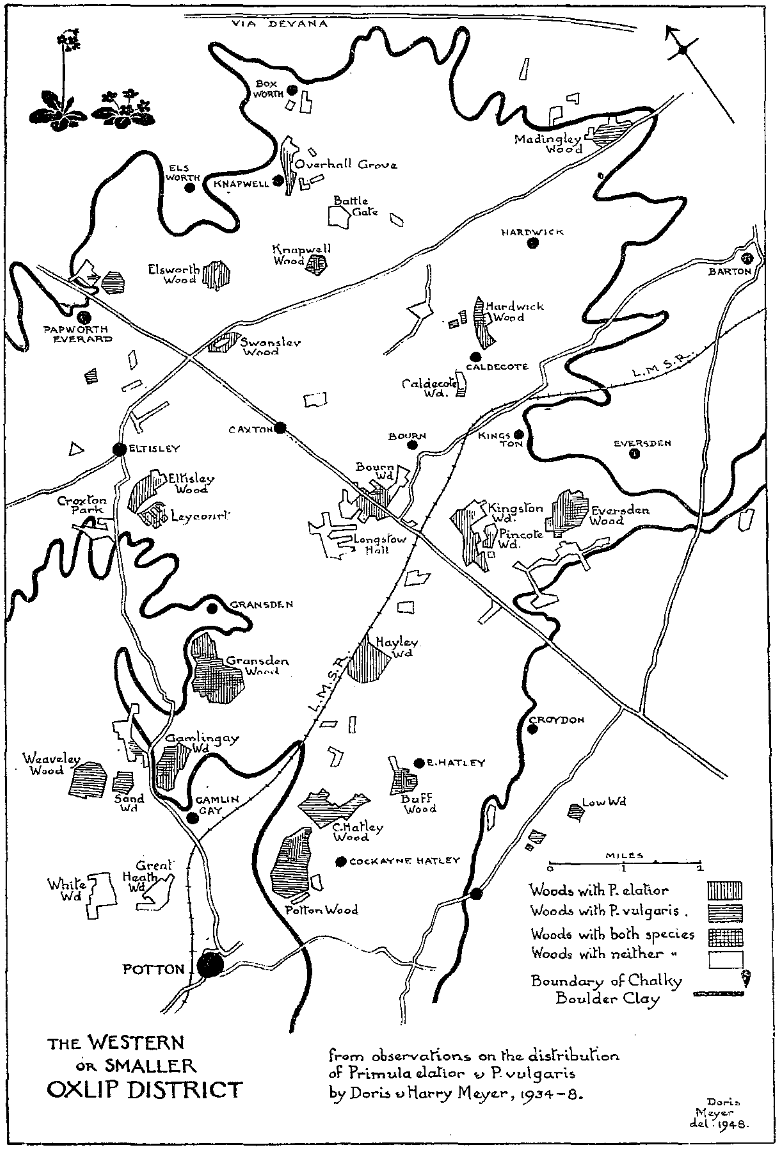


Fig. 19. The distribution of *Primula elatior* in Britain.



The distribution of *Primula elatior* within the Western (smaller) District (see Fig. 19, p. 80).

THE DISTRIBUTION OF PRIMULA ELATIOR (L.) HILL
(Exhibit)

Doris and Harry Meyer.

This exhibit included distribution maps, dried specimens, coloured drawings and photographs of plants *in situ* of *P. elatior* (L.) Hill and also of *P. vulgaris* Huds. and *P. veris* L. and their hybrids.

P. elatior in Britain is confined to East Anglia (Fig. 19) and, apart from a few outlying colonies, it inhabits two boulder-clay plateaux separated by a chalk escarpment. The smaller of these plateaux lies to the west of Cambridge and has been studied in detail by the writers with results as shown on a specially drawn coloured map on the scale of one inch to the mile (Plate I).

This map shows 21 areas of woodland, presumably ancient, as well as a number of plantations, in a district of predominantly arable land. It was found that not only in each individual wood, but also in the area as a whole, *P. elatior* tends to occupy the wetter central parts, and *P. vulgaris* the drier marginal parts, and the hybrids are found in between where the two species meet. There are six "pure oxlip woods" mostly in the centre and north, i.e. the highest part of the boulder-clay plateau; seven "pure primrose woods" around the area; and eight woods, mostly in the south, with a mixed population of *P. elatior, P. vulgaris* and the hybrids between them. In the plantations, both species are almost entirely absent; and this is taken as an indication that both are slow to spread to new ground, *P. elatior* hardly ever doing this.

P. veris is frequent both outside and inside the woods and plantations and its hybrid with *P. vulgaris* occurs in open rides, etc. The hybrid *P. veris* × *elatior* has not been seen.

Larger scale maps (6 inches to 1 mile) had also been prepared of each individual wood to show the various populations in considerable detail.

A similar investigation of the larger eastern district has been commenced and a map showing first results was exhibited.

GEOGRAPHICAL DISTRIBUTION AND ISOLATION IN SOME BRITISH ECOSPECIES

D. H. VALENTINE.

The hybridization of species, leading to the exchange of genes, is hindered or prevented by barriers of isolation, which are of various kinds. The aim of this paper is to estimate the extent and relative importance of geographical barriers of isolation in certain groups of British species. The species selected here are of a particular kind. Often, when allied species meet, hybrids are not formed, or if formed are sterile, and we can say that the species are *genetically* isolated from one another. This may occur for example with species which are not closely related taxonomically, or which stand at different levels in a polyploid series. Such species will not be considered here; for although comparative studies of their geographical *distribution* may be informative, they have little relevance from the point of view of geographical *isolation*. If on the other hand we select allied species which are capable of forming at least a moderately fertile hybrid, we can weigh the importance of geographical against genetical and other modes of isolation; and it is some species of this kind that we propose to examine. The relationship between them has been defined as ecospecific, and they may be classed as gradual-ecospecies, i.e. rather widely distributed groups having the same chromosome number which differ in morphology, ecology and geographical distribution and between which some gene-exchange is possible (Valentine, 1949).

In drawing up a list, certain groups have been omitted, some because we have not enough information about them and others because one of the species concerned is probably an alien. In these categories are *Medicago falcata* and *M. sativa* (n=16) (Gilmour, 1932), *Crataegus monogyna* and *C. oxyacanthoides* (n=17), *Centaurea nigra* and *C. jacea* (n=22) (Turrill, 1940) and *Linaria repens* and *L. vulgaris* (n=6).

The groups which will be considered are listed in Table 1. The nomenclature in the Table and throughout the paper is that of the *Check-List* (Clapham, 1946); the chromosome numbers quoted are to be found in the lists issued by Maude (1939) and Löve & Löve (1948); details of geographical distribution are taken from Meusel (1943), Hegi (1931), Druce (1932) and from British local floras. For each pair of species, we shall give, first details of experimental crosses, then the distribution of the species in Britain and elsewhere, then the frequency of natural hybrids and finally the nature of the main isolating factors, viz. geographical, genetical, ecological or of some other kind.

TABLE 1. PAIRS OF GRADUAL-ECOSPECIES IN THE BRITISH FLORA.

	Names.	*Haploid Chromosome Number.*
1.	*Nuphar lutea, N. pumila*	17
2.	*Viola odorata, V. hirta*	10
3.	*Melandrium dioicum, M. album*	12
4.	*Silene cucubalus, S. maritima*	12
5.	*Geum urbanum, G. rivale*	21
6.	*Epilobium hirsutum, E. parviflorum*	18
7.	*Saxifraga spathularis, S. lactiflora*	14 (probably)
8.	*Primula vulgaris, P. elatior*	11
9.	*Salix caprea, S. viminalis*	19
10.	*Quercus robur, Q. petraea*	12

1. *Nuphar.* Focke (1881) reports the extensive hybridization experiments of Caspary, who showed that artificial hybrids had a pollen and seed fertility of 5-15% of that of the parents; he succeeded in making backcrosses. In Britain *N. lutea* is widespread and fairly common in lowland waters while *N. pumila* is a local northern species, occurring only in Merioneth, Shropshire and ten Scottish vice-counties. Both species extend across Europe into Asia, but *N. pumila* is more northerly, and is absent from the lowlands of Europe (Meusel, 1943). Thus, over fairly large areas the species are geographically isolated. The hybrid is not recorded from Britain, but it occurs in some quantity in Sweden and Russia. Both Caspary and Samuelsson (1934) record hybrids growing with one or both of the parents, and Caspary states that whole populations may consist entirely of hybrids, thus indicating that the isolating factors other than geographical are not very effective

2. *Viola.* Snow and Chattaway (1930) made the cross *V. hirta* ♀ × *V. odorata* ♂ and obtained vigorous hybrids which could be matched with wild plants and whose seed fertility was about one-tenth that of the parents; an F_2 generation was also raised. Both species occur fairly frequently in England but become rarer in Scotland and are absent from the far North. *V. hirta* is found mainly on calcareous soils, often in exposed grassland, and is rare and local in Ireland, while *V. odorata* is found on a variety of soils (Walters, 1946), often in shady situations, and is frequent in central Ireland. In Europe *V. hirta* is generally distributed; it occurs as far north as S. Sweden but becomes rare in the Mediterranean. *V. odorata* on the other hand is regarded by Meusel as a Mediterranean species, doubtfully indigenous in many of its northern stations. It may be noted that *V. odorata* is most abundant in Britain in south-west England and that many local floras, particularly of the north, record doubts as to its status. It thus appears that both ecological and geographical isolation are effective locally; but the species frequently meet and flower together, and hybrids are widespread and not uncommon.

3. *Melandrium.* An account of these species, including distribution maps, has been given by Baker (1948). The species are highly intercompatible and interfertile, so that there is little or no genetical isolation. Both are found over the whole of Britain. *M. dioicum* is typically a woodland plant which increases in frequency towards the north and west, while *M. album* is a weed associated with human activity, most frequent in the south and east of England. Both have a general European distribution, but *M. dioicum* extends further to the north and *M. album* further to the south and east, occurring in N. Africa and Asia Minor, where *M. dioicum* is absent. Thus, as in the species of *Viola,* both geographical and ecological isolation are locally effective, but the species often meet. Differences in flowering-time and pollination mechanism are contributory isolating factors, but hybridization often occurs, and in Britain at least, hybrid swarms are found.

4. *Silene.* Extensive hybridization experiments by Marsden-Jones and Turrill (1928-1950) have shown that these species are highly intercompatible and interfertile. Both occur throughout Britain; *S. cucubalus* is generally a lowland weed, thinning out in the far north, while *S. maritima* is found on beaches and cliffs round the whole coast, occasionally occurring also in the mountains (to a height of over 3000 ft. in Scotland). Outside Britain, *S. cucubalus* is found throughout Europe and Asia, but *S. maritima* is restricted to W. Europe, from Finland and Norway to Italy, Spain and the Canary Is. Thus, both geographical and ecological isolation are effective; in W. Europe the species occasionally meet, but in spite of the weakness of genetical barriers, hybrids are rare.

5. *Geum.* An account of the many experiments made on these species is given by Marsden-Jones (1930), who also obtained hybrids and showed that they were moderately fertile. (From published accounts and our preliminary experiments, it appears that the cross is successful only when *G. urbanum* is the female parent, and that even then it gives by no means a full yield of seed, so that genetical isolation is at least partially effective). In Britain, *G. urbanum,* a plant of woodland and waysides, is common practically everywhere in the lowlands; *G. rivale,* rare in S. England, is frequent in N. England and gradually thins out northward (see map); it is a plant of damp woods and hedges, but it also occurs in exposed places on hills and cliffs (to a height of over 3000 ft. in Scotland). (It may be noted here that the details of distribution of *G. rivale* in many parts of Wales, Scotland and Ireland are lacking; similar gaps occur in our knowledge of the distribution of many other species). *G. urbanum* is found throughout Europe and Asia and *G. rivale* covers a similar area, but goes a little further north and also extends to N. America. Thus, geographical isolation is not effective over most of the range of the two species, and ecological isolation only partly so,

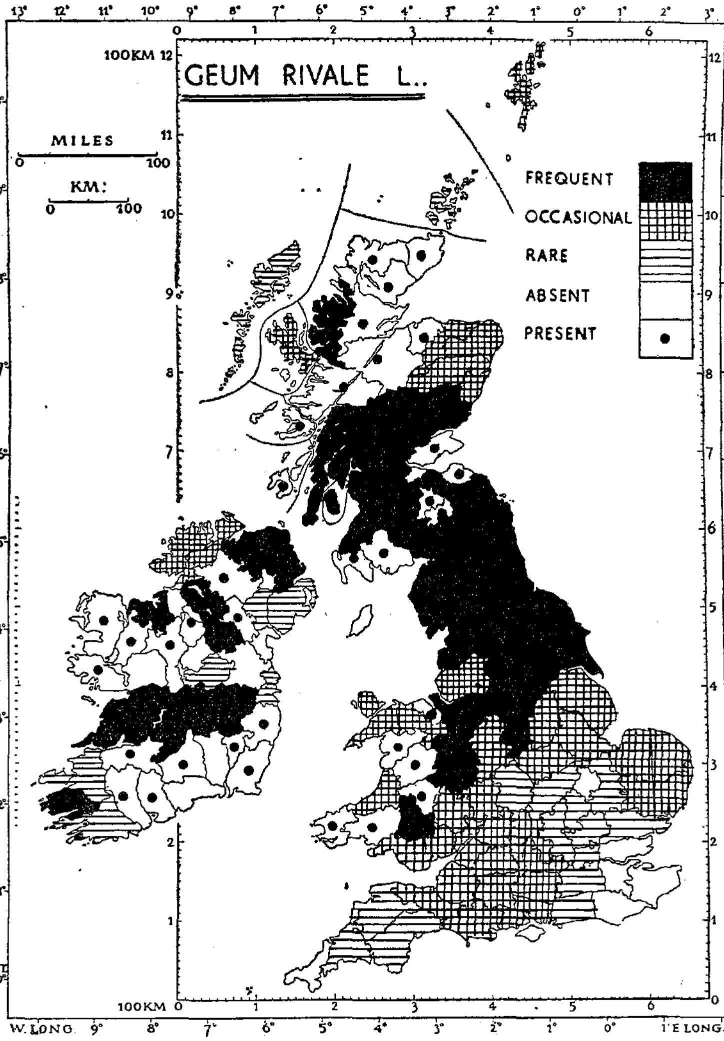


Fig. 20. Distribution of *Geum rivale* in the British Isles.
With acknowledgment to "The New Naturalist" for use of base-map.

but there is a difference in time of flowering. Where the species meet, as they often do, hybrids are generally found, and are in fact recorded from 85 vice-counties in Britain.

6. *Epilobium.* Compton (1913) and Geith (1924) have crossed these species and obtained hybrids. As in many other crosses in this genus, reciprocal hybrids differ in degree of infertility both on the male and on the female side; Geith obtained different results from Compton, but both obtained seeds from some of their hybrids. Both species are common in lowland Britain in marshy places, and it is difficult to distinguish their types of habitat, but *E. hirsutum* becomes less common in the north. Both too have a wide general range throughout Europe and W. Asia, but *E. hirsutum* extends further east and south, to China and S. Africa. The hybrid occurs rather rarely in Britain and occasionally in Europe. It seems likely that the scarcity of the hybrid is due to the high self-compatibility and low cross-compatibility of the species, for neither geographical nor ecological isolation appears to be effective. It may be noted that practically all the British species of the section *Lysimachion* are capable of forming partially fertile hybrids; the two closely related species described here have been selected as typical.

7. *Saxifraga.* Hybridization experiments by Dixon are reported and discussed by Scully (1916); reciprocal hybrids were obtained. *S. lactiflora* has a restricted distribution in Kerry and Cork, while *S. spathularis* has a wider distribution in S. and W. Ireland where it is the commoner plant. It is remarkable that the general distribution of the two species is very restricted and apparently almost identical; both are regarded as native only in N. Spain and Portugal, the Pyrenees and Ireland. Wild hybrids resembling those produced artificially occur in W. Ireland, and it was shown by Dixon that they were fertile. It is not possible to say at present what are the main isolating factors in this interesting case; more work on the taxonomy and the cytology of the species is needed.

8. *Primula.* A summary of hybridization experiments is given by Valentine (1947); reciprocal crosses give about a 20% yield of viable seed, and the seed and pollen fertility of the hybrid is about half that of the parents. *P. vulgaris* occurs throughout lowland Britain in woods and hedgebanks on a variety of soils, while *P. elatior,* as was shown by Christie (1897), is restricted to a small area in E. Anglia, where however it is abundant in damp woods on calcareous clay. *P. vulgaris* occurs along the western borders of Europe and in the Mediterranean, and is absent from Central Europe (Hegi, 1931), but *P. elatior* occurs throughout Europe and W. Asia, ascending higher than *P. vulgaris,* and overlapping its range only in the west and south. Geographical isolation is thus effective, but in the region of overlap hybridization may occur to a considerable extent (Valentine, 1948).

P. vulgaris also often hybridizes with *P. veris*; here, to geographical isolation of the same type as with *P. elatior* is added more marked ecological isolation; there is also a distinct difference in time of flowering.

9. *Salix*. Artificial hybrids between these taxonomically very distinct species have been made by Wichura (quoted in Focke, 1881) and Heribert-Nilsson (quoted in Turesson, 1929). Wichura found that reciprocal hybrids were identical and fertile and he made backcrosses; Nilsson obtained a segregating F_2 generation. Both species are fairly common in Britain, *S. caprea* in woods and hedges, *S. viminalis* in marshes and by streams, where it is sometimes planted; and both occur throughout Europe and Asia, though *S. viminalis* is less frequent in S. Europe. The hybrid is found occasionally in Britain, being recorded from 31 vice-counties, and is scattered throughout Europe; male hybrids are said to be rare. Geographical isolation plays little part here but ecological isolation is probably fairly effective.

10. *Quercus*. Experiments on artificial hybridization are reported by Focke (1881); some of the hybrids produced had normal pollen. Dr. E. W. Jones informs us that recent experiments by Dengler and others have shown that the cross is difficult to make and that, generally, only about 1% of the pollinations give viable seed. Both species are widespread in Britain and Tansley (1939) gives a good account of their distribution and ecology. *Q. robur* is generally dominant on the damper, heavier soils, *Q. petraea* on the lighter and more siliceous soils, especially in the north and west. The general distribution of the two species is similar in Europe, but *Q. robur* extends much further east, into Asia (Meusel, 1943). Wild hybrids occur in a number of places; thus Tansley states that in certain localities in S.E. England the species hybridize freely and produce a number of intermediate forms. It is clear that geographical isolation is important over only a part of the range of *Q. robur*. Where, as in Europe, the species meet, ecological isolation is probably effective; but the experiments that have been mentioned indicate that genetic isolation, due to low interspecific compatibility, may also play an important part. It may be noted that, in some of the other examples quoted, insufficient information about compatibility makes it difficult to estimate the importance of genetical isolation.

DISCUSSION. The information that has been presented can obviously be treated in a variety of ways, but this brief discussion will be limited to matters most closely concerned with geographical distribution. It is based on the useful hypothesis that pairs of ecospecies, of the type considered here, have arisen from a single ancestral form whose area of distribution has been divided into two or more parts. This primary geographical isolation leads to speciation; morphological divergence sufficient to merit taxonomic rank occurs, but for a time at least, the new species are capable of interbreeding and forming a moderately fertile hybrid. In some cases, geographical isolation persists, but in others, for various reasons, the species meet again in the same area, and we have a situation which is illustrated by our examples. Two points arise.

First, during the primary geographical isolation, the species have come to differ in many ways, morphologically, genetically, ecologically and so on. When they are brought together, these differences may either be sufficient to ensure that the species will persist as distinct entities, or they may be insufficient. If the latter is true, the species will not normally be able to exist together in the same geographical area, and will tend to fuse into a single polymorphic population. The *Nuphar* species show this tendency to fusion, and their maintenance as distinct species must depend largely on geographical isolation; but in the remaining examples, other forms of isolation are sufficient, in most circumstances, to allow the persistence of the species as distinct units even where they meet in the same area.

The second point is concerned with the discovery of the causes which have led to the coming together of pairs of ecospecies in the same area, i.e. to the breakdown of the primary geographical isolation. There appear to be two main reasons. The first is concerned with the effects of human interference. The fact that many plants are comparative newcomers to the British Flora is common knowledge; there is a continual influx of alien plants due to the activities of man, who not only causes them to be introduced, but also provides them with appropriate habitats in places where he has destroyed the natural vegetation. It is possible that both *Silene cucubalus* and *Melandrium album* fall into this class; thus, Baker (1948) believes that *M. album* has come into our flora in this way from its original home in S.E. Europe. In other words, the breakdown of geographical isolation between this species and *M. dioicum* has been artificial. In addition, destruction of woodland has driven *M. dioicum* to refuges in hedgebanks where it comes into contact with *M. album,* so that breakdown of ecological isolation is also due to man's activities; the result is the very extensive hybridization which occurs in S.E. England. In the case of the species of *Silene,* ecological isolation has remained effective in spite of the breakdown of geographical isolation.

The other main reason for the breakdown of geographical isolation is provided by climatic change. During the last million years, the whole of N.W. Europe has been subjected to a series of glaciations; there have been repeated and considerable changes in climate, and large areas have been cleared of vegetation for a time and then exposed to re-colonisation from the south and east. Thus conditions in Britain have been such as to suit first one species, then another, and the distribution we see now has to be interpreted in the light of this past history. For example, *Primula elatior* may occupy its present area as a result of a primary invasion when conditions suited it, to be followed by *P.*

vulgaris when conditions changed; or both invasions may have been simultaneous, one occurring from the south and west, the other from the east. At the present time climatic and other conditions are such that the species are roughly in an equilibrium, which, however, may shift in the future as these conditions change. Similarly, *Nuphar pumila* has probably retreated north and west in post-glacial times, to be followed by *N. lutea*; and the same may be true of *Viola hirta* and *V. odorata*, the latter reaching Britain only when the climate became warm enough, and spreading northward, at least to some extent, with the help of man. Similarly, *Geum rivale* may have preceded *G. urbanum*. Hybridization between these pairs of species is still frequent, though genetical isolation is important in all of them as well as ecological. Speculation as to the original homes of the species, at a time when geographical isolation between them was complete, is also possible; e.g. *Primula vulgaris* may have originated in S.W. Europe, *P. elatior* in E. Europe or W. Asia. In a number of the remaining cases, of which the *Epilobium* species provide the best example, practically all trace of the original geographical pattern has been lost, and the species have identical distributions over the greater part of their range; and it seems likely that this is related to their comparatively ancient origin, and to the repeated changes and migrations which have since occurred.

We can sum up our discussion by saying that, with closely related but taxonomically distinct species of the type considered here (gradual-ecospecies), isolating factors are of various kinds, but that, when only a small area, such as Britain, is considered, geographical isolation rarely plays the leading part; and that the extent to which the originally distinct areas of the species overlap or merge is a function sometimes of human activities, more often of climatic changes, recent or remote. If it were possible to extend this discussion to groups of gradual-ecospecies in relation to an extensive area, such as the whole of Eurasia, it is probable that we should have to assign a much more important rôle to geographical isolation; but such a treatment must be postponed until more genetical information, concerning a variety of genera, is available.

May I, in conclusion, make a practical suggestion which is relevant to the theme of this paper? I think it would be of use if the Society were to sponsor the compilation and publication of a list of the interspecific hybrids which occur in Britain and of their geographical distribution. The great value of Focke's work on *Die Pflanzen-Mischlinge*, which was published in 1881 and dealt with all the hybrids of the European flora, leads me to believe that a similar up-to-date work, even if confined to the flora of Britain, would both stimulate interest and promote intensive and critical observation.

I am indebted to the *New Naturalist* for the use of their standard map of the British Isles, and to a number of correspondents for helpful information.

References.

BAKER, H. G., 1948, Stages in invasion and replacement demonstrated by species of Melandrium, *J. Ecol., 36,* 96.

CHRISTY, M., 1897, Primula elatior in Britain (Its distribution, peculiarities, hybrids and allies), *J. Linn. Soc., 33,* 72.

CLAPHAM, A. R., 1946, Check-list of British vascular plants, *J. Ecol., 33,* 308.

COMPTON, R. H., 1913, Further notes on Epilobium hybrids, *J. Bot., 51,* 79.

DRUCE, G. C., 1932, *The Comital Flora of the British Isles.* Arbroath.

FOCKE, W. O., 1881, *Die Pflanzen-Mischlinge.* Berlin.

GEITH, K., 1924, Experimentell-systematische Untersuchungen an der Gattung Epilobium L., *Bot. Archiv, 6,* 123.

GILMOUR, J. S. L., 1932, The taxonomy of plants intermediate between Medicago sativa L. and M. falcata L. and their history in East Anglia, *B.E.C. Rep., 10,* 393.

HEGI, G., 1931, *Illustrierte Flora von Mittel-Europa.* Munich.

LÖVE, A. & D., 1948, *Chromosome numbers of northern plant species.* Reykjavik.

MARSDEN-JONES, E. M., 1930, The Genetics of Geum intermedium Willd. haud Ehrh. and its back-crosses, *J. Gen., 23,* 377.

MARSDEN-JONES, E. M., & TURRILL, W. B., 1928-1950, Researches on Silene maritima and S. vulgaris, *Kew Bull.,*

MAUDE, P. F., 1939, The Merton Catalogue, *New Phytol., 38,* 1.

MEUSEL, H., 1943, *Vergleichende Arealkunde.* Berlin.

SAMUELSSON, G., 1934, Die Verbreitung der höheren Wasserpflanzen in Nordeuropa, *Acta Phytogeogr. Suec., 6.*

SCULLY, R. W., 1916, *Flora of County Kerry.* Dublin.

SNOW, R., & CHATTAWAY, M. M., 1930, An artificial cross between Viola hirta and Viola odorata, *J. Bot., 68,* 115.

TANSLEY, A. G., 1939, *The British Islands and their vegetation.* Cambridge.

TURESSON, G., 1929, Zur Natur und Begrenzung der Arteinheiten, *Hereditas, 12,* 323.

TURRILL, W. B., 1940, Experimental and synthetic plant taxonomy, in HUXLEY, J., *The New Systematics.* Oxford.

VALENTINE, D. H., 1947, Studies in British Primulas I: Hybridization between Primrose and Oxlip (Primula vulgaris Huds. and P. elatior Schreb.), *New Phytol., 46,* 229.

——, 1948, Studies in British Primulas II: Ecology and taxonomy of Primrose and Oxlip (Primula vulgaris Huds. and P. elatior Schreb.), *New Phytol., 47,* 111.

——, 1949, The units of experimental taxonomy, *Acta Biotheoretica, 9,* 75.

WALTERS, S. M., 1946, Observations on varieties of Viola odorata L., *Rep. Bot. Soc. & E.C., 12* (6), 834.

THE GEOGRAPHICAL DISTRIBUTION OF THE BRITISH SPECIES OF THYMUS, AND A BRIEF ILLUSTRATION OF THE APPLICATION OF DISTRIBUTIONAL STUDIES IN ECOLOGY

C. D. PIGOTT.

THYMUS.

As, with the exception of a summary of Jalas' paper on Fennoscandinavian *Thymus* which has appeared in *Watsonia,* no account has yet been published in English literature, I must begin with a short survey of the taxonomy in order to explain the names I have used. At this point I must stress that my exhibit is rather precocious, and that a great deal remains to be done to show that all I shall say is supported by conclusive evidence—however, I have put it out with the hope both of stimulating interest and gaining assistance.

At the present stage of my investigations it appears that three distinct units in the genus *Thymus* occur in the British Isles. These, as my exhibit is planned to demonstrate, differ from each other in their morphology, ecology and geographical distribution. Furthermore, cytological examination has revealed that these three units are distinct in chromosome number and, I suspect that owing to this dissimilarity and to the apparent rarity of hybrids, they are genetically isolated. From the modern concept of the species I therefore agree wth Dr. Jalas in regarding these three units as specifically distinct.

These species can be separated by the following morphological characters:—

a. Plant with ascending shoots arising from a central, tufted, rooted portion, and with short runners. *Internodes of the flowering stems goniotrichous, that is with the hairs arranged in four rows along the corners of the stem, and the intervening faces almost glabrous. Inflorescence elongated and generally interrupted below, in well grown specimens. Leaves often quite large (up to 12 × 6 mm.), of rather thin consistency, with distinct petiole, and generally glabrous, rarely hairy .... *T. pulegioides* Linn.

aa. Plant extensively creeping, and the runners rooting freely at the nodes. *Internodes of the flowering stems not goniotrichous, but holotrichous or with alternate faces glabrous and hairy. Flowers of the hermaphrodite plants with long corolla tubes, and "showy". Inflorescence generally more or less capitate. Leaves small (seldom larger than 8 × 4 mm.), rather thick, often spathulate, glabrous or hairy, and with the nerves prominent on the lower surface in dried material.

  b. Plant forming a rather loose, straggling cushion. The lateral shoots along the runners tending to grow upwards and the internodes long. *Internodes of the flowering

stems more or less terete, holotrichous with short, down-curved, white hairs, evenly distributed ....
T. Serpyllum Linn. em. Miller.

bb. Plant forming a compact, flat carpet. The lateral shoots along the runners growing out horizontally, and the internodes short, so that the leaves tend to form a close mosaic. Leaves coriaceous, glabrous or hairy, sometimes quite woolly. *Internodes of the flowering stems

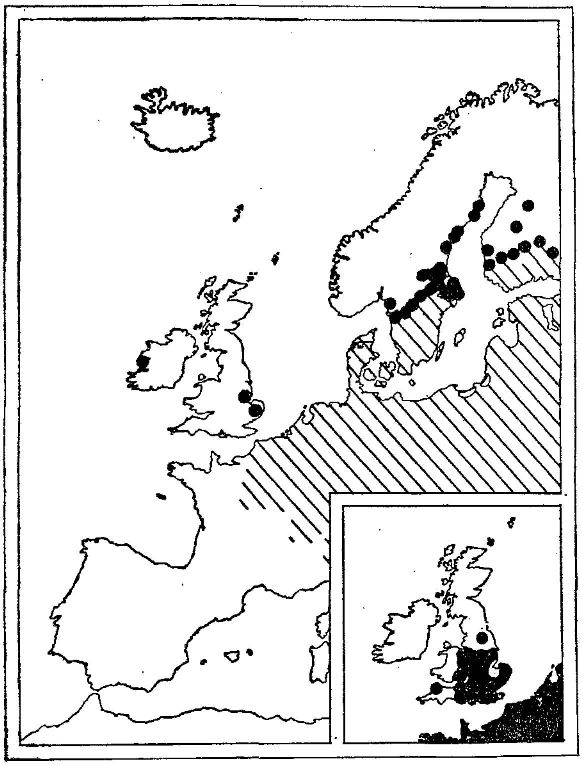


Fig. 21.

North and West European distribution of *Thymus Serpyllum* L. em. Mill. subsp. *rigidus* (Wimm. et Grab.) Lyka em. Jalas. Inset: Distribution in the British Isles of *Thymus pulegioides* L.

*The lower internodes of the flowering stem must be examined, and the internode immediately below the inflorescence neglected.

N.B.—The growth habit characters refer to ungrazed plants, growing in open, unshaded habitats. It is of interest to note, with reference to the growth form, that the common *T. "serpyllum"* of rock gardens, both in the British Isles and on the continent, is *T. Drucei*, which, with its close, matted growth, is most suitable.

quadrangular, with numerous, evenly distributed hairs on two faces, and with the alternate faces glabrous, or sometimes with a few, scattered, short hairs ....
T. Drucei Ronn. em. Jalas
(= *T. Serpyllum* L. em. Fr. ssp. *arcticus*
(Dur.) Hyl. em. Jalas).

The most widespread species in the British Isles is the oceanic *Thymus Drucei* Ronn. em. Jalas, occurring in Greenland, Iceland, the Trondelag region of Norway, the Faeroes, Scotland, Ireland, Wales and England, the west of France and perhaps the Pyrenees. This species has a somatic chromosome number of 54 and may be supposed to be of polyploid origin, and to some extent this explains the great variability it displays. The plant is a frequent member of the Atlantic heath formation on the less acid and better drained soils, and it occurs abundantly in limestone grassland; it is plentiful in the north and west of Britain but becomes rarer eastwards in England. This is the *T. Serpyllum* of most British

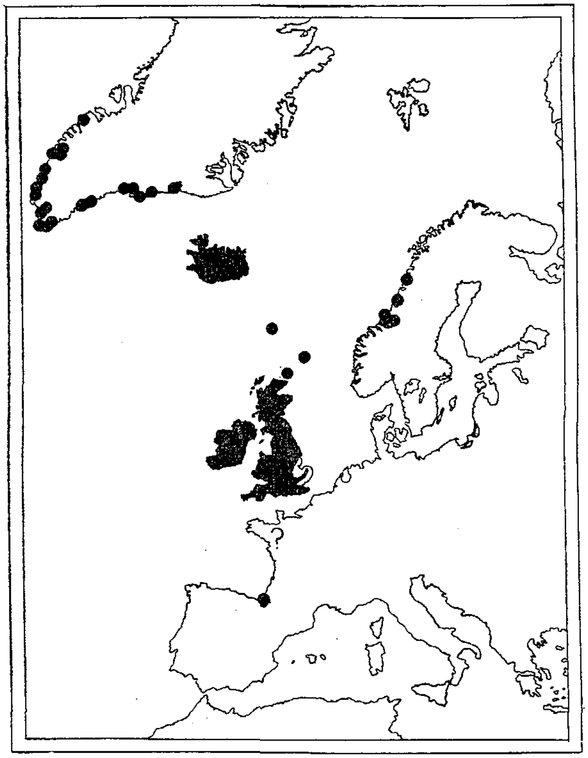


Fig. 22.

World distribution of *Thymus Drucei* Ronn. em. Jalas.

authors and includes most of the Ronniger segregates as distinguished in British material.

Thymus Serpyllum L. em. Mill. with a somatic chromosome number of 24, is ecologically a member of the continental "grass-steppe-sand-heath" formation. At present my studies have only revealed its occurrence in East Anglia and Clare in the British Isles, and this may well be a reflection of its continental nature although I expect it will prove to be more widely spread when more material has been examined. In Europe the species is widespread in the east, becoming rarer westwards and absent from the north of Sweden and the whole of Norway as well as the Faeroes, Iceland and Greenland.

The third species is *Thymus pulegioides* L. which has a somatic chromosome number of 28 and is plentiful in England but rare or absent in Wales, Ireland and Scotland. The continental distribution is very difficult to unravel and I have not attempted to exhibit a map. In England the plant is found both on the chalk downs and in limestone grassland generally, as well as on podsolised sandy heaths.

In conclusion with regard to *Thymus* may I add that the separation of the species in starved or incomplete specimens is often difficult, and that cultivation in garden conditions often results in the most remarkable phenotypic changes. To quote a writer in the *Phytologist* for 1853: "Should botanists not be able to do so [identify them], the sheep will, being the better phytologists: they will readily eat the one, but will not touch the other, on account of its pungency".

Studies of Plant Distribution in a Very Small Area.

In order to fill up at least one gap I will now pass on to a brief discourse on the value of studies of plant distribution in a very small area in relation to ecology. Much has already been contributed by previous speakers which has a direct bearing on this subject, and I should like to draw attention to the ecological data which can be drawn from such studies as Professor Good's book on the Dorset flora, from which I have taken one example. (A map of the distribution of *Filipendula vulgaris* was exhibited.)

Precise maps of the distribution of a species in a very small area form a valuable method of recording and assessing ecological data in general, and to demonstrate this I have taken a few examples from the work of Dr. Hugo Sjors on a bog complex in Bergslagen, Dalarna, Sweden. A special area (300 metres by 350 metres) was chosen and the distribution of important species mapped. The area consisted of two small *ombrogenous raised mosses, parted by a central soakway of *soligenous fen passing down into the marginal *eutrophic belt of *topogenous fen (called the *lagg*). In the *lagg* were situated two small springs, where water rich in base nutrients rises into the *lagg*.

*For defiition see Index.

Thus such an area contains a great variety of habitats, and the different regions in which species occur demonstrate the conditions that they require. It must be borne in mind, however, that each habitat includes a number of different conditions and that these interact in such a way that the influence of any one factor must be considered in relation to the others and cannot be singled out. (Examples taken—*Polygonum viviparum, Scheuchzeria palustris, Calliergon sarmentosum,* etc.)

To conclude, I will summarise by saying that the present distribution of a species is a direct reflection of its ecology in relation to the habitat conditions, both at the present day, and in the recent past. Therefore a close study of autecology is essential for a full appreciation and interpretation of a species' distribution, and the converse is equally true.

*Bøcher, T. W., 1938, Biological Distributional Types in the Flora of Greenland, *Meddelelser om Grønland,* 106.

Good, R., 1948, *A Geographical Handbook of the Dorset Flora.* Dorchester.

*Grøntved, J., 1942, The Pteridophyta and Spermatophyta of Iceland, *Botany of Iceland, 4,* Part I. København.

*Hegi, G., 1927, *Illustrierte Flora von Mitteleuropa, 5* (4). München.

Jalas, J., 1947, Zur Systematik und Verbreitung der Fennoskandischen Formen der Kollektivart Thymus Serpyllum L., em. Fr., *Acta Botanica Fennica, 39.* (Abstract in *Watsonia, 1,* 173-4.)

——, 1948, Chromosome Studies in Thymus, *Hereditas, 34.*

Jorden, G., 1853, Thymus Serpyllum and T. Chamaedrys, *The Phytologist, 4,* 1142-3.

*Mortensen, K. F., 1872, Nordostsjaellands Flora, *Bot. Tidskr., 5.*

*Rouy, G., 1927, *Conspectus de la Flore de France.* Paris.

Sjors, H., 1948, Myrvegetation i Bergslagen, *Acta Phyt. Suec., 21.*

This paper was discussed by Dr. D. P. Young who suggested that the observation reported in the *Phytologist* to the effect that sheep will eat one species of thyme and not another should not be lightly dismissed. He thought that taxonomists might with advantage pay more attention to biochemistry. However, terpenes may not be a reliable guide in this respect, as the same species growing under different conditions may yield oils of substantially different composition. Alkaloids seem to be much more specific, and a difference in the type of alkaloids present in a plant would be good support for taxonomic separation. Mr. Pigott replied that he had quoted the report as a matter of interest but he thought there was considerable doubt about the ability of sheep to discriminate between species of *Thymus.*

*Used for data employed in preparation of the maps reproduced.

A HISTORICAL APPROACH: SOME LATE-GLACIAL SPECIES FROM THE LOWER TEES AREA AND THEIR PRESENT DISTRIBUTION

KATHLEEN B. BLACKBURN.

I fear I must apologise to those members of my audience who make a serious business of mapping plants for a somewhat misleading title. I am really going to try to show how modern methods, particularly pollen statistics, have improved the possibilities of the historical approach to the subject of plant distribution.

The peg on which I propose to hang my remarks is a brick-pit at Neasham, near Darlington, in which, some time ago, an almost complete skeleton of an Elk or Moose (*Alces alces* or *A. malchis*) was discovered embedded in peat. The deposit was examined at the time but is now being re-investigated. Since the locality is relatively close to the area in which the notable rare plants of Teesdale occur to-day, the study of the plant remains at Neasham has a considerable added importance beyond its intrinsic interest.

Attention was first drawn to the Neasham locality by the discovery of the elk bones. The elk is not an extinct animal like the Irish giant deer: it occurs to-day, both in Europe and America, so we can find out something of its habits. One thing about this large, heavy, deer-like animal is its great fondness for water: apparently its food largely consists of plants growing in and near lakes and for this reason it often ends its days by drowning; as, apparently, did the elk at Neasham. The walls of the pit in which it was found consist of a red clay from which bricks are made and running through it is a peaty band. This band widens out at one place to a depth of about three feet and at the same time dips, once, no doubt, a deep place in a pool into which the elk stumbled and fell. A great deal of the importance of this find lies in the possibility of dating it, and it is the peat that must date the elk, rather than the reverse, since there are recorded occurrences of this animal in Scotland up to the 9th century (Ritchie, 1920).

A cleared face of the pit at this locality shows the red boulder clay at the base gradually becoming slightly laminated, indicating the beginning of water action, and then changing to a blue-black colour. Throughout this black clay are rhizomes, leaves and seeds of *Potamogeton praelongus* in extremely good preservation. Above is the peaty pond-bottom mud, here consisting of three layers. The bottom one, which at the right stage of drying will peel off in the thinnest layers like fine tissue paper, contains large numbers of diatoms and green algae, chiefly desmids, and small quantities of the seeds of *Potamogeton praelongus* and other water plants. Immediately above this is a very elastic mud with considerable mineral content. The third layer might be considered a real peat for it consists chiefly of the stems and leaves of *Hypnum scorpioides*. At various places in the quarry this mossy peat was found to contain large quantities of seeds, fruits and leaves from which the vegetation of the pond and neighbourhood could be reconstructed. Water plants were commonest and included *Carex rostrata,* species of *Myriophyllum,* species of *Potamogeton, Ranunculus aquatilis* agg., *Menyanthes trifoliata, Equisetum limosum, Chara* spp. and a *Nitella.* Of land plants the following were found: *Salix herbacea* and *S. phylicifolia, Betula pubescens* and *B. nana, Juniperus, Arctostaphylos Uva-ursi,* a *Vaccinium* and a fruit of some member of the Compositae which has, so far, not been matched among British species: one of the difficulties encountered in this technique is that of identifying species with certainty from seeds or even leaves.

The clay immediately above this peat contains most of the water plants mentioned above in small quantity, also *Selaginella* megaspores, an *Armeria* fruit and *Salix herbacea* leaves. For the first discovery of these I have to thank Mr G. F. Mitchell, M.A., of Dublin, who recently visited Neasham. *Salix phylicifolia* and *Betula nana* also occur there. It will be noticed that *Salix herbacea* and *B. nana* are plants which do not grow in Upper Teesdale now, though the other land plants mentioned do. Above these deposits is clay, amorphous and barren below, but laminated above and with layers of remains of *Myriophyllum verticillatum* and *Potamogeton.* Still further up is a structureless peat yielding results only to pollen analysis.

Let us for a few moments remind ourselves of the methods and possibilities of pollen analysis or, as it is frequently called nowadays, " palynology ". The technique has been most used for studying the changing forest flora in post-glacial time and consists of counting the pollen which is preserved in peat at a series of levels in the deposit, expressing the quantities of pollen of different trees as percentages of total tree pollen and deducing the forest succession of the area from these results. A diagram from a peat near Ridsdale in the County of Northumberland, some 45 miles further north than Neasham, represents the whole period from the end of the ice-age till the present time. Besides illustrating the characteristic regional forest succession, conforming well with the zonation worked out for England in general (Godwin, 1940), this diagram includes the amounts of the most frequently occurring herbaceous plants as percentages of the tree pollen. It is thus possible to discover when the county was completely forest covered, and when it was more sparsely wooded, by comparing the percentages of tree pollen and non-tree pollen at the different levels.

Recognition of less frequent constituents of the pollen-rain is frequently useful in indicating the local conditions, as well as giving evidence of the distribution of individual plants in past times. In the peat mentioned above the occurrence of *Typha* pollen illustrates the former and of *Polemonium* in the earliest post-glacial layers the latter.

We must now consider the results of examining the pollen from the Neasham exposure which are illustrated in Fig. 23.

The junction of the upper clay and the upper peat seems to correspond to the long recognized period at which alder percentages rise suddenly from low values to high ones. This is usually referred to as the Boreal-Atlantic transition of the Blytt-Sernander terminology and is represented in Dr. Godwin's (1940) zonation as the VI-VII boundary. The upper peat thus belongs to the forest period and is very rich in tree pollen, chiefly oak and alder, but elm, birch and lime are also present.

The lower peat, in which the elk was found, is comparatively poor in quantity of pollen and the tree pollen is chiefly birch, whereas the clays above and below it are very poor indeed and

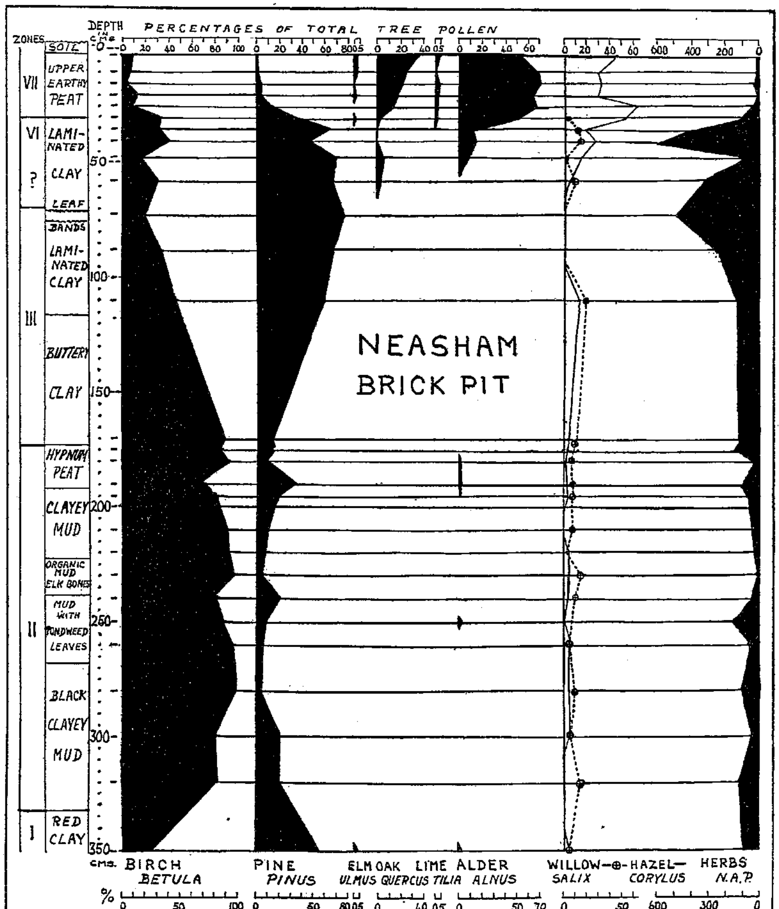


Fig. 23. Pollen Diagram of Late-Glacial Peat from Brick-Pit at Neasham, near Darlington.

the tree pollen is mainly pine. In the clays, non-tree pollen, chiefly grass and sedge, predominates, whereas in the peat birch grains are in the majority. This poverty of pollen might suggest that growing conditions were not good but the implication from my title that the deposit belongs to the end of the ice-age, and not to post-glacial times, needs further consideration.

We must remind ourselves that pollen analysis is a statistical method which depends for its conclusions on the fact that it is a regional study, and consider the results obtained by investigations of the final stages of glaciation in N.W. Europe. There, in many ways, the retreat stages of the last ice-age are clearer, and to them we must look for our geographical evidence.

The last advance of the ice sheet which covered Scandinavia is indicated by a series of terminal moraines, referred to as the Fennoscandian line, passing over parts of S. Sweden and appearing again in Finland, as the name suggests. The rapid retreat from this line is considered the beginning of post-glacial time.

De Geer, studying layers of clay deposited in the deltas of glacial lakes, noticed laminations which he referred to as *varves*. He believed these to be annual deposits and by skilful piecing together of successive depositions came to the conclusion that the time of the moraines was from 8300-7874 B.C.

The west of Denmark was not covered by the last advance of the ice, but the evidence of frozen soils shows that arctic conditions returned to a land which was beginning to warm up and change from tundra conditions to open birch forest. Stratigraphically this temporary warm period is often shown by an organic deposit, such as a lake mud, separating two layers of varved clay. This succession was first observed at a place called Allerød and is referred to as the Allerød oscillation. On the continent the arctic nature of the top and bottom layers, which are referred to as periods I and III, is shown by the presence of *Dryas* (Dryas clays). A map illustrating the general distribution of the known Allerød deposits will show them chiefly in Denmark and the southern shores of the Baltic Sea, but a considerable number are now recorded for Ireland, for which we are indebted to Prof. Jessen and Mr. Mitchell. In Ireland there is however a difference; the arctic clays seldom show *Dryas*; their characteristic plant is *Salix herbacea.* Now if you look at the Neasham diagram you will see that we have, below, a similar succession: clay, pond peat, clay; and, above, more peat. Such oscillations have occurred through the whole Ice age and care is necessary. Prof. Jessen realized this and, when describing the deposits at Ballybetagh, is cautious about correlation, but after studying many more deposits and noticing that the association of plants in the two areas was astonishing similar, he now considers the Irish oscillation to be equivalent to the Allerød on the continent (Jessen, 1949). Perhaps the case may be compared to the post-glacial correspondence of forest succession through the same areas. Just as in post-glacial time there are differences between E. and W. and between N. and S., due to geographical causes, so also in late glacial time differences are to be expected. Firbas (1939) has pointed out that at the time when N. Germany and Denmark were in a tundra condition with no trees, the land to the E. and W. of the ice-covered Alps carried birch and pine forest of varying density whereas further south deciduous forest occurred. The tundra condition followed up the retreating ice and the region of birch scrub also moved north in time of increased warmth and both retreated when the ice readvanced. This oscillation is just what is found in the deposits of the Allerød type: Periods or Zones I and III represent tundra conditions in our latitudes with the characteristic plant either *Dryas* or *Salix herbacea* and no trees. Zone II, the Allerød itself, is a warmer phase in which there is evidence of considerable quantities of *Betula pubescens*. There were also many more species of herbaceous plants at this time. Considering the Neasham deposit, besides the plants already mentioned as discovered from macroscopic remains, there are two, of exceptional interest, found by means of their pollen grains alone: *Helianthemum canum* and some species of *Artemisia*. The significant point of the total list from Neasham is that almost all of the plants identified are characteristic of the Allerød oscillation elsewhere and this gives some further justification for the assumption of this dating for the peat. One puzzle is provided by the occurrence of small quantities of the pollen of hazel, which certainly would not be expected to grow there in Allerød times. Its presence can only be explained by suggesting that it has blown very long distances from S. Europe, just as pine pollen found in Zones I and III is assumed to have done in most of the profiles containing Allerød deposits.

Now considering the present distribution of the plants recorded from the Neasham brick-pit we find that only three do not at present grow in Teesdale—*Potamogeton praelongus, Betula nana* and *Salix herbacea,* though all are found in the British Isles to-day. On the other hand *Dryas octopetala* which is characteristic of the Arctic beds Zones I and III on the continent has not, so far, been found*, yet it grows on Cronkley Fell, in Teesdale, to-day, in company with *Helianthemum canum.*

If we look at present world distribution for the plants involved there are notable differences between them.

Most of the species recorded for Neasham have an arctic area of distribution and most occur in Iceland and Northern Scandinavia, but, on the other hand, all are now living somewhere in the British Isles. The most extreme Arctic-alpines are *Betula nana* and *Salix herbacea. Salix phylicifolia* and *Selaginella selaginoides* are among the sub-arctic forms with alpine distribution (Jessen, 1949).

There is a group of Arctic-Subarctic species widespread in Europe and, as Jessen points out, reaching above the birch zone

*Two fruits of *Dryas* have since been found by Mr. G. F. Mitchell.

in the mountains of Norway: among these are *Juniperus, Menyanthes, Armeria, Carex rostrata* and *Myriophyllum spicatum.* Some reach the arctic circle though not the mountains of Norway; to these belong *Potamogeton natans* and *P. praelongus.* Two remaining plants of the Neasham deposit do not come into the category of arctic plants. The species of the *Artemisia* is difficult to determine, but none of the likely species occurs in the arctic, and it is much more probable that it is a species of the steppes with its main distribution now in Central Asia.

The *Helianthemum canum* at first seems more definite, but again, it is only an aggregate name for a group of species. The pollen of *H. canum* has not so far been distinguished from that of *H. oelandicum,* the endemic species of Oeland, and a map of present localities must perforce include even the Mediterranean subspecies, although the more northern forms are the likely ones and the Neasham one, in particular, may well be the *H. canum* var. *vineale* of Cronkley Fell.

What then can be deduced from the late-glacial fossil plant and animal remains concerning the landscape of that day?

Iversen, describing conditions on the continent, sees a narrow band of real tundra behind the advancing ice, though he thinks that perhaps it was not as cold as the tundra we know. Behind that, " park-tundra " was found with patches of birch trees at more and more frequent intervals of gradually becoming real birch forest. In the park-tundra the open land between the trees carried a variety of plants and in many places probably not in closed communities. The vegetation seems to have had some of the characters of tundra, large amounts of grass suggestive of steppe and some of the features of the alpine flora of central Europe. Steppe animals, Bison, Elk and Irish Giant Deer, roamed in this park-tundra and only disappeared with the approach of closed forest.

Iversen's picture for the continent can be applied to the Teesdale area to give a picture of its changing flora. The land exposed after the retreat of the ice was covered with a tundra vegetation between the numerous lakes in which *Potamogeton praelongus* was a conspicuous feature. Later the climate improved and, in addition to the surviving *Salix herbacea, Betula nana* and other tundra plants, a scrub of *Betula pubescens, Salix phylicifolia, Sorbus aucuparia* and *Juniperus* appeared with *Arctostaphylos Uva-ursi, Vaccinium, Armeria,* and *Helianthemum* growing between the trees. A return of cold conditions killed off the less hardy plants, and in particular the *Betula pubescens,* giving tundra conditions once more. The final warming up of the climate finds the Neasham site covered with oak-alder forest in close stand; the plants of open habitat and of arctic-alpine type have disappeared and have only survived in the upper reaches of the Tees where they remained undisturbed in a habitat favourable to them.

REFERENCES.

FIRBAS, F., 1939, Vegetationsentwicklung und Klimawandel in der mitteleuropäischen Spät- und Nacheiszeit, *Naturwiss., 27,* Heft 6.

GODWIN, H., 1940, Pollen analysis and Forest History of England and Wales, *New Phyt., 39,* No. 4.

JESSEN, K., 1949, Studies in Late Quaternary Deposits and Flora History of Ireland, *Proc. Roy. Irish Acad., 52,* B, No. 6.

JESSEN, K., & FARRINGTON, A., 1938, The Bogs of Ballybetagh, near Dublin, with remarks on Late-Glacial Conditions, *Proc. Roy. Irish Acad., 44,* B, No. 10.

IVERSEN, JOHS., 1945, in The Bison in Denmark, *Dan. Geol. Unders., 2,* Nr. 73.

MITCHELL, G. F., 1940, Studies in Irish Quaternary Deposits, some lacustrine deposits near Dunshaughlin, County Meath, *Proc. Roy. Irish Acad., 46,* B, Nr. 2.

RITCHIE, J., 1920, *Influence of Man on Animal Life in Scotland.* Camb. Univ. Press.

This paper was discussed by MISS LONGFIELD. She said that although the American Elk or Moose (*Alces americanus*) is exceptionally fond in summer of aquatic vegetation for food, both it and the European Elk (*A. machlis*) spend the greater part of their lives in forests, feeding on the buds, twigs, leaves and bark of both coniferous and deciduous trees; the European Elk, at least in Scandinavia, frequenting rather dry woods and browsing often on young maples. She therefore considered that it would not be peculiar if hazel pollen were found in the same deposits as the Elk skeleton as presumably its feeding habits had been much the same as those of the present-day species.

THE SEQUENCE OF THE PLIOCENE AND PLEISTOCENE BRAMBLE FLORAS IN *PERIGLACIAL S.E. ENGLAND (Exhibit)

W. C. R. WATSON.

The line followed in this investigation was to find datable deposits or geomorphological features of Pliocene and Pleistocene age; to identify the bramble species now growing upon them; to discover the distribution of those species in Britain and on the Continent; and then, taking into account the observed means of

*Periglacial—lying beyond the limits reached by the ice-sheet at its maximum extension.

migration and †ecesis, to consider to what conclusions the evidence pointed.

At the Conference lists of the significant species were shown, together with a few selected specimens and a geological section from the Weald watershed to the Pliocene R. Thames running into the North Sea at the R. Blackwater estuary in Essex.

PLIOCENE.

Relict floras were found:—

1. On the Forest Ridge around and to the south of Tunbridge Wells, on Waterdown Forest and Ashdown Forest.
2. On the Lower Greensand Range of extreme E. Surrey and W. Kent at 500-700′.
3. On the North Downs and Lower London Tertiaries above the Lenham Sea coast-line; on the actual Lenham deposits where they still remain; and on the Eocene beds from which the Pliocene deposits have been denuded, down to 250′.
4. On isolated hilltop Lenham gravel deposits in N. Kent and S. Essex, especially Shooter's Hill (424′).

A greater amount of Continental influence is evident in E. Kent.

5. On and near the Lenham deposits on the Downs east of the R. Stour at 600′-500′; and also, especially,
6. On a late Pliocene southern drift at 250′ around Bigbury and Chartham Hatch.

PLEISTOCENE (Interglacial and ‡interstadial).

7. The species occurring on the four successive Lower Thames Gravel terraces in Bucks, Surrey and Kent were listed at nine localities.

Observation in nature and experimental culture, in shade and in exposed situations, on clay and on sand, supplied information as to the effects of frost and snow, heat, drought and excessive moisture upon seeds, seedlings and mature plants. Brambles are pre-eminently forest plants and there can be no doubt that from several causes the Forest Ridge and the Greensand supply ideal conditions for their growth. Continental and home ranges and stations of the species concerned were considered.

The facts found are consistent with the preservation of many Pliocene species on the geological levels given under 1 to 6 above. Their antiquity is sometimes attested by their occurrence as outliers separated from the main mass by barriers subsequently but

†Ecesis—the germination of a seed after its arrival in a new area, its development to a mature plant and its multiplication into a family of descendants.

‡Interstadial—the temperate interval coming between the advance and re-advance of the ice-sheet within each of the series of Pleistocene glaciations.

anciently created; and by the absence of the distinctively Pleistocene species.

Some of the characteristic species have been looked for and found at comparable geological horizons on the Chilterns, in Savernake Forest, and on the Wiltshire Downs.

On the Forest Ridge and more particularly on the Greensand and Pliocene hilltop gravels there are many links with the West of England bramble flora, suggesting a former continuity of distribution, now broken by the S. Hants.-Surrey flora which is in sharp contrast with that of W. Kent.

THE DISTRIBUTION OF THE DIGITALIS PURPUREA COMPLEX (Exhibit)

V. H. Heywood.

The genus *Digitalis* shows two main centres of development—west Mediterranean (Iberian) and east Mediterranean (Balkan-Anatolian). In the west the *D. purpurea* aggregate comprises the major part of this development.

It is not often realised that the *D. purpurea* of this country is only one segregate of a wide-ranging species. The following table sets out the components of the *purpurea* complex and their distribution:

Segregate	*Distribution.*
D. purpurea L., *sensu lato*	W. & C. Europe, N. Africa
ssp. *purpurea*	
var. *purpurea*	Throughout the species' range
f. *alpina* Rivas Goday	Spain, Portugal
var. *gyspergerae* (Rouy) Burnat	Corsica, Sardinia
var. *nevadensis* (Kunze) Amo	S. Spain (Sierra Nevada)
var. *albarracinensis* Pau & Senn.	N.E. Spain
var. *tomentosa* (Hofm. & Lk.) Brot.	Portugal, Spain, Italy
var. *mauretanica* Humb. & Maire	N. Africa
var. *toletana* Font-Quer	C. Spain
ssp. *mariana* (Boiss.) Rivas God.	S. Spain (Despeñaperros)
ssp. *thapsi* (L.) Font-Quer	Portugal, Spain
D. dubia Rodriguez	Balearic Is.
D. amandiana Sampaio	Portugal
D. miniana Sampaio	Portugal

Rivas Goday (1946) has suggested that this array of variants has been derived from a Tertiary archetypal form by three series of migrations: an Atlantic, a Tyrrhenic, and a Balearic. The first of these engendered, *inter alia,* var. *purpurea.*

In the British Isles only var. *purpurea,* the typical form, occurs; it is essentially oceanic in climatic-type and is oxyphilous, but the evolutionary development in the Iberian Peninsula has been towards xeromorphy (var. *tomentosa,* ssp. *thapsi,* ssp. *mariana*), and one form, *D. dubia,* is a calciphile.

The two varieties referring to stem indumentum of plants in this country (var. *nudicaulis,* var. *pubescens*) should be noted; a summary of the other minor variants occurring in this country is given by Turrill (1948). These are, however, forms of the typical race of *D. purpurea.*

This type of distributional pattern—of a wide-ranging polymorphic species represented by only one race in this country—is not uncommon. Attention is drawn to it as it is thought that it might help towards solving some of our distributional problems if more consideration were given to the extra-British distribution and variation of the species of our flora.

Specimens and figures of most of the above forms were exhibited together with a table showing the distribution of the whole genus.

References.

RIVAS GODAY, S., 1946, Sobre la Habitacion de la Digitalis purpurea L. (sensu lato), *Anal. Inst. Mutis Farmacogn.,* 5, 9, 123. Madrid.

TURRILL, W. B., 1948, *British Plant Life,* 226. London.

THE TOPOCLINE IN ULMUS CORITANA Melville (Exhibit)

R. MELVILLE.

The Coritanian Elm is an example of a plant in which continuous variation occurs within the natural range of distribution of the species. This variation does not occur haphazardly but follows a regular topographical sequence, and is conveniently referred to as a *topocline.* That is not to say that every individual in any one locality will be of the same form, although on occasion this may be so, but rather that the nature of the population changes in a fairly regular manner as one proceeds across the range of the species in a particular direction.

In *Ulmus coritana* slightly asymmetrical round-leaved forms occur in the southern parts of the specific range in southern Essex and to the north of London. Strongly asymmetrical narrow-leaved forms are found in the central and northern parts of Norfolk. Forms with leaves of intermediate shapes occur in the intervening region and to some extent mingle with the narrow-leaved forms in the north and the round-leaved forms in the south.

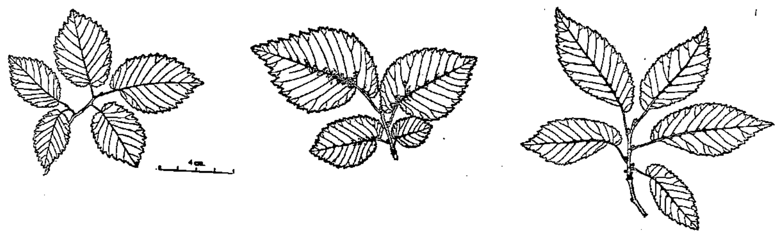


Fig. 24. The end and middle terms of the topocline in *Ulmus coritana* are represented by these short shoots from var. *rotundifolia* (left), var. *angustifolia* (right) and var. *media* (centre).

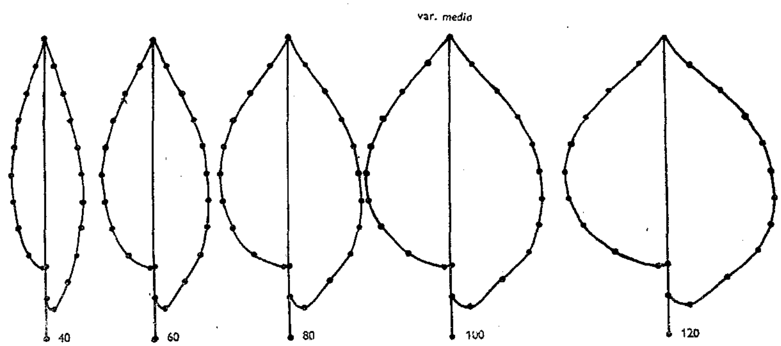


Fig. 25. A series of leaf shapes calculated from the mean leaf shape of subdistal leaves of *Ulmus coritana* var. *media* Melville (100) forming part of an arithmetical series differing only in breadth. The numerals indicate percentage breadths.

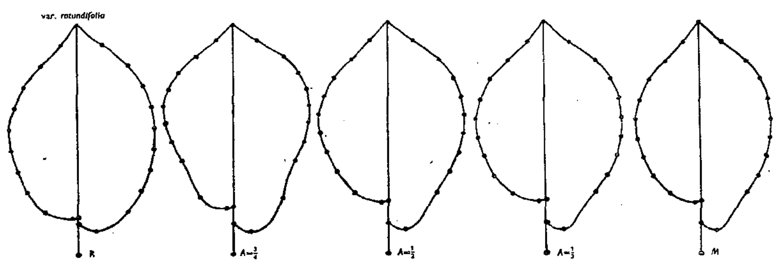


Fig. 26. A series of leaf shapes calculated from the mean shape of subdistal leaves of *Ulmus coritana* var. *rotundifolia* Melville (R), illustrating the nature of the differences in leaf shape between var. *rotundifolia* and var. *media*.

The Topocline in *Ulmus coritana* Melville.

Reproduced with permission from *Journ. Linn. Soc., Botany*, **53**, 263-271, 1949

Narrow-leaved forms have not been found, so far, in the south, nor broad-leaved forms in the north.

A series of herbarium sheets was exhibited to demonstrate the changes in leaf-shape correlated with the distribution of the species in East Anglia. This was supplemented by the distribution map and the drawings used in illustration of the original description of *U. coritana* in *J. Linn. Soc., Bot., 53,* 263-271, 1949. The existence of a wide range of intergrading forms within a species may provide a difficult problem for the taxonomist. It is obviously impracticable to describe every form. Where, as in *U. coritana,* the sequence of variation is linked with distribution, it can be described as a topocline, which may be sufficiently defined by stating its limits and the mean. This plan was carried out by describing a typical median form as var. *media,* while the round-leaved and narrow-leaved ends of the sequence were defined as var. *rotundifolia* and var. *angustifolia* respectively.

The characteristic leaf shapes occurring on normal short shoots of the three varieties are shown in Fig. 24. The leaves are of a bright, rather yellowish-green and somewhat coriaceous in texture. The serrature is rather blunt and axillary tufts of hairs are usually well developed in the vein axils along the midrib on the lower surface of the leaf. In habit, the tree is rather spreading, with ascending to spreading branches well spaced and giving a more or less open crown.

For the purpose of studying the variation, measurements were made of the distal and subdistal leaves (i.e. the apparently terminal and the next below it) of normal short shoots of a number of individuals by a method earlier described (*Ann. Bot.,* Lond., n.s. *1,* 673, 1937). The mean leaf shape of subdistal leaves of the type tree of var. *media* is shown in Fig. 25, the outline being drawn to pass through the tips of the serrations. The forms linking var. *media* with var. *angustifolia* differ mainly in the breadth of the leaf. Once the coordinates needed to define one of these leaf shapes have been obtained, it is a simple matter of proportion to alter the breadth without altering the other elements of the leaf shape. The outlines in Fig. 25 form part of an arithmetical series calculated from the mean shape of var. *media* as 100. The 60 per cent. member of this series closely resembles the shape measured from the type of var. *angustifolia.*

The transformation of the leaf shape of var. *rotundifolia* into something resembling that of var. *media* is slightly more involved. Here the most striking difference is a marked increase in the asymmetry of the lower half of the leaf while the upper half and the relative breadth remain almost unaltered. Supposing the leaf were elastic and decreased regularly in elasticity from the base to the apex, the effect is such as one would obtain by holding the tip and pulling the petiole to increase the length of the leaf. Such treatment would cause the base to elongate much more than the apex. In treating the problem mathematically, it was assumed that the extension decreased logarithmically from base to apex. The effect of applying different logarithmic factors without altering the breadth measurements is shown in Fig. 26. When the factor $\frac{1}{3}$ is used a close approximation to the shape of var. *media* is obtained and by adjusting the breadth measurements in arithmetic proportion, as at *M*, the shape is a very close fit to the measured shape of var. *media* in Fig. 25.

The control of leaf shape within the plant is, presumably, governed by a balance of growth-promoting hormones. Evidently different growth balances are reached in different individuals. In *U. coritana* the balance of growth factors appears to change in a comparatively regular manner as one passes across its territory from north to south. One would suppose that environmental factors must be in some way responsible for the changes. What these factors are is an open question. Changes in temperature, rainfall and other meteorological factors, across such a comparatively small distance as the 100 miles or so of English countryside in which the cline occurs, do not seem to provide an adequate explanation. Nor have I been able to link up any soil changes that might be responsible.

THE ANTARTIC ORIGIN OF SOME BRITISH "CARICES" (Exhibit)

E. Nelmes.

The word "Carices" in the above heading is in quotes, because if my theory of their Antarctic origin be correct they are not true *Carices* but derived from *Uncinia* or uncinioid ancestors. The species under consideration are *Carex microglochin* Wahlenb. and *C. pauciflora* Lightf.

The genus *Uncinia* is a very natural one. There are about thirty known species and they all have a terminal, unispicate, androgynaeceous inflorescence, their utricles are usually nerveless, often with a plumbagineous surface, often gradually tapering above to a beakless or shortly beaked, truncate-hyaline apex. There is invariably a vestigial axis or rhachilla arising from the base of the ovary, adpressed to the mature achene, protruding, usually considerably, from the mouth of the utricle, and strongly hooked at the apex.

It is extremely likely that *Uncinia* has had an Antarctic origin. Its present area of distribution comprises the western half of South America, the eastern half of Australasia and Malaysia, and most of Polynesia. In addition to this large south Pacific area, the genus is linked up across the ocean south of South Africa.

There is one species of *Uncinia, U. Kingii* Boott, restricted to extreme South America, the hook of which is much less strongly developed, and it is not difficult to accept this as a transition

BRAINS TRUST

Question Master—Mr. J. S. L. Gilmour.

Mr. J. P. M. Brenan.	Dr. J. M. Lambert.
Dr. R. C. L. Burges.	Dr. W. B. Turrill.
Mr. R. A. Graham.	Prof. T. G. Tutin.

The following selection from the questions put to the Brains Trust, with summaries of the replies, has been chosen from those which had some reference to the subject of the Conference.

Can the Brains Trust give a definition of "growing wild"—as distinct from "cultivated"—with particular reference to the admission of a species as a wild plant in a Flora?—"YARD-STICK".

DR. TURRILL suggested that a "wild" plant might be defined as one that had not been deliberately sown or planted and had extended itself by natural means—this held good even if the plant grew in a garden. PROF. TUTIN agreed, but thought that for the purpose of a Flora it was necessary to qualify the definition so that only species which maintained themselves by seed or as perennials for a number of years, or occurred repeatedly, were included.

DR. LAMBERT thought that the idea of competition was important. She thought that plants growing on a waste space had less claim to be considered "wild" than those in natural communities such as *Impatiens capensis* found in primary swamp.

MR. BRENAN thought that to insist on a species withstanding competition before it could be regarded as "wild" raised difficulties. He instanced open communities on sand-dunes where aliens frequently got established and were subject to little competition.

DR. BURGES also thought that insistence on withstanding competition narrowed the field too much. Plants found on rubbish dumps sometimes spread and grow freely in competition elsewhere. Perhaps the solution might be to include such plants in a Flora in brackets. PROF. TUTIN remarked that some undoubtedly native species, such as *Aira praecox,* avoided competition. DR. LAMBERT said that by competition she intended competition with external factors as much as competition with other species. Larkspur could maintain itself from seed in gardens. DR. TURRILL said that if a gardener did not want such plants he said they were 'going wild'.

In summing up MR. GILMOUR remarked that the discussion had brought out very clearly the distinction between "growing wild" and "being native"—two concepts often confused.

Should future local floras follow the main lines of the "Flora of Gloucestershire" or those of Good's "Geographical Handbook of the Dorset Flora"?—"IGNOTUS".

MR. GRAHAM thought that if a local flora was intended to serve the purposes usually associated with such works it should follow Gloucestershire. PROF. TUTIN suggested that perhaps local floras would be unnecessary when the projected series of maps was published!

DR. BURGES thought that the answer must depend on whether a comprehensive Flora on traditional lines had already been issued for the area concerned. If so it might be desirable to break new ground, but a volume of the Gloucestershire type was most desirable for every county. PROF. TUTIN remarked that plants which catch the eye often do not get detailed localities in local Floras. Botanists should record the common plants more. For example, in Leicestershire *Chenopodium Bonus-Henricus* was more local and less plentiful than *Atriplex hastata* but one would not suspect this from the *Flora* where a long list of localities is given for the former and no specific ones for the latter.

MR. BRENAN thought that the proper function of a county Flora was twofold—it should show the distribution of plants in relation to (1) the geography of the county and (2) soil and other similar factors.

MR. GILMOUR summed up by saying that the discussion had shown that there would still be a need for local Floras, even of the modified kind, after the project for the publication of the maps had got under way.

Some people are very fond of transplanting rare and beautiful wild flowers to fresh localities either for experimental purposes or, as they say, to increase a thing of beauty. Should this be deplored or encouraged?—"COUNTRY-LOVER".

PROF. TUTIN said that such actions were to be deplored and especially if the person doing the transplanting had no serious reason for it. When experiments were necessary they should be recorded in a suitable journal—such as *Watsonia*. MR. GRAHAM concurred but thought there was one justifiable exception—when it was necessary to transplant a rare species otherwise doomed to certain destruction. He instanced *Schoenus ferrugineus* which would be "drowned" by the raising of the level of Loch Tummel. DR. BURGES thought that even this exception should not be made; he deplored the whole thought of moving plants.

DR. TURRILL suggested that the views of his colleagues on the Brains Trust were too extreme. He thought that knowledge would be advanced by establishing scheduled transplant areas for experimental purposes. Such areas should be set up fairly widely over the British Isles and kept under strict control. DR. LAMBERT thought that in such an idea very careful consideration should be given to what would happen when the experiments came to an end; surely there was a risk that transplanted species might extend outside the areas.

As an example of a justified transplant into a natural habitat, DR. TURRILL mentioned the male *Ranunculus acris*. Only one plant was found—only one had ever been found. This was dug up and multiplied vegetatively and then one part was sent back for replanting in the place where it was found.

MR. GILMOUR in summing up suggested that the projected National Nature Reserves might be able to supply limited areas for transplant experiments under constant supervision.

Will the Brains Trust please explain the meaning of the word "Cybele" in "Cybele Britannica"?—ANON.

This led to some interesting observations and, with help from the body of the hall, *Cybele* was explained as a term introduced by H. C. Watson to describe a systematic treatise on the geography of the plants of a specified area, being applied by analogy with the term *Flora* which has long been used for a systematic description of the families, genera and species of an area. In Greek mythology, Cybele was the Phrygian goddess of nature and fertility and was chosen by Watson as a suitable parallel to Flora, the Roman goddess of flowers.

(See H. C. Watson, 1847, *Cybele Britannica, 1,* 2.)

Does the Brains Trust view with alarm Dr. Valentine's suggestion that the Society might compile a sort of Comital Flora for hybrids?—"MONGREL".

PROF. TUTIN thought that it was worthwhile recording the distribution of hybrids which reproduced vegetatively (e.g. *Mentha*), and also apomicts which showed a gradation to plants known to be straight hybrids.

DR. TURRILL thought that it was first necessary to define the term "hybrid"—did it mean in this case hybrids between species? He thought that experimental evidence was essential before such a list could be published and he was strongly opposed to guessing hybrid origin from no more evidence than morphological characters provided. He suggested that many recorded "hybrids" may be merely mutations.

DR. LAMBERT stressed the lack of permanence of many hybrids which made them unsuitable for a work on the lines of *Comital Flora*. DR. TURRILL then reminded the meeting that a number of plants entered as "species" in published lists of the British flora are really hybrids—for example the hybrid swarms of *Centaurea* which occur in Britain and Holland and perhaps elsewhere.

Finally, DR. VALENTINE was asked if after hearing the discussion, he still thought his suggestion could be carried out. He replied that he still thought a list of interspecific hybrids with British records could and should be prepared.

CONCLUDING REMARKS BY THE PRESIDENT

Mr Gilmour, in his concluding remarks, referred to the various concrete proposals that had been put forward, and especially to the plan outlined by Professor Clapham for the preparation and publication of a series of distribution maps of the British Flora; it had been agreed that this should be referred to the Council of the Society for consideration and action.

He hoped that the proceedings of the Conference would be published by the Society as were those of the last one in 1948. In conclusion, Mr. Gilmour thanked all those who had contributed to the success of the Conference, both as speakers, exhibitors, organisers and helpers and he mentioned particularly Dr. J. G. Dony, Hon. Secretary of the Field Work Committee, and Mr. W. R. Price, Hon. Assistant Secretary of the Society.

FIELD MEETING AT QUENDON WOOD, N. ESSEX, SUNDAY, APRIL 2, 1950

On the day following the Conference a party of about 60 members and visitors travelled to Quendon Wood by coach to study *Primula elatior* (L.) Hill, under the leadership of Dr. D. H. Valentine and Mr. H. and Miss D. Meyer.

The species was chosen as offering an early flowering example of a plant with a very interesting and restricted distribution in Britain (see p. 81). At Quendon Wood, near Saffron Walden, it grows in woodland of the oak-ash-hazel type on Boulder Clay. Hybrids with *P. vulgaris* and back-crosses were plentiful. It was demonstrated that *P. elatior* is a plant of the "high coppice" phase of the woodland while *P. vulgaris* occurs around the borders of the wood and along some of the rides.

The field meeting provided an excellent opportunity for the continuation of informal discussions on the work of the Conference and for English botanists to exchange views with the three foreign visitors who were able to attend. A more detailed account of the occasion will appear in the Society's *Year Book, 1951*.

POSTSCRIPT

Readers will be interested to know that pursuant to the resolution passed at the close of the general discussion, the Council of the B.S.B.I. discussed Prof. Clapham's suggestion for the preparation and production of a series of maps of the British flora and at their meeting of May 11th, 1950, a Committee was appointed to consider the part that the Society might play in the project. Professors A. R. Clapham and T. G. Tutin, Dr. E. F. Warburg, and Messrs. J. E. Lousley, E. Milne-Redhead and E. C. Wallace were appointed to this Committee, which at its first meeting elected Prof. Clapham as Secretary. To carry out the task successfully must inevitably entail several years' work and the Committee is at present engaged in investigation of the practical difficulties with a view to formulating a definite plan.

Captain Diver's suggestion that close co-operation should be established between the Society and the Nature Conservancy has also been implemented.

J. E. Lousley,
Hon. General Secretary, B.S.B.I.,
December 31, 1950.

INDEX

Figures in heavy type refer to pages on which maps or illustrations appear.