

PROGRESS IN THE STUDY OF THE BRITISH FLORA

BEING THE REPORT OF THE
CONFERENCE

HELD IN 1956 BY
THE BOTANICAL SOCIETY OF
THE BRITISH ISLES

EDITED BY
J. E. LOUSLEY

ANDRÉ LAWALRÉE

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EDITORIAL NOTE

Study of the British flora has made outstanding progress during the past decade and this is therefore an appropriate time to review the methods employed and to consider the most favourable lines for development. The fifth conference sponsored by the Botanical Society of the British Isles was arranged with this object. Consideration of old techniques brought out aspects which have been neglected or misunderstood; accounts of modern methods were illustrated by examples of current work; the review presented an overall picture of available methods which those present at the Conference were able to apply to their own lines of research. The papers and discussion brought out in the clearest possible way two broad lines of development which offer the greatest promise at the present time (see page 124).

All the papers read and the accounts of exhibits are published in this book together with the discussion. They are arranged in the sequence used at the Conference except that the exhibits are brought together after the main papers. The scientific names are those used by the speakers except that all trivials are spelled with an initial small letter in accordance with the general policy of the Society.

The arrangements for the Conference were in the hands of the Meetings Committee of the Society. Much of the work fell on Dr. J. G. Dony, then Honorary Meetings Secretary, and to his energy and enthusiasm, together with that of the other members of the Committee, and other officers and members who assisted, the success of the Conference was due.

I am grateful to J. P. M. Brenan, D. H. Kent, N. Y. Sandwith, Dr. S. M. Walters, P. J. Wanstall, and Dr. E. F. Warburg, members of the Society's Publications Committee, and to E. B. Bangerter for assistance in proof reading.

J. E. LOUSLEY.

CONFERENCE PROGRAMME

PROGRESS IN THE STUDY OF THE BRITISH FLORA

FRIDAY, April 13th

- 10.15 a.m. A welcome to the Conference
Prof. T. G. TUTIN
- 10.30 The early development of a knowledge of the British flora
Rev. Canon C. E. RAVEN
- 11.30 The Eighteenth and Nineteenth Century background to the study of the British flora
Dr. G. TAYLOR
- 12.15 p.m. Interval for luncheon
- 2.00 The contribution of the Exchange Clubs to knowledge of the British flora
Mr. J. E. LOUSLEY
- 2.45 The place of the local Flora in the study of the British flora
Dr. J. G. DONY
- 3.30 Interval
- 3.45 The progress of the Biological Flora
Prof. P. W. RICHARDS
- 4.30 Interval for tea
- 5.30 EXHIBITION MEETING
- Exhibits will be displayed in the Botany Department, close to Tuke Hall, and may be seen at any time during the period of the Conference. During the evening exhibitors will explain their exhibits and answer questions regarding them in Tuke Hall.
- 6.00 p.m. The status of *Viola lactea* Sm.
Mr. D. M. MOORE
- 6.15 Natural Selection in favour of the hybrid *Agrostis stolonifera* × *tenuis*
Mr. A. D. BRADSHAW
- 6.30 *Alchemilla vulgaris* L. agg. in Britain
Miss M. E. BRADSHAW
- 6.45 A comparison of the spread of *Galinsoga parviflora* and *G. ciliata*
Dr. W. S. LACEY

- 7.00 The Species Problem in *Galium pumilum*
Mr. K. M. GOODWAY
- 7.15 Variation and distribution in *Erica mackaiana* Bab.
Mr. P. A. GAY

SATURDAY, April 14th

- 10.15 a.m.—Some aspects of plant variation—the Grasses
Mr. K. JONES
- 11.00 The importance of Experimental Ecology in the study
of the British flora
Dr. F. H. WHITEHEAD
- 11.45 Interval
- 11.55 The importance of relict and disjunct distributions in
the interpretation of the history of the present
British flora
Dr. F. ROSE
- 12.45 p.m. Interval for luncheon
- 2.30 Distribution Maps of plants—an historical survey
Dr. S. M. WALTERS
- 3.30 The study of our flora as a part of a whole
Prof. D. H. VALENTINE
- 4.30 Concluding remarks by the President
- 4.45 Close of conference

SUNDAY, April 15th

FIELD MEETING IN THE NEIGHBOURHOOD OF HITCHIN, HERTFORDSHIRE

The programme printed above is as circulated before the Conference. It was carried out as stated, except that the President, Dr. George Taylor, was unable to be present. As he was also unable to prepare his paper, Canon C. E. Raven kindly expanded his account of "The Early Development of a Knowledge of the British Flora" into the time allowed for Dr. Taylor's paper in the programme. The proceedings on the second day were closed by Professor T. G. Tutin.

**LIST OF MEMBERS AND GUESTS WHO ATTENDED THE
CONFERENCE, April 13 and 14, 1956**

D. E. Allen, Miss M. C. Allott, Dr. K. L. Alvin.
P. W. Ball, P. D. W. Barnard, Miss F. M. Barton, Mrs. D. L. Bennett, Miss D. Bexon, R. A. Blakelock, Miss I. Blewitt, Dr. H. J. M. Bowen, A. D. Bradshaw, Miss M. E. Bradshaw, G. M. Brown, Miss J. Buchanan, Miss K. I. Butler.
Miss D. A. Cadbury, J. F. M. and Mrs. Cannon, A. J. Carpenter, Miss S. Carter, K. E. Cockshull, T. G. Collett, Miss A. Conolly, A. Cridland.
Mrs. H. R. Davies, Miss O. R. Dewey, Dr. J. G. Dony, D. Dupree, T. R. Eagles, D. St. J. Ecclestone, Rev. E. A. Elliot, Dr. A. G. Erith.
R. S. R. Fitter.
P. B. Gahan, P. A. and Mrs. Gay, Miss E. J. Gibbons, Mrs. A. N. Gibby, J. L. Gilbert, J. B. Gillett, D. R. Glendinning, W. J. Goddard, Miss C. M. Goodman, K. M. Goodway, R. A. Graham, Miss M. Gregory, P. Greig-Smith, H. C. Grigg, E. W. Groves.
P. C. and Mrs. Hall, Miss Halliday, D. E. Hardy, R. Harley, Miss Harvey, Dr. J. G. Hawkes, J. H. Hemsley, F. N. Hepper, T. F. Hering, Miss S. S. Hooper, Miss M. A. Hudson, Mrs. B. A. Hulme.
Miss M. Isaac, Miss E. M. C. Isherwood.
L. James, A. C. Jermy, Miss H. Jenkins, K. Jones.
D. H. Kent, Miss M. P. H. Kertland.
Dr. W. S. Lacey, Dr. J. M. Lambert, J. Latham, W. N. and Mrs. Lawfield, G. F. Lawrence, Dr. V. E. Lloyd, Dr. L. Lloyd-Evans, Miss C. Longfield, J. E. Lousley.
D. McClintock, P. H. McNally, R. D. Meikle, Dr. A. Melderis, Dr. R. Melville, B. Miles, R. Minor, M. S. Moon, D. M. Moore, Miss B. M. C. Morgan.
P. J. and Mrs. Newbould, P. M. Newey.
Miss W. T. M. O'Connor.
Mrs. A. T. Peppercorn, F. H. Perring, D. W. Pickering, D. L. H. Porter, T. F. Preece, Dr. C. T. Prime, Miss E. A. Pringle, N. M. Pritchard.
J. A. Ratter, Canon C. E. Raven, Miss Rawlins, R. C. Readett, B. W. Ribbons, Mrs. M. Richards, Prof. P. W. Richards, Dr. R. Riley, Miss M. F. Roberts, C. A. Robinson, N. K. B. Robson, Dr. F. Rose, M. D. Ross, Dr. E. M. Rosser, J. Rossiter, Mrs. B. H. S. Russell.
R. E. and Mrs. Sandell, Miss M. Sands, N. Y. Sandwith, Mrs. N. Saunders, J. P. Savidge, D. Schofield, Miss M. Scholey, P. D. Sell, Miss E. Shaw, K. C. and Mrs. Side, Dr. E. Smithson, J. L. Southern, Miss J. Stevens.
R. F. Turney, Prof. T. G. Tutin.
Prof. D. H. Valentine, Miss D. E. de Vesian, Miss B. M. Vizard
Dr. S. M. Walters, P. J. Wanstall, Dr. E. F. Warburg, W. E. Warren, Mrs. W. Boyd Watt, Mrs. B. Welch, Dr. C. West, A. W. Westrup, Dr. F. H. Whitehead, Miss M. M. Whiting, J. E. Willé, Miss A. F. Wood, S. R. J. Woodell, J. E. Woodhead.
P. F. Yeo, Dr. D. P. Young.

INTRODUCTORY REMARKS

The Conference was opened by Professor T. G. Tutin, a Vice-President, who said:—

It gives me great pleasure to welcome members of the Botanical Society and our guests to this Conference. Our subject is "Progress in the Study of the British Flora" and it is evident from the programme that we are about to be given an extensive prospect and retrospect of this wide field.

You will, I am sure, be sorry to learn that the President is unable to be with us; his absence leaves us with a gap in the history of the study of the British flora, the subject with which most of the early speakers are concerned. Towards the end of to-day and throughout to-morrow we shall hear about various lines of recent progress in this many-sided subject, and finally Professor Valentine will be giving us a glimpse of a fascinating future. In the first half of last century, when Europe was recovering from the Napoleonic wars, Babington attempted the great task of correlating our insular flora with that of the continent. In spite of his efforts and those of other botanists, the insularity of British workers has not been entirely broken down, and we have still to learn to look on our flora as a small part of that of Europe.

This wider view can have important consequences for the future progress in the study of the British flora. A few examples will perhaps make clear what I mean. In this country *Veronica spicata* and *Veronica hybrida* appear to be distinct species, having different distributions and being reasonably well characterised morphologically. A study of the plant in Europe makes it clear that these two taxa can at most be regarded as subspecies.

We know *Lathraea squamaria* in this country as a predominantly whitish plant with a tinge of dull purple; what is supposed to be the same species in Denmark is dark purple with no whitish colour about it. Two chromosome numbers are recorded for the species. Are they correlated with the differences in colour, and are there also undetected morphological differences? The answer to this and probably many other similar questions can only be obtained by abandoning our insularity more completely. Dr. Prime in his recent work on *Arum* has demonstrated that *A. maculatum* in these islands and in Scandinavia has different chromosome numbers, and certain morphological differences also. It is evident that to know our own flora properly we must enlarge our scope. A start has already been made in this direction by experimental taxonomists and by specialists in certain genera.

It seems to some of us that the most pressing need is for what might be called an alpha flora of the whole of Europe to link up with, but not overlap, the *Flora U.R.S.S.* Plans for fulfilling this need are well advanced, though it must necessarily be a number of years before the work can be completed.

The B.S.B.I. could greatly assist in breaking down our insular outlook and at the same time could greatly widen our knowledge of our own flora by organizing excursions, to begin with to the western fringes of the Continent, and by inviting the co-operation of botanists in the country to be visited. It would also, I think, be of great advantage to everyone if a few foreign botanists could be encouraged to join our major excursions in this country. May I be allowed to offer these few suggestions for the consideration of our Council?

Finally I would like for a moment or two to look to the future in a different direction. Our next Conference, whether it is held in two or three years time, will coincide with the centenary of what is probably the most important event in the history of biology. On 1st July 1858, the famous essay by Darwin and Wallace outlining the theory of evolution was read to the Linnean Society, and on 24th November in the following year the first edition of the *Origin of Species* was published. I think it is fair to say that this theory was the seed, rather slow in germination perhaps, from which the fine flowering of our Society in recent years has sprung.

Our next Conference, therefore, will be of peculiar significance to the Botanical Society, as well as marking the centenary of an event of the first importance in biological thought.

**THE EARLY DEVELOPMENT OF A KNOWLEDGE OF THE
BRITISH FLORA**

C. E. RAVEN

To many of you—and indeed when I was first invited to give this paper at the start of our Conference to me also—it seemed reasonable to ask why we should now concern ourselves with the early development of knowledge of the British flora. We all know that the craftsmen who carved the foliated bosses and capitals in Southwell or Ely had a singular appreciation of the diverse plants which they depicted and an exact observation of their forms and habits of growth. We also know that this accuracy of definition was wholly lacking in the stylised and stereotyped woodcuts which adorned, but certainly did not illuminate, the mediaeval bestiaries and herbals. If botany is, as I believe, the first science to deserve that name, then it is perhaps significant that it owed its precocity rather to the superb draughtsmen who followed the inspired lead of Leonardo and of Durer, rather than to the herbarists and druggists, the gardeners and agriculturists, whose lives were devoted to plant lore. We all know how rapidly the complete chaos which our own first botanist William Turner so vividly describes yielded to a satisfying and synoptic, though not of course a complete, classification; and how by the end of the seventeenth century the subject had advanced to such a degree of achievement that, apart from adding new records of plants from other countries, it made virtually no scientific advance for a century and a half. You may disagree with me that naming new species (which Linnaeus defined as the criterion of botanical excellence) is not in itself science but only nomenclature, and that at best taxonomy is only the handmaid of Madam How and Lady Why, but, in any case, why at such a meeting as this should we bother over these early days of our studies?

Yet, on further reflection, it has become clear to me that even if the general history of botany in this country is well and widely known, nevertheless the records do indicate that in our field more, I think, than in any other, the foundations were from the first well and truly laid. Subsequent events, though geology and chemistry, physiology, genetics and cytology have added much, and enabled growth and clarification, have not with us as they have in other subjects produced any revolutionary changes. There have been periods when development was rapid, and others when study seemed to be diverted from issues of real importance to the pursuit of relatively trivial and even superficial

enquiries. I am not myself clear that our science is at the present moment sufficiently concerned with matters of real significance, but, be that as it may, botany has in the main followed a fairly steady course; and the chief lines of its career were indicated by the time of the death of John Ray. He and his contemporary Nehemiah Grew, and to a lesser degree his disciple John Morton, may be said to have attained a high standard of excellence in identification, description and classification; to have recognised and studied topographical problems, and indicated the significance of ecology, to have begun the study of plant physiology and opened up elementary enquiries into the relationship of form to function, and to have glimpsed the facts and the importance of hybridisation. It is, I think, open to question whether any advance of great value was made until a century and a half later.

If we look now at the story of this first phase of scientific botany, we find that early in the sixteenth century as a result of the recovery and the wide circulation of the Greek and Latin botany books and pharmacologies, a simultaneous effort was made in Italy, France and Spain, and pre-eminently in the Rhineland and Switzerland, to compare the plants described by Theophrastus and Pliny, or Dioscorides and Galen with those growing in the fields or gardens of the countries mentioned. Our own William Turner, the Northumbrian who was at Pembroke College, Cambridge, in the second and third decades of the century, is an excellent example of this first group of scientific botanists. His efforts to identify a bird like the pelican or a flower like the Narcissus involved a minute comparison of classical authorities, and then what might be an impossible search for a native specimen which filled the bill. As soon as he travelled and came across the dried herbaria of Luca Ghini, and the admirable pictures in Brunfels, his task became manageable: but even then the flora of Greece and the Mediterranean is not by any means easy to discover in our island climate. The discipline which this primary business of nomenclature involved was an exacting and therefore, I believe, a very valuable preparation for botanical studies: it certainly gave to these early students a power of detailed observation and minute discrimination which have seldom been surpassed. Anyone who studies Ray's work, whether in the Cambridge Catalogue or in the final edition of the *Synopsis*, will be amazed that he hardly ever confuses species that we distinguish or, unless he is relying on hearsay records, describes plants which we cannot easily and accurately name.

The exploration and identification of our British flora, traceable by anyone who will glance through W. A. Clarke's *First Records* (a book which ought now to be revised and brought up to date), was the work of a notable and varied succession. Biologists like Thomas Penny, doctors like Peter Turner, apothecaries like Gerard and his emendator Thomas Johnson,

naturalists like John Goodyer and George Bowles, botanists like John Parkinson and Mathias de l'Obel—these and a number of others, James Cargill of Aberdeen, Mistress Thomasin Tunstall of Ingleborough, and Thomas Lawson of Westmorland all contributed; and Ray himself, through Willoughby, Robinson, Hans Sloane, and his many other pupils and friends brought the different strands into a coherent and scientific unity. Anyone who considers such a list will see the absurdity of the attempt lately made in a recent history of science to separate the naturalist from the biologist: that field workers and laboratory workers have on occasion been separated is regrettably true—and has been disastrous for both: but to segregate the study of any living organism into supposedly distinct provinces is as foolish as to insist that all historians are either novelists or chroniclers.

The developments to which this primary business of naming and its sequel in arrangement and classification gave rise are threefold:—First, there is the fixing of the habitat—the observation of the locality in which a species is found both in general, mountain, woodland, wayside or water, and in particular. This latter was at first only a guide to other collectors, and in early herbaria was all too often omitted. There was at the beginning no real consideration of the significance of topography; for geology was not yet; and the difference between one type of soil and another, though certainly known to farmers, had not attracted the attention of herbarists. Ray may himself be accounted the first Englishman to recognise its significance when he added to his first Catalogue the detailed lists of plants found in special localities round Cambridge—Chesterton, Ditton, Gogmagog Hills, the "Hill of Health" (now Mount Pleasant, the south slope of Castle Hill), Hinton "the lanes and closes" and "the moor and the water there".

Secondly, and as a natural consequence, Ray's friend, the historian of Northamptonshire, John Morton was perhaps the first to apply the agricultural knowledge of different soils, sandy, clay, stoney and limey, to the botanist's recognition of the grouping of various plants. He fully recognised that soil affects the presence and the rate of growth of plants, but, in the absence of chemical analysis, or even of the chemical differences between acid and alkaline, no obvious explanation of the distribution of species could be reached. It is, I think, curious considering that the knowledge of the value of particular types of soil for fruits or crops goes back to very early days, how very long a time elapsed before a scientific ecology was outlined.

Thirdly, such enquiries lead back to problems of plant structure and physiology. Turner had noticed and described the parasitism of the Broomrapes; Ray as his basis for classification had studied and fastened upon the importance of the seed-leaves or cotyledons, and had investigated and experimented upon the rise of sap; Grew had been the pioneer in the study of botanical anatomy, and along with Robert Hooke had examined plant-

fibres under the microscope. Such work did not amount to very much, and was in fact handicapped by the acceptance of supposed analogies between plants and animals—an acceptance which still affects botany in its approach to genetics. But it revealed as clearly as did medical practice the urgent need for advance in the field of physics and chemistry. Here, as in biology generally, the seventeenth century had got as far as was possible until the basic sciences emancipated themselves from magic and tradition. If, after Ray, botany marked time, it was because until the time of Lavoisier and Lamarck it was not possible for it to get further. During the century of enforced stagnation, nomenclature and exploration of new botanical areas were alone available for progress; and the consequent developments, useful as they were in their very narrow field, could not but give a false perspective to the whole subject by focussing attention away from the principal problems of botanical science.*

Prof. T. G. TUTIN said that although Linnaeus was, of course, mainly a taxonomist he did interest himself also to some extent in other branches of botany. For example, he was an ecologist in a primitive way as is evidenced by the account in his *Skånska resa* (Stockholm, 1751) of what amounts to a transect at Tjörnedala, in S.E. Sweden. This transect can still be seen with most of the species mentioned in Linnaeus' account.

Mr. J. E. LOUSLEY said that the reaction of the Conference to Canon Raven's quotation of Linnaeus' comment (that naming new species should be the criterion of botanical excellence) was a clear indication that the botanists of to-day no longer regarded taxonomy as an end in itself. It had now been put in its proper place as the handmaid of Madam How and Lady Why, but instead there had arisen a new danger that the importance of accurate identification would be overlooked. This was obviously essential to the value of published work in, for example, ecology and cytology; and yet students and workers, with so much else to study, were liable to be led to regard naming their material as a matter of very secondary importance. There would always be a need for botanists with a thorough knowledge of the British flora and competent to assist research workers to give accurate names to their material.

Canon RAVEN agreed with this. He felt also that taxonomic studies of critical groups—such as *Hieracium*—were valuable as a preliminary leading on to the study of apomixis, which in turn opened up larger biological questions in the interpretation of evolution.

Dr. S. M. WALTERS suggested that, with increasing specialization in every branch of botany, our need is for co-operation between a num-

*As there was time available owing to Dr. Taylor being unable to read his paper, Canon Raven then continued his address with a brilliant extempore talk covering later phases of the history of British botany. Some of the matters referred to in the discussion which followed arose from comments made by Canon Raven which are not included in his paper as printed.—EDITOR.

ber of specialists to unravel such problems as apomixis. Some division of labour is essential if only because human life is too short, and we need the co-operation of field botanists, geneticists and laboratory workers. He welcomed signs of a reaction against excessive geneticist specialization, and an increasing tendency for geneticists to take their studies outside the limits of the experimental garden.

Dr. E. F. WARBURG enquired how Canon Raven would rank Dillenius as a botanist. Work done by Mrs. H. N. Clokie recently has shown that the so-called Dillenian Herbarium at Oxford was not, in the main, the collection of plants on which the third edition of Ray's *Synopsis* was based. Most of the British plants described for the first time in this work are in the Sherardian Herbarium and can be seen at Oxford. It seems likely that the Dillenian Herbarium was a collection made by Dillenius for a further work which was not published. Canon RAVEN replied that his own work had not extended beyond the death of Ray and he had not worked on Dillenius. Where would Dr. Warburg put Dillenius? Dr. WARBURG said he regarded Dillenius as an extremely good and careful botanist, and in some ways ahead of his time. It was of interest that his specimens were occasionally localised.

Prof. D. H. VALENTINE pointed out that Canon Raven's reference to Dr. Mills' rediscovery of *Veronica spicata*, in the locality where it had been recorded by Ray, illustrates in yet another way the value of old records; for it would seem that *V. spicata* has been unable significantly to extend its range during a period of 300 years; and this at once stimulates enquiry into possible explanations, such as low frequency of seed-setting and inefficient means of dispersal, and provides a starting point for new investigations.

Mr. R. S. R. FITTER asked if Canon Raven could explain why a dichotomy arose between field and indoor naturalists. Canon RAVEN said this occurred when a mechanistic as opposed to a vitalistic attitude became prevalent. The contrast was very evident in a comparison between the works of Ray, which were concerned almost solely with problems of living organisms, and those of the theologian Paley, which were purely in terms of the machine. In Paley's time the problem of the living organism had almost disappeared. The change occurred when chemical analysis and laboratory technique came in and replaced the observations of field naturalists. It followed the development of professional science in the 19th century, when the professionals looked down on the amateur naturalists. An example of this is the reaction of the great anatomist Owen to Charles Darwin, because the latter was an amateur. In turn, Huxley was looked down at by the aristocratic members of the Royal Society because he was a poor man and a professional. This snobbery did much to discourage work in the field.

Mr. FITTER then enquired if Canon Raven considered that the rationalist movement of the 18th century had anything to do with the tendency to divert attention from field observations. Canon RAVEN replied that the development of rationalism was parallel to the transformation of an agricultural into a manufacturing country. The

change was similar to the one which swung naturalists over from observations of nature to weights and measures.

Miss C. LONGFIELD observed that the B.S.B.I. had been outstandingly successful in co-operation between amateurs, with their field notes, and professional botanists, and expressed the hope that the present balance would be maintained. Canon RAVEN, in reply, said that he was quite sure that the co-operation of the two is vital.

Dr. S. M. WALTERS said that in his view the cleavage was not between amateurs and professionals, but between field and laboratory workers. In this respect the cleavage was greater within the professionals, than it was between professional botanists as a class and amateurs—in the latter case he was doubtful if to-day any cleavage existed.

**THE CONTRIBUTION OF EXCHANGE CLUBS TO KNOWLEDGE OF
THE BRITISH FLORA**

J. E. LOUSLEY

There is now no botanical exchange club for vascular plants in Britain. By a resolution passed at our Annual General Meeting last year the work of the exchange section was suspended—the first deliberate break in an activity which had been carried on since 1836. This would, therefore, seem a fitting opportunity to review the contribution which exchange clubs have made to knowledge of the British flora.

There has been considerable misunderstanding about the activities of these clubs, and much of this may be due to the somewhat unfortunate choice of title. Claims that they caused damage to our rarer species have built up a bias against their work to an extent which makes it difficult to review their efforts dispassionately. For this reason, and although the present paper is concerned solely with their contributions to scientific knowledge, it must be pointed out that some of the criticism is based on incorrect assumptions, and much of it fails to relate past events to the background of conditions at the time. The critics have shifted emphasis from critical plants, which for the last century were the primary and proper subject of the club's activities, to rarities, which were not.

As a result of this false emphasis, exchange clubs have sometimes been dismissed as small groups of amateurs exchanging specimens for their private herbaria on much the same basis as stamp collectors swap their duplicates. A glance at a few of the reports will show that in fact the most active members were usually the keenest field botanists of the day, taking their botany extremely seriously, and contributing material mainly with the object of threshing out difficult problems and bringing new facts to the notice of their fellow workers. The system used by the two clubs operating during the present century was essentially as follows:—

Contributors were asked to send in a minimum of 10 sheets of each gathering with sufficient labels, which were later branded with the club's stamp. They also supplied a spare "label" to be used in preparing the report, and this provided an opportunity for the addition of habitat and other field notes, and for discussion of the characters and classification of the plant. In the case of critical groups it was the duty of the distributor to submit *the whole gathering* to the appropriate referee, who was asked to comment on the determination, and to confirm that the gathering was homogeneous. From the returned material, sheets were set aside for certain public herbaria, and the remainder distributed

to members, who were asked to provide further notes on plants which interested them. It often happened that when the distributor had carried out his work skilfully these further notes proved as valuable as those of the official referees. All these comments were brought together in the printed report, of which three copies were sent to each contributor so that he could cut out the appropriate sections to attach to the herbarium sheets with the specimens.

The advantages of the system were considerable. Fundamentally it provided sets of standard sheets represented in a number of herbaria, and, although mixed gatherings slipped through occasionally, in general, botanists scattered over the country could be reasonably confident they had similar specimens before them. The system had many of the merits of exsiccata with printed notes, but also the advantage that the notes often represented the views of several botanists. This, so far as I know, was a purely British institution characterised by freely expressed and often conflicting opinions. It represents something different from exsiccata distributed in other countries, in which the printed notes on each gathering were normally the work of only a single botanist. Each exchange-club specimen, with the extract from the report attached, provides a standard which can be cited with an epitome of the views of contemporary botanists.

TABLE 1.

*BRITISH SOCIETIES AND CLUBS WHICH HAVE
ORGANISED THE EXCHANGE OF HERBARIUM
SPECIMENS*

BOTANICAL SOCIETY OF EDINBURGH (1836→)
BOTANICAL SOCIETY OF LONDON (1836-1857)
BOTANICAL EXCHANGE CLUB (OF THE THIRSK NATURAL HISTORY SOCIETY) (1858-1865)
LONDON BOTANICAL EXCHANGE CLUB (1866-1868)
BOTANICAL EXCHANGE CLUB (1869-1878)
BOTANICAL EXCHANGE CLUB OF THE BRITISH ISLES (1879- 1908)
BOTANICAL EXCHANGE CLUB AND SOCIETY OF THE BRITISH ISLES (1909-1914)
BOTANICAL SOCIETY AND EXCHANGE CLUB OF THE BRITISH ISLES (1915-1946)
BOTANICAL SOCIETY OF THE BRITISH ISLES (1947→)
WATSON BOTANICAL EXCHANGE CLUB (1884-1934)
THE BRITISH LINNAEA FOR EXCHANGE OF PLANTS WITH CONTINENTAL CLUBS (1886-? 1889)
THE PHYTOLOGICAL CLUB (in connection with the Pharma- ceutical Society) (1853-?)

This was the system in its most highly developed form evolved as a result of many years' experience. But before it reached this stage, other less refined systems had been employed which did valuable work when viewed against the background of the requirements of the times. At this point I would like to turn to a brief review of the history of exchange clubs in Britain. The names of the Societies concerned are set out in Table 1.

HISTORY

Large-scale organised exchange of herbarium specimens in this country dates from 1836, when facilities for studying dried material were very limited indeed. The Botanical Branch of the Natural History Department of the British Museum had just been formed and had charge of the Sloane and Banksian herbaria but little else. The collections at Kew were not started until seventeen years later. At Oxford, they had several fine old herbaria, but these were hardly in a condition for easy reference. At Cambridge, they had the collection of John Martyn to which Henslow was adding, but the period of expansion under Babington was to come later. Edinburgh also had a few collections. In 1836 facilities for comparing herbarium specimens were thus extremely poor. Transport was still mainly by coach, and botanists scattered about the country had little opportunity of standardising their determinations, and discovering where they were going astray in interpreting the descriptive floras of the time. Contemporary botanists were keenly aware of the need for the interchange of specimens; without it the advance of knowledge could only be slow.

The Botanical Society of Edinburgh was founded on March 17th 1836, and its objects were given as "... the advancement of Botanical Science, by means of periodical meetings, correspondence and the mutual interchange of specimens amongst its members". Under its by-laws, specimens contributed were used to build up the Society's own herbarium, and the surplus distributed, after "collation", to those members who had sent in at least 50 "*species*", or who had commuted at the rate of £1 for 50 "*species*". The arrangement was an immediate and outstanding success. In the first year no less than 61,200 specimens were contributed, of which 30,000, representing 1400 "*species*", were British. Plants were distributed to 57 members. In the second year, it is stated that between 90,000 and 100,000 labels had to be written or printed by the officers, and 20 *species* contributed were regarded as new to the British flora. In the third year, 40,200 specimens were sent in, of which 31,500 representing 3,300 "*species*" (i.e., gatherings) were British. Material was distributed to 84 widely scattered members. For a time the exchange was pursued with great enthusiasm, the Society even contributing to the expenses of collectors on journeys into the Highlands and elsewhere, but the number of specimens received had dropped to 25,000 in 1841-2, and thereafter the quality and quantity fell

away. *A Catalogue of British Plants* was published by the Society in 1836 for the purpose of enabling members to mark their desiderata. The second edition, issued in 1841, was the work of Balfour, Babington, and Campbell.

No doubt, it was the initial and obvious success of the Edinburgh Society which prompted the formation of the Botanical Society of London. This arose from a meeting convened on July 27th 1836, and one of the objects was "To form herbaria of British and foreign plants, for the reference of the members, and exchange with other Societies or individual collectors, and thus be the means of producing many valuable herbaria, which otherwise would not have been completed or even commenced". The arrangements were similar to the Edinburgh plan, and in the first year 4,819 specimens of British plants, and many foreign, were received. In the second year the total rose to 18,592 British, and upwards of 10,000 foreign, and included plants received in exchange from the Edinburgh Society. In 1844, the Society published the *London Catalogue of British Plants* and in the Annual Report for this year it is said that "... it has always been considered that the Society's highest utility would be found in the exchange of specimen _____", and certainly this branch of its activities was pursued with outstanding success.

By this time, H. C. Watson was taking an active part in the affairs of the London society and using his influence to improve the standard of accuracy in material distributed. At first there had been little effort to correct the names given by contributors and thus the object of standardising "nomenclature" was hardly supported. Watson corrected many of the irregularities which were taking place, and raised the standard to a much higher one. He published in *The Phytologist* critical notes on the more interesting plants distributed. Although these represented the views of an individual, they initiated the series which led later to the valuable discussions on plants distributed which were a feature of later exchange clubs. At the end of 1850, Syme* resigned the Curatorship of the Botanical Society of Edinburgh to become Curator of the herbarium of the Botanical Society of London. He followed Watson's precedent of publishing notes on the more interesting plants distributed, and maintained the standard which had been set. The distribution was still running at the level of some 20,000 British specimens a year in 1853, when, in a review of the fourth edition of the *London Catalogue*, it was stated that the Society had outdistanced every competitor in "the exchange of well-named specimens". In the following year there was an announcement of a "Foreign Exchange Club" to dispose of some of their duplicates, and for this J. T. Syme was to act as "Distributor", which is apparently the first use of this term. Early in 1857 the affairs of the Society were in a state of abeyance, and the herbarium and duplicates sold to F. Y. Brocas.

*John Thomas Irvine Boswell, né Syme, afterwards Boswell-Syme.

During these twenty years the Edinburgh and London Societies had distributed vast numbers of specimens. They had made it standard practice to use separate labels giving the locality and date of collection, employed a referee to ensure greater accuracy in the determinations of plants distributed, and made a start on publishing notes on the more interesting plants sent in. The improvement in the scientific value of their work during the period was considerable, and largely due to the support of Watson and Syme.

In November 1857 "pending the abeyance of the Botanical Society of London", the exchange activities were taken over by the Thirsk Natural History Society. The annual reports, with the sub-heading "Botanical Exchange Club", included critical notes by the curators, to which other experts contributed. When J. G. Baker joined the staff of Kew, the club was renamed the London Botanical Exchange Club in 1866. Two years later J. Boswell-Syme became Curator and we read that the object of the Club was "to facilitate the exchange of dried specimens of British plants, *especially of critical species and varieties*". This emphasis was to continue for the remainder of the history of British exchange clubs. The report for 1868 shows that comments were no longer restricted to the views of the Curator. Thus, on an *Aster* from Derwentwater, comments by Watson, Baker, Syme and Babington were printed in addition to information about the habitat by the collector. "London" was dropped from the title of the Club in 1870, and it became the Botanical Exchange Club of the British Isles" in 1879. I need not here refer to the further changes in title in the history of our present Society.

Reading through the long series of reports one is impressed by the increasing interest in critical plants and particularly in the Batrachian *Ranunculi*, *Rubi*, *Hieracia* and *Rosae* and in smaller groups like the species of *Fumaria*, *Viola*, *Sorbus*, *Epilobium*, *Euphrasia*, *Mentha*, *Rumex*, *Salix* and certain grasses. The custom grew up of printing lengthy notes by the collectors giving details of the habitat and characters not easily observed in dried material, together with the often divergent opinions of the referees and others. In 1905, for example, there were 54 gatherings of *Hieracium*, 14 of *Carex*, and 10 of *Mentha*, and other critical groups were also represented. Our exchange activities were suspended after the 1954 distribution.

The Watson Botanical Exchange Club was formed in December 1884 "to promote more intercourse, help and exchange between working botanists, and particularly with regard to critical species". Within six weeks there were 34 members, and the first distribution took place in February 1885, when 2250 sheets were sent out. By the third year, the total rose to 4971 sheets but, in general, the figures were well below those of the B.E.C. It came to an end in 1934, having been the means of distribution of 120,033 sheets during its fifty years of existence. Supported by many leading botanists, it was a small friendly club,

with a wonderful spirit for encouraging youngsters. In 1927, I acted as Distributor when I was 19, following D. G. Catcheside, and followed by E. C. Wallace, who were both about the same age.

The history of the principal British exchange clubs thus falls into three main periods as follows:—

(1) 1836-1856. During this time vast numbers of specimens were sent out by the Botanical Societies of Edinburgh and London supplying a need for properly localised material on which

TABLE
STATISTICS OF BRITISH

	B.E.C.					
DECADE	NUMBER OF PARCELS ¹		SHEETS OF SPECIMENS ²		NUMBER OF PARCELS ¹	
	Total for Decade	Average per year	Total for Decade	Average per year	Total for Decade	Average per year
1879	36	36	4,800	4,800	—	—
1880-89	(1 year only) 293	29	38,826	3,882	161 (6 years only)	27
1890-99	248	25	35,045	3,505	218	22
1900-09	258	26	38,738	3,874	256	25
1910-19	324	32	64,559	6,456	215	22
1920-29	304	30	46,671	4,667	181	18
1930-39	208	21	22,178	2,218	65 (4 years only)	16
1945-54	118	12	10,357	1,036	—	—
Totals	1,789	26	261,174	3,678	1,096	21
	Total number of distributions—71.				Total number of	
	Average contribution per member per year—147 sheets.				Average contribution	
	Peak year was 1912 when 34 members contributed 8,656 sheets.				Peak year was 1886	
	The activities of the Exchange Section were suspended from 1940 to 1944 inclusive.					

¹The number of parcels contributed is given here—the number sent out was usually slightly higher.

botanists could work. Both societies stimulated interest in the geographical distribution of plants, and the Edinburgh Society had a scheme devised by William Brand for dividing the country into 42 districts which was the forerunner of H. C. Watson's later geographical work. The latter and J. Boswell-Syme effected a gradual improvement in scientific standards.

(2) 1857-1878 was a transition period with the B.E.C. as the only organisation operating. No statistics are available about the numbers of specimens distributed. Emphasis had passed

EXCHANGE CLUBS, 1879-1954

WATSON		B.E.C. & WATSON COMBINED	
SHEETS OF SPECIMENS ¹		NUMBER OF PARCELS ¹	SHEETS OF SPECIMENS ²
Total for Decade	Average per year	Total for Decade	Total for Decade
—	—	36	4,800
21,283	3,547	454	60,109
18,425	1,842	466	53,470
25,537	2,554	514	64,275
25,956	2,596	539	90,515
20,421	2,042	485	67,092
8,411	2,103	273	30,589
—	—	118	10,357
120,033	2,400	2,885	381,207
distributions ... 50		Total number of distributions—121.	
per member per year ... 108 sheets		Average contribution per member per year—132.	
/87 when 35 members contributed 4971 sheets		Average number of sheets per distribution—3,150.	
		The peak year was 1912 when 56 parcels included 11,830 sheets. For 1913 and 1915, 11,292 and 11,116 sheets were contributed to the two Clubs.	

²The number of sheets of specimens contributed is as given in the reports. Some distributors included, and others omitted, packets of fruits and seeds and foreign specimens in their statistics.

from mere exchange to the study of critical plants as recorded in the reports. J. G. Baker, H. C. Watson and J. Boswell-Syme took leading parts.

(3) 1879-1954. In addition to the B.E.C., the Watson Club functioned during part of this period, and the number of specimens distributed is shown in Table 2 (pp. 24-25). The numbers (which were very much lower than those of the first period) reached their peak in 1912-1915, and then gradually fell away. Although some members belonged to both clubs, there is no evidence that the formation of the Watson had any effect on the support of the B.E.C. During this period emphasis was on critical plants and the work was supported by many leading botanists.

THE CONTRIBUTION OF THE EXCHANGE CLUBS

I would now like to summarise the ways in which the exchange clubs advanced knowledge of the British flora. Clearly their main purpose was to make herbarium material available, and there is little need to remind anyone who makes use of the larger herbaria of the success they had in this field. The proportion of labels branded with the stamps of the leading clubs is very large indeed. These sheets provide a series of standard gatherings likely to be represented in most of the larger collections. In many cases the relevant extracts from the reports are mounted with the specimens, but if this is not so, they are still available for consultation.

Without this material our work to-day would be greatly handicapped, but the benefits which accrued at the time of distribution were even greater. Discussion of the plants contributed stimulated research and brought new plants to the notice of botanists. Sometimes the exchange clubs were used as a testing ground before publication—as in the case of *Spartina townsendii*—at others, plants not generally understood were distributed so that people could learn to recognise them and arouse interest—a good recent example is the fine series of *Oxalis* sent in by Dr. D. P. Young. The printed discussion often encouraged people to put on record facts which would otherwise have been lost, and where extracts from the reports are mounted with the specimens they are automatically filed where they are most readily consulted.

For over a century the clubs played an important part in educating and encouraging young botanists. However isolated these were geographically, they could soon find out to what extent their identifications of the plants they contributed met with the agreement of the leading workers of the day, and they could use the specimens received in exchange as standards. Looking down the old lists of contributors it is interesting to see what a large proportion of the names are well known to-day as authors of important papers and books—a striking tribute to the efficiency of the training. In this connection a word of warning may be

useful: many of these well known workers joined the clubs at a very early age and care must be taken to avoid placing the same reliance on statements made when they were inexperienced as is due to their mature judgment.

The effort made by the clubs to insist on well prepared material, selected to show the characters necessary for study, did much to improve the standard of herbarium specimens in this country. As I can confirm from personal experience, the well deserved comments of the referees on poor material were a most effective stimulus to improvement and, although some contributors never learned their lesson, the majority showed steady improvement as they gained experience.

IS THERE A NEED TO-DAY FOR THE FACILITIES WHICH THE
EXCHANGE CLUBS PROVIDED?

For the most part the facilities provided by the exchange clubs catered for the times in which they operated. There is now abundant herbarium material available, and the need is to add to this selected specimens, rather than additions contributed at the whim of members of a club. Individual botanists no longer have the same need to receive dried specimens, since better transport facilities make it possible for even the most isolated workers to pay occasional visits to one or other of the larger herbaria, where facilities have improved greatly during the past century. It is also much easier to see the growing plants, so that wide experience can be gained independently of the use of dried material. For these reasons I think it clear that there is no longer any need for an exchange club on traditional lines.

By suspension of the activities of the exchange section, however, we have lost several important facilities which are still very much needed. There is now no machinery for distributing material of newly recognised segregates or new discoveries to the main public herbaria. Anyone revising a group can prepare a short series of exsiccata and distribute them himself, but a botanist adding a single plant to our list is less likely to consider it worthwhile to pack up and post a single specimen to each of half a dozen institutions. There is a case for setting up a receiving centre from which material would be distributed to the British Museum, Kew, Edinburgh, Cardiff, Dublin and other important collections. The Society might encourage authors contributing accounts of new or critical British plants to our publications to supply a few sheets for this purpose, subject, of course, to conservation safeguards.

The facility of free discussion is very much more difficult to replace. It is modern practice to treat papers in botanical periodicals almost as *ex cathedra* pronouncements, and it is very rare indeed for those able to correct or add to the statements to commit themselves to print. We have, fortunately, lost the acrimonious controversies which disgraced the correspondence columns of a century ago, and now, less fortunately, we have lost

the outlet for the expression of diverse views provided by the exchange clubs. There is no machinery for collecting the views of other botanists unless they happen to be known to be interested in the group concerned, and these are not always the only people with useful knowledge to contribute. Here we have lost something of real value.

I fear that the same applies to the exacting training in accurate identification and the preparation of herbarium specimens provided by the clubs. The amount of time wasted to-day in trying to solve difficulties in identification which have no other foundation than the poor selection and careless preparation of specimens is frightening. The art of preparing satisfactory material cannot be acquired from a few brief demonstrations, and it is difficult to suggest any way in which the discipline of the exchange clubs can be replaced.

I have endeavoured to show that the work of these organisations was a serious and important contribution to the study of the British flora. The clubs provided herbarium material as an essential tool of taxonomic research, and collected together much useful information which would otherwise have been lost. By focussing attention on variations they brought to notice almost all the segregates which cytology or other modern methods have shown to be of importance. Although they concentrated too much attention on minor differences, and thus diverted interest from other aspects, members did attempt to test the value of these differences by cultivation and other methods available to them. Many hints for useful new work could still be found by examination of old reports and the specimens to which they refer.

No doubt some of their efforts may not seem very impressive in the light of greater knowledge available to-day; undoubtedly some of their methods and the abuse of their organisation deserve serious criticism; but, by and large, they did much in their time to advance knowledge of our flora. The scientific value of the work of exchange clubs was considerably greater than is sometimes appreciated.

REFERENCES

References for the statements not based on the writer's personal experience will be found in the *Reports*, *Year Books*, and *Proceedings* of the Botanical Society of the British Isles and its forerunners (as set out in Table 1, p. 20) with the addition of the following:—

Botanical Society of Edinburgh, Annual Reports 1-8, for sessions 1836/7-1843/44, 1837-44.

Gardeners' Chronicle for 1857, 648, 1857.

Hooker's Journal of Botany, 9, 379-380, 1857.

Phytologist, 1-5, 1841-1854; N.S., 1-2, 1855-1858.

Watson Botanical Exchange Club, Reports 1-4, 1885-1934.

The paper was illustrated by an exhibit demonstrating some of the features of exchange club work mentioned in the paper. These included an analysis of the members contributing to the Botanical Exchange Club in 1883 (selected at random) showing that out of 33 contributors, 16 produced a total of 24 local floras, 2 produced series of papers equivalent to local Floras, 1 wrote the text for *English Botany*, Ed. 3, 3 wrote important monographs, 7 others are still well known as serious workers, and only two are little known to-day. Other features were illustrated with specimens and extracts from the reports to show (1) the value of collected opinions, (2) the value of the clubs' work in drawing attention to variations and segregates, (3) the facilities for circulating lengthy and useful collectors' notes and (4) the use of the clubs for circulating material of new taxa before and after publication to the main herbaria and other botanists.

Mr. N. Y. SANDWICH deplored the loss of large private herbaria scattered all over the country. Their owners had an intimate knowledge of the British flora which they used, in effect, to provide centres for the accurate identification of plants found in the districts.

THE PLACE OF THE LOCAL FLORA IN THE STUDY OF THE BRITISH FLORA

J. G. DONY

Local Floras defy definition, for if they are to be described as lists and studies of wild plants of a restricted area, they will include all the studies many of us have made for the Nature Conservancy and the numerous lists which feature so much in ecological studies. Valuable as these are, they cannot be considered to be Floras. If a narrower definition is adopted, that of accounting for the occurrence of all the wild plants known in an area at least as large as the smallest British county, it will exclude such useful studies as Kent's "Notes on the flora of Kensington Gardens and Hyde Park" and Hepper's "Flora of Caldey Island", which have appeared recently in our publications. Both definitions will include check lists, not considered by their compilers to be Floras but in many cases proving to be more useful than some works which have passed as such. This paper will consider mainly the larger local Floras, that is those which deal with the study of a wide group of plants in a reasonably large area. It will not deal with studies of small groups of plants such as ferns, trees and orchids, nor with ecological studies, valuable as these are to students of plant life of a restricted area. Local Floras, thus defined, have had at different periods of time a remarkable uniformity, greater than would be expected even from the common nature of their subject, yet, at the same time, a diversity which generally gives to each work an individuality of its own.

The story of how our local Floras came into being has been told recently in an admirable way by J. S. L. Gilmour. Little can be added to this. He has shown that the middle of the nineteenth century was the period of their greatest output, and that before 1820, and again in the present century, relatively few were published. Gilmour's view is that the Victorian popularity of the local Flora was largely the result of the 'back to nature' spirit of the Romantic Revival. It was assisted in no small measure by the adoption of the Linnean system of plant nomenclature and the publication in English of books on the British flora. Gilmour probably jumps too quickly from Hudson's *Flora Anglica* (1762), with its only limitations of being in Latin and using the Linnean system of classification, to Lindley's *Synopsis of the British Flora* (1829), Babington's *Manual* (1843), and Bentham's *Handbook* (1856). The years between Hudson and Lindley had seen Withering's *Botanical Arrangement* (1786),

the numerous editions of which speak for its popularity, and Smith's *English Flora* (1824), both written in English. Even before Withering, there had been attempts to simplify the subject for English readers, perhaps too much so, by Jenkinson in 1775 and Robson in 1777. But while these volumes rested safely on the library shelves botanists could go into the field fortified with some excellent forerunners of Hayward's *Botanists' Pocket Book* in Broughton's *Enchiridion Botanicum* (1782) and Galpine's *Synoptical Compend of British Botany* (1806).

Local patriotism played a large part in the development of the local Flora. If Relhan could publish three editions of a Cambridgeshire *Flora* in 1785, 1802, and 1820, and Oxford take up the challenge with Sibthorp's *Flora* in 1794; if Abbot, contemplating financial ruin (he left a will which mentioned his insurance policy but little more), could produce a *Flora* of so unpromising a county as Bedfordshire in 1798; it was a further challenge to more floristically attractive counties. Floras soon followed for Northumberland and Durham (1805), Nottinghamshire (1807) and Devon (1829). Failing a county to work, some botanists travelled in each direction from home, a distinct advantage if they lived near the county boundary. No less a person than John Ray had done this, and many of the earliest local Floras were centred on a town. Among these are Blackstone's Harefield list (1737), Deering's Catalogue for Nottingham (1738), Warner's *Plantae Woodfordiensis* (1771) and H. Smith's *Flora Sarisburiensis* (1817).

In this period the first Scottish local Floras appear in the *Flora Glottiana* (1813) for the neighbourhood of Glasgow, Woodforde's *Catalogue of Plants round Edinburgh* (1824), Greville's *Flora Edinensis* (1824) and Johnston's *Flora of Berwick-on-Tweed* (1829). Ireland was earlier in the field with Wade's *Flora* of Dublin county in 1794.

These early local Floras are to us mainly dull and uninteresting, but it is well to remember that they were not written for our generation and that the authors had many difficulties to contend with. Citation was one, and in all the Floras this tends to be long. Warner and others, writing before the Linnean system was fully accepted, used Ray's long and tedious names as well as the Linnean. Most cite many authors and Abbot cited plates as well. Few stations are given, and these seem to have no significance to the authors. Austerity appears to be the hallmark of the Floras of this early period, for few allow the privilege of a personal comment; indeed, there would be little room for it, as they included the whole of the plant kingdom. It is difficult to find a purpose behind them except that they were most obviously finding their way. Where the path was leading is not always clear, and exceptions to the general pattern are consequently of interest. Wade, in a period when authors gave English names, even if they wrote entirely in Latin, was logical and gave names in Gaelic. It would be interesting to know

more of Wade, for it is certain that this must have annoyed the alien overlords in Dublin Castle. An interesting Flora by Davies of Anglesey (1813) gave Welsh names and a list of the Welsh names translated into English and Latin, with copious notes in Welsh. Abbot was frivolous enough to introduce a few personal notes: 'of all our natives', he wrote of *Alchemilla vulgaris*, 'this is the most elegant plant'. Greville, not content, as most were, with the Linnean system of classification which they followed serving as a rough key, keyed out all his species, adding good descriptions and rather more stations than did most of his contemporaries. The result is a voluminous Flora, for its period, of over 550 pages, but without doubt the best of the early Floras.

By the 'forties the Floras change rapidly, the mosses and fungi are omitted, or become relegated to lists in an appendix; the descriptions also go, but maps appear. The number of stations given increases and these become related to geological formations. But the romantic element is at its height and one opens a local Flora of this period expecting it to be dedicated to 'the young ladies of England' and inscribed 'Consider the lilies of the field' or 'Many a flower is born to blush unseen'. It was good to know that Abbot had a soul, but the botanists of the mid-century lay their souls bare in their over-enthusiastic personal notes. Poetry abounds, and Webb and Coleman's *Flora Hertfordiensis* (1848) is as much verse as botany. There are, however, some good Floras of this period, and new influences are at work. Leighton's *Flora of Shropshire* (1841), in addition to numerous stations and an index of localities, gave good descriptions in English, and useful diagrammatic sketches showing characters of sedges. It is a Flora which it is still possible to use in the field. Webb and Coleman divide their county into districts based on river drainage, a plan which was to be followed by most subsequent authors of local Floras, except that Babington, in the *Flora of Cambridgeshire* (1860), tried to queer the pitch with natural regions. Thus began a fierce controversy which divided British botanists to the extent of not speaking to each other, or only with venom when they did.

Behind much of this was H. C. Watson, and there can be no doubt that his was the greatest influence in the large amount of work being put into the study of the British flora. As early as 1835 he had written: 'it is hoped that botanists . . . ere long will bestir themselves; and if wishing to write at all, not confine themselves to the mere list-making labour of a local Flora'. He wrote off the bulk of the early works and reduced the number of acceptable local Floras which had appeared before the time he was writing to thirteen. Even these, he complained, were faulty, as they did not contain many species which were known to appear in the areas they were supposed to represent, and, still worse, they included without sufficient authority many species which were in fact absent from those areas.

Watson maintained that a local Flora should be more than 'mere nomenclature' and the collecting together of information on rare species; but he was ready to admit that others before him had realised this. There is evidence that the first persons to do so were not botanists, as such, but farmers. In the Napoleonic War period, when efforts were being made to bring fresh tracts of land under cultivation, and to introduce new methods of farming, the self-styled Board of Agriculture conducted surveys of all the British counties. These *General Views of Agriculture* contain much sound botanical information which would well repay study. The first botanist to make use of new methods was probably N. J. Winch of Newcastle, whose *Botanist's Guide through the counties of Northumberland and Durham* (1805) was of the list form against which Watson so loudly proclaimed. His paper on the *Geographical Distribution of Plants in the counties of Northumberland, Cumberland and Durham* (1819) broke new ground, introducing such concepts as northern and southern limits of range of distribution, coastal range and continental elements. Some of the new principles he adopted in his *Flora of Northumberland and Durham* (1831).

To Watson good local Floras could serve a definite purpose, for they could show in miniature the distribution pattern which he was working out for the country as a whole. They could serve a double purpose, for Watson envisaged regional Floras, or as he would have called them provincial Floras, as intermediates between the purely local and the national Floras. A regional Flora could be compiled from local Floras, and a reliable national Flora from the regional ones. In addition, Watson stressed the need to study the conditions controlling the growth of the plants. The army of local botanists who rallied to Watson's cause were in most cases the very people who, caught up in the enthusiasm, went on to produce the local Floras. At the height of their popularity they must have been profitable, for supplements were published and second and third editions appeared. Since 1840, six editions of Floras of the Liverpool district have been published.

The earlier botanists were fortunate as they were treading virgin soil; but in time it would become necessary to account not only for the flora as the author found it but also for the work done previously. This was to be done in an incomparable manner by Trimen and Dyer in their *Flora of Middlesex* (1869), the best of the local Floras of the Watsonian period, and it set a pattern which British botanists, for good or ill, saw little reason to depart from until our own day. It is perhaps as well to enquire what this pattern was. It was firstly to account for the history of botanical study in the area covered by the Flora; secondly to examine the factors governing the distribution of wild plants within that area; and thirdly to list the plants of the area in botanical districts which were best based on river drainage. Austerity appears again, for all extraneous matter was deleted.

as were descriptions and keys. The latter has astonished most foreign botanists, who have tended to use keys in all their Floras; the authors of local Floras in Britain assumed that the reader had at hand a national Flora.

The standard set by Trimen and Dyer was high, but this did not deter others. Local Floras became fewer; they also became larger; as the introductions dealt with geology, physical geography and history in attempts to interpret the flora. It is doubtful whether they became better, for the reader was lost in a maze of information that was difficult to interpret. Pryor's *Flora of Hertfordshire* (1887) was twice as large as Webb and Coleman's with all its verse, but attempting to be scientific, cut out the English names and used strange Latin ones which it is difficult for even a botanist to recognise. I was pleased to notice a fortnight ago, when discussing a plant with a keen, but not expert, botanist, that he went to his bookshelf to consult Webb and Coleman rather than Pryor. The blame for the nature of his *Flora* was not entirely Pryor's, for he died before its publication. Watson, too, was dead, and the splitters had the field entirely to themselves. Authors found it necessary to account for the distribution of varieties and forms, and much appeared in the body of the Floras which would best have been published elsewhere, if at all.

Good Floras continued to appear, and outstanding among those of the post-Watsonian period were Druce's *Flora of Oxfordshire* (1886, second edition 1927), and his *Flora of Berkshire* (1897). His *Flora of Buckinghamshire* (1926) was poor by comparison (it is not surprising that it lost him £600), and his *Flora of Northamptonshire* (1930), is a disappointment to us as we trust it was to him. There was also still a market for the popular local Flora, and Green's *Flora of Liverpool* (1902) had over 800 good drawings of the more common species.

It is impossible to judge the worth of a local Flora until it has been tested in the field. Gilmour, who has no doubt used it, considers White's scholarly *Bristol Flora* (1912) to be among the best, a view with which other friends of mine, whose opinions I value, agree. I have never had need to use it, but in prospect find it disappointing. White is less austere than most of his contemporaries and his personal notes are those of a botanist for botanists to read. But compare his comments on the increase of *Geranium pyrenaicum* with those of Trimen and Dyer. Much the same is written, but more concisely in the case of the latter. Contrast White's long account of *Geranium pyrenaicum* with what must be an all too short one of *Radiola linoides*. It is obvious on almost every page of the *Flora* that White knew his plants exceptionally well: his dilemma was that of all authors of local Floras, that if much is written of one species less must be written of another, or the Flora will be too large to publish. White's *Flora* is a book to have by one's bedside; Trimen and Dyer's is certainly not.

In recent years local Floras have become very large. The Devon Flora had 802 pages, the Gloucester 849, and the Leicester 985. These are all large counties, though smaller than Lincolnshire, which still lacks a Flora. Splitting has been largely responsible for the great increase in size, but the volume of past records of species which we now find to be rare takes up much room. The very size of these works discourages otherwise keen local botanists, some of whom have manuscripts almost ready for the press, but are alarmed at their size. The short cut to publication taken by Evans in the *Flora of Cambridgeshire* (1939) is no solution of what has become a serious problem.

The local Flora has played an important part in the history of British botany. More local Floras have been published compared with the total number of works on British plant life than there have been local Faunas compared with the number of works on British animal life. They have been largely responsible for making Britain the best botanised part of the world. With their assistance it is possible to show reasonably well the distribution of many species and to collect a great deal of information on the behaviour of our plants. Unfortunately there are many gaps, and, for many parts of the country, the only Flora is so old that it is now of little use. Annotated copies of the older Floras in these areas are very important and much might be done in collecting details of them.

Local Floras have added few plants to the British flora, for most of our native species were known before the compilers of the nineteenth century Floras got to work. Splits, it is true, appear, especially when the author was interested in a critical group; but even here, as with the discovery of a new species, excitement led the finder to go to press as early as he could and publication was made in a national journal. The description of new species and varieties, and the making of new combinations, in local Floras has usually been discouraged. Some appear and we are to be thankful that they are so few. The making of new records was, however, often done by local enthusiasts in the routine examination of apparently unpromising country, an occupation which at least kept some botanists from rushing, at every available opportunity, to Teesdale, Lawers and the Lizard to see what was already known.

There are, perhaps, some serious limitations in our local Floras in the too ready way in which their compilers followed the lead of the national Floras. This is to be seen most often in the notes on status, habitat and the time of flowering of the plants. As it is partly on the information in the local Floras that the authors of national Floras must depend, there is every opportunity here for a vicious circle to be formed.

Is there a future for local Floras? This depends very much on the demand there will be for them. It is useful at this stage to analyse the motives which will lead a person to buy such a

work. There are a few, a very few, collectors of local Floras as such. Libraries will buy a certain number—local libraries more than national ones. In every district there are a number of persons who will subscribe to or purchase any book of a purely local character. County ties are probably stronger here than those of the town, which may account in part for the popularity in the past of the county Flora. The local sale, other than to botanists, will depend very much on the price and attractiveness of the volume and little upon its contents. Botanists will buy the book in proportion to the use that they think it will be to them. With increased library facilities, the sales to botanists will depend also on price. Many botanists or would-be botanists, before buying a local Flora, will ask two questions. Does the book lead me with a reasonable degree of accuracy to the discovery for myself of a local species in which I am interested? If I visit this area and find a species of whose identity I am uncertain, is this book likely to assist me in finding its name? The final demand for a local Flora will depend, as it does for all commodities, on usefulness and on price. More people are likely to buy a local Flora of 400 pages at £2 than one of 800 pages at £4, unless they think that the former has little use and the latter a great use.

The production of a local Flora is a more simple matter to determine. Illustrations, which are essential for good sales, increase costs, and maps are very expensive. Costs of printing, with plates and maps, diminish with the number published. It costs little more to print 750 copies than 500. An issue of 500 copies of a 400-page book could not sell at less than £3, a similar issue of an 800-page book could not be marketed at less than £6. An issue of 1,000 copies in each case could be sold at little more than a half of these prices. It is this margin between 500 copies (and some local Floras have sales lower than this) and 1,000 copies (which probably no local Flora has reached), which is of great consequence. This would make it unprofitable to publish a local Flora for a thinly populated county, such as Huntingdonshire, most of the Scottish counties or many of the Welsh counties. Most local Floras in recent years have been published by a local society prepared to face a loss and in some cases raising a fund in anticipation of the loss. If local Floras can still serve a useful purpose, it is for us, as botanists, to master the problem of their size and to pursue the question of greater financial support for their publication.

There is evidence of new approaches to the study of local botany which can be compared only with that of the Watsonian period, and there is much encouragement for the future. We have by no means solved the problem of variability, but it is not one to worry the purely local botanist as much as it has in the past seventy years. The new *Flora of the British Isles* of Clapham, Tutin and Warburg should bring a stabilising effect comparable with that of Bentham and Hooker, and in McClintock

and Fitter's *Pocket Guide* we have the handbook that can be put safely into the hands of the rawest amateur. The work now in progress with the Distribution Maps Scheme has produced an interest in local botany very similar to that which culminated in *Topographical Botany* (1873-4). We badly lack a modern 'Hayward' and there is surely a field of work there for someone.

The tools are with us, but it is the new methods of study which should interest us most. Godwin has shown what can be done with a purely ecological approach in the study of a local flora. The only criticism that can be made of it is that it is hidden away in a relatively obscure publication which few of us have the opportunity to consult. The *Geographical Handbook of the Dorset Flora* (1948) by R. D'O. Good opened up a new field but failed to satisfy the needs of the field botanist. These new methods should do much towards solving the problem of the long and wearisome introductions which have featured so much in our local Floras, but do little towards solving the problems of listing the species which still remain. The methods being used by the team of workers engaged in the revision of the Warwickshire Flora most deserve our attention. Similar methods are in use for work on the Derbyshire and Cambridgeshire Floras, and there is reason to believe that Rose is departing from tradition in his proposed *Flora of Kent*.

There is hope that from these new methods a fresh pattern may arise, but the challenge remains for a younger and as yet unknown botanist to take up. Trimen and Dyer were both 26 when the *Flora of Middlesex* was published. By contrast, Riddelsdell was 75 when he died with his Gloucestershire Flora still unpublished. The field is one for younger men; and perhaps the greatest safeguard for successful work is to be sure that one is alive in body and spirit when it is finished.

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Prof. D. H. VALENTINE enquired to what extent our British system of local floras was represented abroad. Mr. D. McCLINTOCK said that for Germany, at least, there were some excellent local floras. For example, he had one for Württemberg which he regarded as almost ideal—it was a convenient size for the pocket, and in addition to localities included brief descriptive details.

Mr. F. H. PERRING said that for the Flora of Cambridgeshire which was in preparation, data were being collected in lists of species from 1-kilometre squares, and presentation of the data was a more serious problem than their collection. The classical Flora of up to 1,000 pages is too large to take in the field and too expensive for present-day publication. Therefore, in contemplating the possible form of the new Cambridgeshire Flora, they were considering dividing the county into a number of equal areas, such as 5-kilometre squares, which would give 100 such areas. The data could then be presented in the book by much the same method as was used for *Comital Flora*—by giving the numbers of the squares in which each species has been recorded. Dr. Dony suggested that there was no reason why a book containing, say, a thousand maps could not be produced cheaply. Line blocks cost little more than type which occupied the same space and, if printers could be persuaded not to charge for the displaced type which they did not set up when blocks were used, the cost of a book of maps need not be greatly in excess of a book of type the same size.

Mr. R. D. MEIKLE suggested that an ideal flora should be a compromise between a mere list of species represented and the other extreme of the elaborate lists of localities as set out in the *Flora of Gloucestershire* and the *Flora of Devon*.

Mr. R. C. READETT pointed out that the revision of the Warwickshire County Flora was being carried out on the basis of kilometre squares: thus fitting readily into a National Scheme like the Distribution Maps Scheme. It was intended to publish as many maps showing the distribution of species by kilometre squares as possible. In the case of rare species—and others, if it were found impossible on financial grounds to produce maps in all cases—lists of squares where the particular species has been recorded would be published. Thus any future worker would have either a map showing the distribution, or the data from which to construct such a map. If, as seemed likely, it was found impossible to survey every one of the 2595 kilometre squares, and a random sampling of say one in four was taken in some areas, it would be indicated which squares were not in fact surveyed. When these were done at a later date the information could be published as a supplement.

Mr. A. D. BRADSHAW suggested that there was a danger that too great an interest in mapping distributions by wholesale methods would mean that information about the small scale distributions of species would be forgotten. The latter is essential if we are to understand the ecology of species, and is lost in a grid square system. Mr. PERRING replied that for Cambridgeshire such information is being collected at the same time as the general grid square information.

Dr. J. G. HAWKES added that the Warwickshire Flora as planned would show particulars of habitat by means of symbols on all distribution maps included. This information would also be given in all cases where species distributions were listed and not mapped.

Dr. R. MELVILLE pointed out that for some purposes dots on maps were insufficient and it was necessary to give localities so that people can go and collect material. As an example he instanced his experience when organising the collection of drug plants during the war, when the localities in local floras proved of great value.

THE PROGRESS OF THE BIOLOGICAL FLORA

P. W. RICHARDS (University College of North Wales, Bangor)

The aim of the *Biological Flora* (or to give it its full title, the *Biological Flora of the British Isles*) is to provide information about the 'biology' and ecology (in the widest sense) of British vascular plants, native and naturalized. The welcome it has received, since the British Ecological Society first launched it in 1940, shows that it has met a real need which has both practical and purely scientific aspects. The main cause of discontent has been its somewhat slow rate of publication; at the present rate it will be many years more before even a considerable fraction of the British flora has been included. Now, after it has been in existence for just over 15 years, it is perhaps a good moment to glance back over its past history and to consider whether anything could be done to increase both its usefulness and its rate of publication. Since it is a co-operative enterprise, depending on co-operation between its editors and contributors, and between those most closely concerned and those outside, this Conference might like to consider whether anything could be done by co-operation between this Society and the British Ecological Society to increase the value of the flora and hasten its progress.

But first, as there must be many here who do not know the history of the *Biological Flora* or may not fully understand its aims and methods, let me briefly explain how it came into existence, what it sets out to do and how it tries to do it.

Our traditional floras are mainly descriptive works, collections of plant descriptions. They are often provided with keys and other aids to identification and are basically a modern development of the mediaeval and Renaissance herbals, the primary purpose of which was to be a manual for the recognition of plants of real or supposed medicinal values. Modern floras differ from their ancestors in dealing with all plants impartially, regardless of possible uses, and often give fairly complete information on distribution and other matters not necessarily useful for identification. In recent years it has become increasingly clear that plant species differ, not only in the characters of the kind usually mentioned in floras (which are mainly fairly easily visible morphological characters), but also in the sum total of their characters, ecological, genetical and physiological, as well as morphological. If information under all these headings were to be included in a flora on the traditional plan, it would become cumbersome and its primary purpose, identification, would be frustrated. Hence arises the need for a flora of a different kind, a 'biological' flora.

The first hint of such a work can be found in a remark of J. D. Hooker in the first edition of his *Students' British Flora* (1870). The time was then not nearly ripe for such an enterprise and nothing more was heard of a biological flora of Britain* until 1928, when a committee of the British Ecological Society adopted a scheme put forward by its convener Sir Edward (then Professor) Salisbury who was appointed editor of the new work. A questionnaire indicating the kind of information needed appeared in the *Journal of Ecology* and the *Journal of Botany*, and a specimen account of the biology of *Endymion non-scriptus* was published in the latter. Unfortunately the scheme did not receive the support it deserved and it also became plain that one man, even if his whole time could be devoted to the task, could not accomplish such a task on his own.

At a meeting of the Ecological Society at Oxford in December 1940, the subject was revived, and it was suggested that work on a biological flora might be the sort of work which could be done in war-time when long-term ecological investigations were mostly impossible. It so happened that Professor (then Dr.) A. R. Clapham and myself had recently worked on the ecology of species of *Juncus* and we were asked to prepare for publication accounts of four species, *J. effusus*, *J. conglomeratus*, *J. inflexus* and *J. subnodulosus*, following a schedule which we prepared with the help of various people interested. When these accounts had been prepared the Council of the Society agreed to launch the *Biological Flora* and appointed three editors, Professor Pearsall as editor of the *Journal of Ecology* (afterwards Dr. H. Godwin), Professor Clapham and myself. Since then every volume of the *Journal of Ecology* has included accounts of several species. These accounts are included as part of the *Journal of Ecology* and are also reprinted and sold separately.

The scheme begun in 1940 differs from that proposed in 1928 in being co-operative, a different author or authors being responsible for each part, and in the parts being issued as soon as ready and therefore not in a systematic or any other order. The editors impose certain limits of length and endeavour to ensure a minimum of uniformity in the accounts, bearing in mind that the nature of the material will vary both from species to species and according to the opportunities and interests of the authors. An excessive striving for completeness must be avoided and also the premature publication of accounts based on too limited an experience of the species. The editors' aim is to publish accounts which are in the nature of progress reports on the ecology of each species, rather than little monographs.

*In 1900, G. C. Druce announced that he had in preparation "An Ecological Flora of the British Isles", in which he hoped to show "more particulars as to the exact place of growth, altitude and distribution, than is given in the usual text-books" (*J. Bot.*, **38**, 240, 1900). Nothing came of this project beyond the information on the lines specifically mentioned in the announcement which was included in his *Comital Flora* published in 1932.—EDITOR.

The editors divide their functions. Professor Clapham keeps the list of accounts in preparation; intending contributors should write to him and he will provide them with the Schedule for Contributors (revised in 1947 and to be revised again shortly) and with a blank map for showing distribution. Accounts ready for publication should be sent to me; since there are always problems in arranging and presenting the material it is desirable to send a draft for comments before completing the final version of the manuscript.

Up to date (May, 1956), accounts of 74 species and several genera have been published, the work of a large number of contributors, including both amateur and professional botanists. Over 160 more accounts are in various stages of preparation. New contributors are welcome, as well as data from those who may not feel able to undertake the writing of complete accounts. Such data should be sent either to the contributor responsible for the species (whose name can be found from the published list of "Accounts in preparation") or to one of the editors. Where an intending contributor has not ready access to libraries the editors can sometimes help, and sometimes where the contributor is an amateur botanist without laboratory facilities something can be done to assist. Arrangements exist for co-operation with the Distribution Maps Scheme so that the fullest data on distribution are available.

The paper is thrown open to discussion in the hope that the audience will ask questions and offer constructive criticism.

Mr. J. E. LOUSLEY said that the parts of the *Biological Flora* which had appeared had shown very clearly the great value of autecological studies, which were urgently needed in connection with several aspects of botany, including conservation. There was a great deal of scattered information, some published and some unpublished, but collecting this together was a major task, and uneconomic when separate workers attempted to go through the whole of the literature independently for individual species. Moreover, valuable information was lost because botanists were not sufficiently encouraged to send in minor field observations which collectively could be of importance. Records of population fluctuations are an example. We need a central office for the collection of this information—an ecological counterpart to the B.S.B.I. Maps Scheme—in which a folder would be kept for each British species. The first step would be to index published information, a set of abstracts from B.S.B.I. publications might be cut up as a start towards this, and the central office would also organise the provision of new data—much as the Maps Scheme office has done. Assistance and encouragement could be given to volunteers. The work could never be completed—that could never be said of a biological project—but if a grant could be obtained to finance a small staff for a five-year period, most of the information at present available could be collected and the progress of the *Biological Flora* greatly accelerated.

This, of course, is primarily a matter for the Ecological Society, but the B.S.B.I. and other Societies could provide considerable practical assistance.

Mr. KEITH JONES then suggested that although the *Biological Flora* is a most valuable publication as it stands, consideration might be given to an expansion of the cytological information. At the VIII International Botanical Congress held in Paris, 1954, Professor Stebbins suggested that writers of floras should become informed on nine stated points. Amongst these were included (1) chromosome numbers adequately obtained and recorded, (2) structural heterozygosity, (3) presence and type of polyploidy. At the time the Congress considered that floras would become far too cumbersome if information of this type was included. However, the *Biological Flora* is unique in form and it would be possible to make adequate references to these points. In particular, it would be of great value if it could be clearly stated whether determinations of chromosome number have been made on plants collected from natural populations or on seedlings raised experimentally from collections of seed.

Mr. A. D. BRADSHAW deplored the use of foreign counts in putting down chromosome numbers without comment. This could be most misleading. He agreed with Mr. Jones that there is a very great need in the *Biological Flora* for attention to be paid to chromosome number and behaviour and resulting fertility, since these may profoundly affect the whole biology of the plant and are therefore a cardinal part of the Flora. To report a chromosome number $2n = 35$ for instance is surely not enough, since this inevitably means the plant is sterile and must be surviving vegetatively and therefore that the position should be examined more closely.

Prof. D. H. VALENTINE enquired if vice-county or grid-system distribution maps would be used for later contributions, and observed that some of the maps already published in which whole vice-counties had been blacked-in gave a very unsatisfactory picture of the real distribution. Prof. RICHARDS replied that they were well aware of the shortcomings of some of the published maps and as soon as the necessary information was available for the construction of grid-system maps they were prepared to consider using them.

Mr. N. Y. SANDWICH said that contributions seemed to be getting longer and fuller, and asked if this was due to any change in policy. Prof. RICHARDS replied that he did not agree that contributions were tending to get longer. There had been no change in policy on the part of the editors but the accounts necessarily varied considerably in length according to the material available.

Mr. SANDWICH then suggested that better use could be made of the facilities of the *Biological Flora* for publication of really full descriptions. For practical reasons this was seldom possible in descriptive floras and hence it is often difficult to refer to descriptions of, for example, seeds and seedlings. This was supported by Prof. VALENTINE, who said he thought it a very important point. Full descriptions even of many common plants are not available, and he would also like to see varieties and hybrids described in detail. Prof. RICHARDS replied

that he thought these were very useful suggestions, which the editors would endeavour to implement, but for practical reasons he felt that it was hardly possible to include full descriptions of all varieties and hybrids as well as species.

Mr. P. J. WANSTALL suggested that it would be very helpful to contributors to have a panel of cytologists prepared to receive and examine material. Prof. RICHARDS said this was a very welcome suggestion and they would appreciate volunteers from cytologists prepared to assist in this way.

Mr. F. N. HEPPER said he thought the importance of growing material from various wild sources in the garden for comparison should be impressed on contributors. When a species is variable the locality from which each particular fact recorded is observed should be included in the account.

SOME ASPECTS OF PLANT VARIATION: THE GRASSES

KEITH JONES (Welsh Plant Breeding Station, Aberystwyth)

INTRODUCTION

In recent times cytology has played such a significant role in the study of species and species evolution that a conference dealing with "Progress in the Study of the British Flora" would be incomplete without some reference to chromosomes. At the same time there seems little need to enumerate the ways in which cytology can assist the botanist or the breeder, for on a number of occasions these have been listed and discussed by others. It would be more appropriate to our conference theme to consider some aspects of the subject which, although undeniably important, have not received the attention due to them. I refer in particular to those variations in chromosome number and chromosome behaviour which may occur *within* the species, a fuller understanding of which must lead to improvements in cytotaxonomic methods and so to progress in floristic studies.

The variation which is characteristic of all living organisms is most apparent in external morphology, but we now know that it occurs also at the chromosome level. This has been shown primarily by the discovery that a species is not necessarily characterized by one chromosome number alone, but may embrace forms having two or more different numbers. This is common knowledge these days, but perhaps it is not so well realised that there can also be pronounced intraspecific variation in chromosome pairing at meiosis. It is necessary that both aspects be taken into account in species studies if an accurate assessment of the cytological make-up of the species is to be made. This is the point I wish to emphasise in the following account, which will describe some of the more recent work on cytological variation, particularly in the grasses, the group which is my main concern.

VARIATION IN CHROMOSOME NUMBER

The wide range of chromosome numbers found in the grasses is due both to the occurrence of at least seven different basic numbers in the group, and to the very high incidence of polyploidy. Polyploids are present in almost every genus so far examined, *Lolium* and *Melica* being two notable exceptions, and about 70 per cent of the grass species are of this type. Of particular interest to the present discussion, however, is the fact that well over 100 species contain several different chromosome forms in a polyploid series. There are also some species, mainly

apomicts, which have a wide range of chromosome numbers not exact multiples of the basic number of the species (aneuploids). There is thus ample evidence of intraspecific variation in chromosome number in the grasses, and I shall now discuss the two main types of variation under separate headings.

Intraspecific Polyploidy

A few examples of species with intraspecific polyploid chromosome races are listed in Table 1. The data here represented are taken from the published papers of several authors, more than one of whom has, in some cases, worked on the same species. The chromosome races listed do not necessarily, therefore, occur in the same region or country. It will be noticed that some species show a wide series of numbers ranging from diploid to high polyploid, whilst others have a restricted series in which the diploid is not represented. There are some also which show marked gaps in the series which may yet be filled in by further research.

TABLE 1

Polyploid chromosome races in some grass species

Species	Chromosome Number $2n$							
	14	21	28	35	42	49	56	70
<i>Agrostis stolonifera</i>	—	—	x	x	x	—	—	—
<i>Holcus mollis</i>	x	—	x	x	x	x	—	—
<i>Calamagrostis brewerii</i>	—	—	x	—	x	—	—	—
<i>Calamagrostis epigejos</i>	—	—	x	—	x	—	x	—
<i>Festuca rubra</i>	x	—	—	—	x	—	x	x
<i>Festuca ovina</i>	x	x	x	—	x	x	x	x
<i>Alopecurus pratensis</i>	—	—	x	—	x	—	—	—
<i>Agropyron repens</i>	—	—	x	—	x	—	—	—
<i>Agropyron duvalii</i>	—	—	—	x	x	—	—	—
<i>Phalaris arundinacea</i>	—	—	x	x	x	—	x	—
<i>Bromus ramosus</i>	x	—	x	—	x	—	—	—
<i>Bromus erectus</i>	—	—	—	—	x	—	x	—
<i>Bromus inermis</i>	—	—	—	—	x	—	x	x

Any investigation of a species must naturally be confined to a very small percentage of the plants in that group. If, therefore, it is attempted to make an accurate estimate of the chromosome number of a species, the plant sample must be as representative as possible. It is of particular value, therefore, to know whether forms with varying chromosome numbers will occupy different areas. Although only a very few species have been studied intensively from this point of view, it is possible to see that chromosome forms may be distributed according to ecological or regional requirements, or they may occur at random showing no correlation with habitat type.

Perhaps the most thorough survey of chromosome races in the grasses is that carried out by Dr. Watson of the Scottish Plant Breeding Station, on *Festuca ovina*. She has found that the diploid form of this species ($2n=14$) occupies the east coast of Scotland, an area north of the lowlands and the east coast of England. The tetraploid race, on the other hand, exists exclusively in Wales, Ireland, south and west England and south-west Scotland. There is thus a very clear pattern of distribution in this case which seems to be on a regional, rather than an ecological, basis (Watson, 1954). Similarly in America, Nygren (1954) discovered that the tetraploid ($2n=28$) and the hexaploid ($2n=42$) races of *Calamagrostis breweri* occupied southern and northern areas respectively.

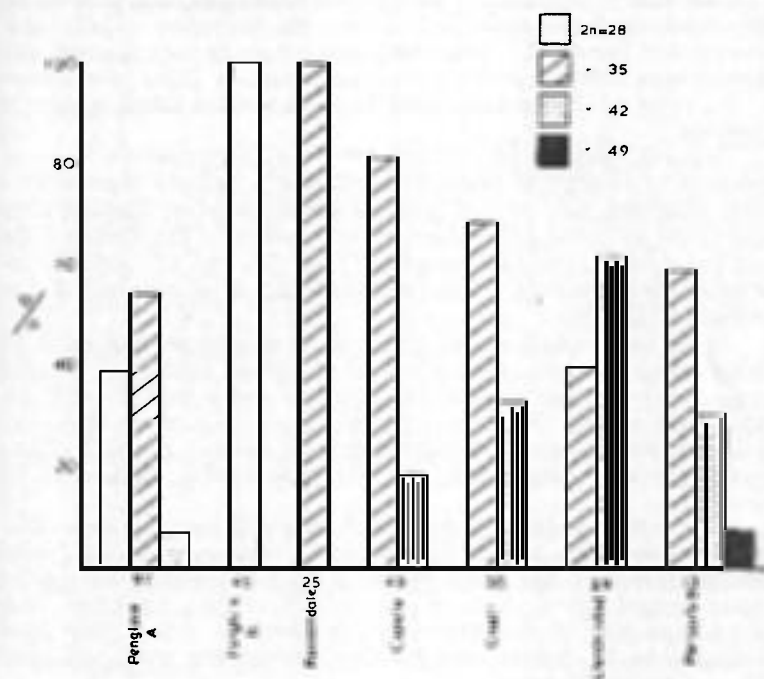


Fig. 1.

The relative frequencies of chromosome races in populations of *Holcus mollis* ($2n = 28, 35, 42, 49$).

Investigations which I have been making, in collaboration with A. R. Beddows at the Welsh Plant Breeding Station, on the genus *Holcus* suggest that the chromosome races of *H. mollis* ($2n=28, 35, 42, 49$) (Beddows and Jones, 1953; Jones, 1954) show some tendency to ecological specialisation. The histograms in Fig. 1 show the relative frequency of these types in some woodland areas of England and Wales, and in one arable area

(Penglais A). Only the tetraploid is present in one of these, whilst in the others the pentaploid occurs either alone or in conjunction with the hexaploid. Only two plants of the heptaploid have yet been recorded. Because the tetraploid has been found in only one of the woods examined it is not possible to be sure whether soil moisture is the essential factor in its distribution. However, there is evidence that the pentaploid and hexaploid thrive under conditions of high water content of the soil, with the hexaploid the more frequent in the wetter areas. It must be mentioned that all the races occur in a random assortment in areas disturbed by ploughing, tree-felling, etc., as in Penglais A. The pattern of distribution is apparent, therefore only, in well-defined ecological habitats. Clearly then, this species is in need of more study, particularly on an ecological basis, and it is to be regretted that the ecological studies of Ovington (1947) and Jowett and Scurfield (1949, 1952) were made at a time when the species was thought to be purely tetraploid. Here is evidence of the value of chromosome counting as a routine check wherever possible.

Another example of the distribution of chromosome races in relation to ecology is *Festuca rubra*. In a private communication, Harberd, also of the Scottish Plant Breeding Station, suggests that although most plants of this species in the British Isles are hexaploids ($2n=42$), octoploids ($2n=56$) can be found in extremely dry habitats. This is something of a reversal of the picture in *Holcus*.

Little can be said of the distribution of chromosome races in other grasses because of the lack of published evidence. It does seem, however, that the races of *Agrostis stolonifera* ($2n=28, 35, 42$), examined by Björkman (1954), sometimes occur together; whether this means that they generally show a random distribution, or only occasionally, as in *Holcus mollis*, remains to be seen.

The few examples quoted above are sufficient to show that chromosome races can be distributed in various ways, and, until an investigation has been made, it is not possible to predict what sort of distribution will occur. It follows, therefore, that a small sample of the species is not likely to give a very good estimate of its chromosome number particularly when collected from a restricted area.

There is still much work to be done on the comparative morphology of intraspecific races, but in general it seems that members of a series do not show any major taxonomic differences, and in some instances, such as *H. mollis*, it has not been possible to discover any qualitative differences. The lack of morphological differentiation may not be surprising when we realise that a pure reduplication of chromosome sets rarely brings about a morphological change as marked as that which can be caused by a single gene mutation. Nevertheless, polyploidy does have an important influence on the species in initiating genetic

discontinuity. From this beginning the species can break up into several groups which may eventually receive separate taxonomic recognition. Although this may not happen until morphological differences have developed, it is essential that the taxonomist from the very outset recognizes the chromosome types. The argument against this is the difficulty of identification, but in these days when cytological techniques have been improved and simplified, chromosome counts can easily be made by all who have access to a microscope. We might then consider chromosome number as a good taxonomic character, so that instead of involving ourselves in tedious and prolonged biometrical studies to separate the diploid and tetraploid forms of *Dactylis* or *Anthoxanthum*, we can resort to a chromosome count and be sure of our identification. Cytology should be regarded as a useful and very desirable aid to all species studies rather than as a regrettable necessity in a few cases.

Aneuploidy

The normal sexual species, and in particular the multivalent-forming polyploids, such as *Dactylis glomerata* and *Anthoxanthum odoratum*, occasionally give rise to progeny having a few chromosomes in excess of, or less than, the normal chromosome number. Such types are called aneuploids. In *Dactylis* they have been recorded as occurring with frequencies of 15 per cent (Müntzing, 1937), 40 per cent (Myers and Hill, 1940) and as little as 3-4 per cent in my own studies. Such deviations in chromosome number are the result of slight irregularities in chromosome pairing at meiosis and seem to be of no evolutionary or taxonomic significance in these cases. In apomictic species, however, the aneuploid can be much more frequent and assumes a greater importance. In the apomictic Poas, for instance, the bulk of the plants investigated seem to be aneuploid and there can be a very wide range in chromosome number, e.g. *P. pratensis* $2n=48-124$, *P. subcaerulea* $2n=82-147$, *P. arctica* $2n=39-92$, *P. alpina* $2n=31-57$ (see Gustafsson, 1947, for references). Such types are the result of pronounced irregularities that can occur in chromosome behaviour in the EMCs. of apomictic species. It is interesting to see that there are species which are insensitive to chromosome unbalance, in contrast to *Agrostis stolonifera* and *Holcus mollis* which seem to show selection against aneuploidy.

Both these species show marked meiotic irregularities in their pentaploid and hexaploid forms, and chromosome counts made on seedlings raised from these races after open-pollination or intercrossing, are indeed mainly aneuploid. This is well illustrated by the data in Table 2. It will be seen that practically all the seedlings are aneuploid and yet only one or two such types have been detected in the large samples of plants collected from natural populations. It is thus quite clear that in making determinations of chromosome number, we must distinguish

TABLE 2

Chromosome numbers of the progeny of the 28, 35 and 42 chromosome races of *Holcus mollis* and *Agrostis stolonifera**

Species	2n=21	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>H. mollis</i>	7	1	3	2	4	11	20	7	3	1	5	4	2	2
<i>A. stolonifera</i>							3			5	6	8	9	13

Species	2n=36	37	38	39	40	41	42	43	44	45	47	49	62
<i>H. mollis</i>	1		6	1	3	1	1		2	4	1	1	1
<i>A. stolonifera</i>	11	7	3	6	2	3	1	2		4			

between the *potential* chromosome number of the species, as found in artificially-reared seedlings, and the *actual* chromosome number that exists in the natural population. Since it is the species as it exists that is of the greatest interest to the experimental taxonomist, we should examine chromosome number after, and not before, natural selection has operated. Although there is little doubt that aneuploids are common in the Poas, most of the chromosome counts that have been made were on experimental seedlings raised in the greenhouse or garden. It would seem more profitable, in estimating the frequency of aneuploids in various regions of the world, to collect plants *in situ* for such an examination.

B-chromosomes

In many species individual plants can be found having one or more B-chromosomes in addition to the normal complement. Chromosomes of this type are generally smaller than the normal and show no homology with them; neither do they appear to have any qualitative effect on the external phenotype. I do not wish here to discuss the origin or significance of the B-chromosomes except in their relation to the accuracy of chromosome counting. Within the species, and even within the individual, B-chromosomes can vary in number, and often it is difficult to distinguish their presence in root tip counts. B-chromosomes can be mistaken for additional normal chromosomes in such instances and a plant may erroneously be considered to be a true aneuploid. Observations of chromosome pairing at meiosis will usually solve this difficulty. B-chromosomes have been discovered in *Festuca pratensis* (Bosemark, 1954), several species of *Poa* (Müntzing, 1946, Müntzing and Nygren, 1955) and *Agrostis*, (Björkman, 1951, Jones (unpublished)), the diploid and tetraploid forms of *Dactylis* (Jones, unpublished), *Alopecurus pratensis* (Johnsson, 1941), *Anthoxanthum aristatum* (Östergren, 1947), and many others.

*Björkman (1954)

VARIATION IN CHROMOSOME PAIRING

Chromosome pairing at meiosis can give important information relative to the nature and evolutionary origin of a species. Its study in hybrids helps to understand species relationships, and taxonomic classifications may be affected as a result. It is important therefore that data on pairing are representative of the species or its hybrids. A knowledge of the possible extent of pairing variation in the species will assist the cytotaxonomist in drawing his conclusions.

Unfortunately, little has been done to investigate the range of pairing variation in a normal sexual species. Our studies have usually been confined to but a handful of plants or have been concentrated on the abnormalities of meiosis. In the course of intensive investigations on the genus *Dactylis*, which are being made in co-operation with my colleague Dr. Martin Borrill, I have had occasion to examine in detail at meiosis 136 plants of *D. glomerata* collected from a number of localities in Europe, and the Mediterranean area. In addition F_1 hybrids between plants from different areas, as well as samples from commercial and pedigree strains, have been analysed. The results of these researches are summarized in Table 3, and show that, as judged by quadrivalent formation, pairing is very uniform and is unaffected either by hybridization, or selection for fertility over a large number of sexual generations, as must occur in strain building. The hybrids further show that despite extreme differences in morphology between ecotypes there is no appreciable degree of chromosome differentiation.

TABLE 3

The cytology of *Dactylis glomerata* ($2n=28+$)

Material	Per cent aneu-ploids	Per cent plants with B-chromosomes	Per cent plants with AI laggards†	Total plants	Mean quadri-valent	Per cent trans-location hetero-zygotes	Total plants
Ecotypes (10)*	3.7	9.7	13.0	216	2.97	10.9	64
Ecotype × ecotype (6)**	1.9	—	15.4	52	2.49	2.7	37
Bred strains (4)***	2.7	—	13.5	37	3.04	—	35

† Any plant with more than 15 per cent of AIs with laggards recorded.

* Ecotypes from Silesia, Austria, France, Norway, Finland, Portugal, Sicily, Cyprus, Israel, Turkey I and II.

** Ecotype F_1 crosses = Cyprus × Cornwall, Cyprus × Israel, Scilly × Cyprus, Scilly × Israel, Scilly × France, Cornwall × France.

*** Strains = American, Danish, S.26, S.143.

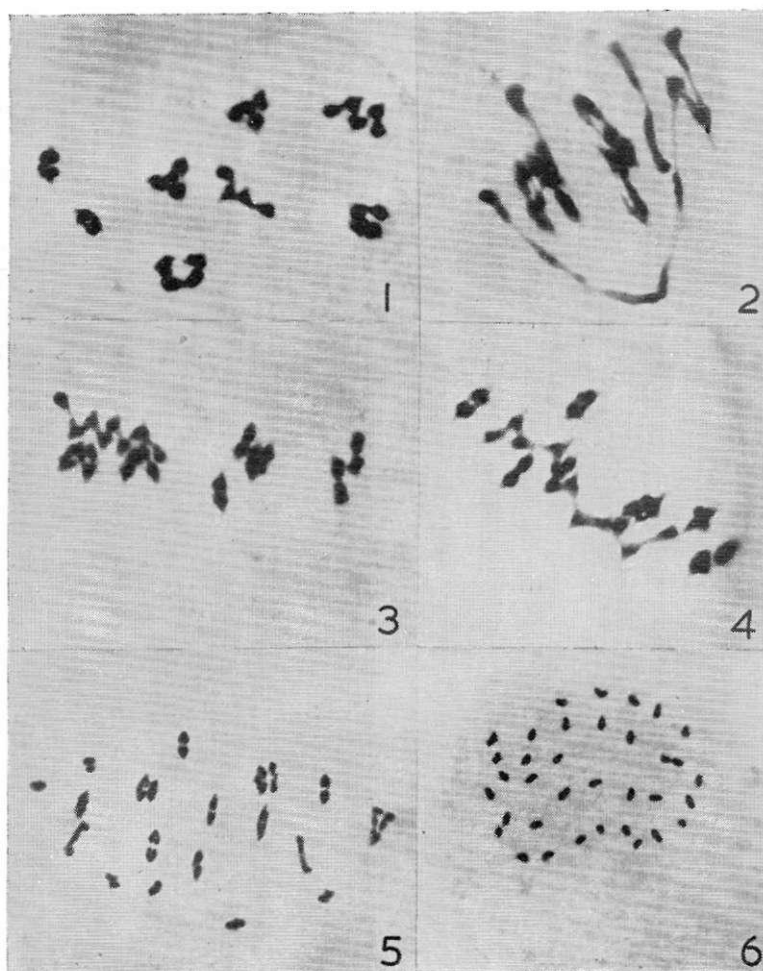
The survey of the species shows for the first time that 10.9 per cent of the plants from natural populations are translocation heterozygotes. These have associations of 6, 8 or even 12 chromosomes at metaphase I of meiosis (Plate I, Figs. 3 and 4); 2.7 per cent of the hybrids were of this type and none was present in the strain material of which only a small sample has yet been examined. Laggard univalents were present in more than 15 per cent of the first anaphases in approximately 15 per cent of all the plants examined. Whether this is due to the environment or not, will be seen in the coming season. The survey is being continued but already we have a good picture of the cytology of this species which enables us to see in true perspective the significance of the cytology of any individual plant which may later be examined.

Similar studies are being made on *Anthoxanthum odoratum*. This is also a quadrivalent-forming species and my analysis of four populations collected by Dr. Borrill shows that meiosis is again uniform with all plants having means of about 2.5 quadrivalents. The most interesting result of this investigation to date, however, has been the finding that every plant examined is heterozygous for at least one translocation; commonly, an association of 6 or 8 chromosomes occurs at meiosis in addition to the quadrivalents (Plate I, Fig. 2). We thus have a species in which there is a high degree of hybridity selection similar to that known in *Oenothera* species. Only the analysis of a wide range of material can reveal such a situation.

The results obtained on the above two species are not surprising. In particular, the uniformity in chromosome pairing may have been expected as they are species which rely on sexual reproduction for their successful propagation. Natural selection has therefore acted to produce the most efficient type of pairing for good fertility and has resulted in the species showing the optimum degree of quadrivalent formation. It may be significant that there is no evidence of a "shift" to bivalent formation in any of the groups studied.

Meiosis may be less uniform in those species in which sexual reproduction is not at a premium. The pentaploid and hexaploid races of *Holcus mollis*, for example, show very marked intraracial differences in this respect. In the pentaploid race plants show all types of pairing, from that in which there are only a few univalents to those in which all the chromosomes are unpaired, (Plate I, Figs. 5 and 6); they differ also in the type and degree of multivalent formation, and, of course, in their fertility. The hexaploid race shows similar but less extreme variation. There is no doubt that the pairing differences in these plants are not due solely to the external environment although this must have some effect. They are due rather to the genetic and chromosomal constitution of the individuals, which in this case may be of somewhat different origin despite their uniform appearance. However it is clear that the whole range of variation must be

PLATE I.



First metaphase of meiosis in some grasses.

Fig. 1. *Dactylis glomerata* ($2n = 29$) Aneuploid, 1v 4iv 4

Fig. 2. *Anthoxanthum odoratum* ($2n = 20$).

Translocation heterozygote, 1vI 1iv 5II

Fig. 3. *D. glomerata* ($2n = 28$).

Translocation heterozygote, 1vIII 4iv 2II

Fig. 4. *D. glomerata* ($2n = 28$).

Translocation heterozygote, 1xII 8II

Fig. 5. *Holcus mollis* ($2n = 35$). 1III 13II 6

Fig. 6. *H. mollis* ($2n = 35$). Asynaptic plant, 35

examined if the nature of the races and their reproductive method are to be known. It might be mentioned here that although the races can produce a good quantity of germinable seed, we have already seen that most of it is aneuploid and incapable of producing mature plants in the field. The appearance of fertility is thus deceptive, and the plants are effectively sterile under natural conditions. Such a situation may well occur in other grasses and we should be careful to distinguish between "yield" and "fitness" when considering the significance of seed production.

The apomictic grasses can exhibit all types of transitions between meiosis and mitosis in their generative tissues. The irregularities of the division are usually more pronounced on the male side because selection operates on female, rather than on male, fertility. It is also possible for meiosis to occur in the PMCs, whilst at the same time divisions in the EMCs. are exclusively mitotic. We can, therefore, find in the apomicts, not only intraspecific variation but also intraplant variation. The classic study of apomixis in the grasses is that of Nygren (1946) on *Calamagrostis* spp. in Scandinavia. The three species *C. lapponica* ($2n=42-112$), *C. purpurea* ($2n=56-91$) and *C. chalybea* ($2n=42$) show a most interesting range of behaviour in their PMCs, from very disturbed meiotic divisions with some mitosis in *C. lapponica*, to practically complete mitosis in *C. chalybea*. Chromosome behaviour in the EMCs. was more uniform in the three species. I would refer you to Nygren's excellent paper for further details. The most important aspect of his studies, from the point of view of the present discussion, is the demonstration that chromosome behaviour in the apomicts can be profoundly affected both by the physiological state of the plant and by the external environment. One plant of *C. purpurea*, fixed in its first year of growth, showed only meiosis in both its EMCs. and PMCs. Fixations of florets of varying ages in the second year showed fewer meiotic and more mitotic divisions with the percentage of mitoses increasing with the age of the floret. Differences in temperature as between alpine and sub-alpine regions were also able to affect the divisions, though not to the same extent. Here then we can see that the behaviour of the chromosomes is a product of the interaction of genotype and environment, but that in apomicts the genotype is more responsive to changes in the internal and external environments than is the case in most sexually reproducing species. Nygren points out that if the environment has an important part to play in conditioning the reproductive method we should endeavour to make fixations of such plants in their natural environment rather than from transplants in the experimental garden.

Finally, a word may be said about pairing variations in hybrids. Gaul (1953) has demonstrated such variation in hybrids of *Triticum aestivum* and *Agropyron intermedium* where F_1 hybrids between the same two species had univalent means

ranging from 14 to 38 per plant. In my own experience F_1 hybrids of *Agrostis tenuis* and *A. stolonifera* had means of from 4 to 14 univalents per plant (Jones unpublished). These differences were not attributable solely to the effects of the external environment but were a reflection of the chromosomal constitution of the individual hybrids. Patently, it would not be possible to place reliance on a single individual when drawing phylogenetic conclusions from pairing. It must be remembered, of course, that when we deal with outbreeding grasses the F_1 is a segregating generation.

CONCLUSION

A wide field has been covered in this talk, and the examples chosen, though perhaps extreme, demonstrate that it would be unwise to ignore cytological variation in species studies. What bearing will this knowledge have on cytotaxonomic methods? It must, I think, influence methods of sampling. Studies based on one or two individuals are of limited value, whether they be species or hybrids, and it becomes necessary to examine a much larger number of individuals which have been collected in a wide range of ecological conditions. Invariably it would seem better to collect plants rather than seed for, as we have seen, the seeds may represent not only the potential *biotypes*, but also the potential *cytotypes*. However, it is often impossible to obtain plants, and reliance may have to be placed on experimental seedlings. In such cases great variations in chromosome number should be looked upon with suspicion until population plants have also been examined. Above all it is important that the source of material used for chromosome determinations should be clearly stated in publications so that the reader can see for himself whether or not the actual population plants have been investigated.

Studies of chromosome pairing in sexual species can safely be made on cultured material but the apomicts should wherever possible be studied in their natural environment. Whether the species is sexual, apomictic or hybrid, however, the intensive type of investigation will yield more fruitful results than that which embraces a number of species but only a few representatives from each.

Quite clearly there are many ideals in cytological investigations which for several reasons may be unattainable. However this may be we cannot fail to profit if, at least, we are aware of the limitations of our methods and avoid gross generalizations.

Most of you will be familiar with these pitfalls; if, however, by re-emphasizing them one can encourage the intensive approach to the study of the British flora then one may feel that a contribution has been made.

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Prof. T. G. TUTIN said that if *Festuca ovina* is diploid on the east coast and tetraploid on the west, it would be interesting to know what happened in the middle. Mr. JONES replied that he was quoting from Dr. Watson's paper, and she did not say.

THE IMPORTANCE OF EXPERIMENTAL ECOLOGY TO THE STUDY OF THE BRITISH FLORA

F. H. WHITEHEAD (University of Oxford)

Of the problems concerning the distribution of plants I would like to confine my talk to that of the plant and its habitat. It needs little more than a cursory glance to be convinced that habitat and plant distribution have some connection; closer examination usually discloses how complex the relationship may be.

The descriptive side of these problems has received considerable attention but far less experimental work has been attempted. I hope to show that suitable experimental methods and techniques can contribute greatly to our understanding of the underlying causes of plant distribution.

It seems to be far from generally realised that the description of a problem is not its solution, and, to go one stage further, the demonstration of a correlation is no proof that the factor concerned is causal. For example, it would be possible to show on a calm sunny day that there is an inverse correlation between barometric pressure and photosynthetic rate. Experiment would show that there was no causal connection, but that both barometric pressure and photosynthetic rate are independently associated with a third factor, namely the intensity of radiation from the sun. It is this type of complexity of factor relationships which is so often found in plant ecology and which only experimental methods can elucidate.

As would be expected, correct scientific approach is of the greatest importance in the investigation of these problems at whatever level they are made. Briefly, it can be said that descriptive ecology discloses the existence of problems, and often includes some correlation of distribution and habitat factors. Such correlations permit the making of working hypotheses, and then experimental ecology tests these hypotheses, either demonstrating their validity, or leading to new hypotheses and further experiments.

The investigations can be carried out at various levels of refinement, and the examples given are chosen to illustrate the different types of problem and approach. At what may be termed the first level of investigation, we have the type of experimentation which consists of transplants. There is a considerable body of data on this type of experiment. To choose a few, there is the work of Gaston Bonnier (1894), of Clements *et al.* (1950), and the Potterne experiments of Turrill and Marsden-Jones (1930).

These last contributed very greatly to taxonomic knowledge and to ecology. Their experiments were designed to test the effects of different soils on selected species of the British flora, and, amongst other findings, demonstrated that adult plants are often successful on soils other than those on which they are usually found, but that their performance is frequently affected considerably by changes from their usual soil. As a supplement to this investigation it would be very interesting to see if seedlings could establish themselves. Very frequently it is at this stage that elimination takes place, thus deciding distributions.

At the other extreme from the Potterne experiments, we have the very detailed work of Blackman & Rutter (1946-1949) on *Scilla*, and Harley *et al.* (1953) on the mycorrhiza of beech. I would like to mention one small part of this latter work as an illustration of its nature. It is often claimed that the distribution of certain mycorrhizal plants is determined by the needs of the associated fungi, and Harley's work is an investigation of the nature of the relationship between beech, its mycorrhiza, and the environment. It was found by the use of radio-active isotopes that the uptake of phosphorus and potassium was greatest at an oxygen concentration of about 20%. It seemed that the oxygen tension in the region of the feeding roots, i.e. in the litter, would be an important factor. No data were available but by an ingenious technique this was measured in the field. It was found that the oxygen concentration throughout the year fluctuated about the 20% value. This demonstration of the agreement between field and laboratory results shows the value of such experiments.

An example of experimental ecology I should like to discuss in more detail was carried out at Oxford by Rorison (1956). Why some plants are found on chalk soils, and others only on acid soils, has always intrigued ecologists, and this work was an attempt to see what part mineral nutrition, competition, etc., played in this phenomenon.

Two calcicoles, *Scabiosa columbaria* and *Asperula cynanchica*, and two calcifuges, *Holcus mollis* and *Galium saxatile*, amongst others, were studied both in the field and the laboratory. The minerals most closely studied were calcium, potassium and phosphorus. Plants were grown in water culture using Analar chemicals. Replicates were made up in a series of varying amounts of *Ca*, *K*, & *P* including approximations to the soil types used in the field. One series was adjusted to a high pH the other to a low pH. No very significant differences in performance were found in the growth of *Scabiosa*. Plants grown from seed sown in the field, however, all died on the soils with low pH. From this it was concluded that there was present in the acid soil something, or some condition, that was absent from the water culture. Further water cultures were set up, using soil extracts from the acid and alkaline soils in place of the nutrient solution, and these again were adjusted for pH. *Scabiosa* grew quite well in the soil extracts from both soils when they were

adjusted to a high pH, but growth was poor, particularly in the acid sand extract, at low pH. From this it was concluded that the substance affecting growth was water-soluble and relatively abundant in the acid soil. It was thought that aluminium might be a possible substance. To test this hypothesis aluminium was added to the Analar culture solutions again at two pH levels, and the plants grown on these showed the same symptoms and performance as those grown on the soil extracts—i.e. growth was satisfactory at the high pH and poor at the low pH.

The symptoms themselves are of great interest, since the effects noticed were the malformation of roots and the very small amount of root system formed in the solution at low pH. Since *Scabiosa* requires a well aerated soil for growth, it seems likely that, in the presence of aluminium and in soils with a low pH, the root system is inadequate to supply the plant with its necessary water in the seedling stage, and death is probably from drought in such soils.

It seems likely then that the distribution of *Scabiosa columbaria* in Britain is determined by either a high pH in the soil or a lack of aluminium. Since the latter is rare in the British Isles, and since here the only common soils with high pH are those containing calcium carbonate, the distribution of *Scabiosa* has previously been considered as being determined by calcium, whereas these results show that this is not necessarily so. The results for *Asperula cynanchica* were very similar to those for *Scabiosa*.

Results for *Holcus mollis* and *Galium saxatile* were less easily interpreted, and at the moment it is perhaps best to sum them up as probably showing that these species have large potassium demands and that for some reason the uptake of potassium appears to be interfered with or inhibited by any large concentration of calcium ions.

These experiments have shown fairly clearly the broad outline of the ecological distribution of *Scabiosa*, etc., and something of the physiological processes underlying them.

Finally, I should like to refer very briefly to some experimental ecology of my own. Although the field work was not carried out in this country it is probable that similar conditions can be found here. This work is on the relationship of vegetation and the effects of wind. An aerodynamic parameter Z_0 can be used as a scale by which to indicate the degree of shelter which a rough stony surface gives to plants. The larger the stones the more shelter and the greater the value of Z_0 . It was found that those criteria of vegetation which can be grouped collectively under the term luxuriance are all related to the value of Z_0 . Thus, in the most exposed community (type Area A) where the stones are small there are very few species, a smaller range of life form, smaller % cover, lower % yield (grams per square metre), a lower average plant height, etc., than in the most sheltered area. Intermediate values are exhibited by communities with intermediate

values of Z_0 , so that the figures present an intergrading series from the most exposed to the most sheltered community types.

Alternative explanations, e.g. shading, might be advanced or it might be argued that these findings are mere coincidence. A very simple experiment sufficed to settle both points. If the characteristics of the vegetation depend on the nature of the surface, then if the surface is altered there should also be a change in the vegetation. This experiment was carried out by building low stone walls around quadrats in the most exposed area where the vegetation had been accurately mapped. These were orientated so that the cardinal points lay on the diagonals of the squares. Thus one corner pointed north, the opposite one south, etc.

In this particular region because of local topography the wind is strongest from the west. Now, if shading is the causal factor, the greatest increase in height would be against the S.W. and S.E. walls. In fact it was found that the greatest increases in height were against the N.W. and S.W. This shows that the operative factor is a western component and not a southern, thus indicating that shelter from wind is more important than shading from the sun in this particular situation.

Experiments in the laboratory have yielded valuable results concerning how these variations in height are produced. They have also shown that for many plants there is a critical "wind speed/time exposed" value which, if exceeded, ends in the death of the plant. It is this factor which appears to be determining to a great extent plant distribution in these mountain top areas.

From these few examples, it can be seen that experimental ecology is beginning to discover some of the underlying explanations of distribution. There are at present far too few data to justify the announcing of general principles. For instance, it is by no means certain, or even probable, that the findings with regard to *Scabiosa* and *Asperula* are applicable to all calcicoles. Indeed, it can be said that one of the most important conclusions to be drawn from most experimental ecology, is that problems are far more complex than was thought at one time. However, it can also be said that the results indicate that their solution is not an impossibility.

In conclusion, I would like to make a special plea for more experimental work, especially of an autecological nature. Descriptive ecology has disclosed a wealth of such problems which need investigating by experimental methods. Besides advancing our knowledge of plant distribution it is more than likely that the results would have important practical applications.

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Prof. D. H. VALENTINE expressed full agreement with Dr. Whitehead about the value of work on experimental ecology. To add another example to those which had been quoted, he referred to the series of papers by Dr. V. M. Conway on *Cladium mariscus*. By combining experiments in the laboratory with observations in the field, she was able to demonstrate very convincingly the mechanism of the aeration of the rhizomes and roots of this fen plant. Dr. WHITEHEAD suggested that it was a pity that Conway's work was not followed up.

Prof. T. G. TUTIN said that he had been very interested in the contrast between the behaviour of *Scabiosa columbaria* and *Asperula cynanchica*, which he had transplanted into his garden near Leicester. This was on boulder clay, with soil with a pH about 6—it was sufficiently acid for Rhododendrons and other calcifuges to grow well. *Scabiosa columbaria* survived for only a few years after introduction and then died out; *Asperula cynanchica*, on the other hand, became a garden weed regenerating freely each year from seed. This suggested that it was less sensitive than the *Scabiosa* to competition.

**THE IMPORTANCE OF THE STUDY OF DISJUNCT DISTRIBUTIONS
TO PROGRESS IN UNDERSTANDING THE BRITISH FLORA**

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In this paper I propose to draw attention to some new ideas about the history of some parts of our flora, but to comparatively few new facts. This paper is, indeed, the result of pondering about our "wild" British flora and vegetation after some years' experience of studying its structure and distribution in the field, and also of considering the valuable results of modern work on pollen analysis and peat stratigraphy. It is hoped that it may do a little to stimulate further experimental work on the autecology of our flora.

We now have, from the brilliant and painstaking researches of Godwin (1940, 1947, 1953) and his co-workers, a fairly clear picture of the main phases of vegetational climaxes in Britain in the Late- and Post-glacial Periods, from about 12,000 B.C. to the present day. We also know, from Godwin's work (1940, 1949), that the problem of the per-glacial survival of a part of our flora, though of academic interest, is of little practical significance to-day, because in the Late- and early Post-glacial periods widespread open conditions enabled a great many species, not only arctic-alpines but also those types we now find either as weeds of cultivation or in open calcareous habitats, to spread widely over Britain. For example, in the Late-glacial, *Potentilla fruticosa* occurred in the Lea Valley (Godwin, 1949); and *Polemonium caeruleum* in the Lea Valley (*ibid.*, 1949); at Hawks Tor in Cornwall (Conolly, Godwin & Megaw, 1950); and in Surrey, North Hants. and Berks., Norfolk, Hunts., and Shropshire (Godwin unpub.). These and others, such as *Helianthemum canum*, are now very rare or local.

So modern plant distributions must in general be studied and interpreted in relation to post-glacial historical changes, rather than in terms of spread from per-glacial "refuges". This fact was appreciated many years ago by Watt (see discussion with Salisbury and Wilmott in *Proc. Roy. Soc., B*, **118**, 197-241, 1935).

The first major historical change in the Post-glacial Period was the spread of forest and blanket-bog over nearly all the surface of Britain with the development of the warmer climate of the Boreal and Atlantic Periods (zones IV-VII of the pollen-analyst). This must have restricted those species of open habitats, intolerant of shade or of forest competition, to a limited number of refuges where open conditions persisted for one reason or another, such as mountains above the tree-limit, cliffs or steep

slopes, both inland and coastal, sand-dunes, and certain types of fen, marsh, and lake-shore communities.

In the early Post-glacial Period, when men were few and their organisation little developed, they appear to have had little more effect on the vegetation and flora than the wild animals, but, later on, the biotic effect of man became much more pronounced, not only on the areas which he completely modified into arable lands or built-up areas, but on the vegetation as a whole, including what we now call "wild" vegetation. It is with the study of the possible course of some of these effects that this paper is concerned, particularly with the effects shown in terms of changes in the distribution of certain "ecologically significant" species.

Let us first consider what vegetational changes due to early man there are of which we have positive historical evidence.

Godwin (1944) and Godwin and Tallantire (1951) have shown that, while until Neolithic times (about 2600-1600 B.C.) the Breckland region of East Anglia carried mixed oak forest, from this time onwards forest clearance took place, as is shown by the marked reduction in the proportion of tree-pollen and the increase in that of non-tree-pollen (of grasses, sedges, and heaths particularly). This change apparently received an impetus in Bronze Age times (about 1600-500 B.C.), so that by the close of that period many of the East Anglian chalk grasslands and Breckland grass-heaths must have already come into existence. Though positive evidence is not yet available in detail, much the same sort of clearance probably took place in other regions of dense Neolithic and Bronze Age occupation in England (e.g., in Wessex, the Cotswolds, and the South Downs in the Neolithic Period, and on the Greensand and Bagshot Sand areas of S.E. England in the Bronze Age). On the other hand, some areas (such as the Low Weald, the Boulder Clay plateau of East Anglia, much of the Midland Plain, the Chiltern plateau, and much of the North Downs) show little sign of prehistoric colonization, probably due to the heavy clay soils of these areas which were difficult to clear and to cultivate; and, indeed, several of these areas are known to have remained dense forest until relatively late historical times.

We are left, then, with the following fairly well authenticated picture of post-glacial vegetational history: (1) A wide, more or less continuous distribution in the Late-glacial and early Post-glacial of many species of open, usually calcareous habitats; (2) A later elimination of these species by the spread of forest and blanket-bog, except from certain refuges of the types mentioned above, so giving disjunct, relict distributions; and (3) a second spread of some of these species after forest clearance to new open habitats created directly or indirectly by man, while others have been unable to take advantage, for one reason or another, of any recent increase in the area apparently made available to them.

Pigott and Walters (1954) originated this hypothesis, and they discuss it in considerable detail with regard to "calcicole" species, mainly of the Continental type of distribution in Matthews' (1937, 1955) sense. Indeed, this paper owes much to the stimulus of their ideas. A similar glacial relict hypothesis has been developed for Sweden by Sterner (1922).

I wish to bring forward in this paper further hypotheses about the distributional history of some of the calcicole plants of open habitats, and also some ideas on the possible history of other, contrasted, ecological and distributional groups of species in our English lowland flora, which in my view show similar signs of phases of spread and subsequent restriction to disjunct, relict habitats.

The groups of species showing possible relict distributions that I propose to consider are:—

- (1) The calcicole species of dry open habitats, mainly of "Continental" distribution in Matthews' sense.
- (2) The calcicole species of wet open habitats, some of which are of "arctic-alpine" distribution.
- (3) The calcifuge species of wet open habitats, e.g. lowland valley bogs and wet heaths in areas below the present treeline.
- (4) Forest relict species of "Oceanic" type.
- (5) Forest relict species of "Continental" type.
- (6) Coniferous forest relict species of "Continental Northern" or "Northern Montane" type.

GROUP (1).

In this group come most of the species considered by Pigott and Walters (1954), and considered briefly above. The fact that many of these "Continental" species are calcicoles appears to be correlated with the Continental type of climate (see Walters, 1953). The problems I wish to consider here are (a) the possible sites of some of the refugia of these species, and (b) the possible routes and nature of subsequent spread of some of these species. These refugia may have been in the areas where the plants are now most plentiful; or they may have been at a distance from the areas of present abundance.

The most interesting distributions are perhaps shown by those species which are at present concentrated down the east side of England, but are absent in S.E. England for no apparent ecological reason. *Anemone pulsatilla* is a good example of this kind. Until recently it was distributed from Piercebridge on the Tees down the Magnesian Limestone to S.W. Yorkshire, down the Oolite from N. Lincs. to N.E. Northants, and along the East Anglian chalk from N.W. Norfolk to Tring in Herts; an outlying area occurs in the Cotswolds, and another on the chalk of N. Berkshire (see Lousley, 1950, p. 216). Although now believed to be extinct in Yorks, it formerly occurred in several localities

on the Magnesian Limestone near where rivers cut through it to form steep cliffs or slopes, as at Piercebridge on the Tees, Knaresborough on the Nidd, Thorpe Arch on the Wharfe, Brotherton on the Aire, and at Smeaton Crag on the Went. Some of these sites may well have provided refugia for this species: at Knaresborough, for instance, the cliffs still support *Silene nutans* and other species which are intolerant of competition, and which I have seen in southern Germany growing together with *A. pulsatilla* on cliffs surrounded by dense beech forest, in which these species are absent. Subsequent spread may have occurred southwards at, or after, the time of the Neolithic forest clearances, down the Oolite through Lincs. and Northants., and across the Fens (possibly by means of the feet of animals over this area which was, in part, dry in Bronze Age times, see Godwin and Clifford, 1935), into the East Anglian chalk country, where *Anemone pulsatilla* was formerly far more abundant over the open sheepwalks than today (see Babington, 1860). Its present restriction there, and in Lincolnshire, mainly to old earthworks and road verges is an interesting example, historically documented, of a species becoming confined to small refuges for a second time; apparently this time to refuges, not from the forest, but from the plough.

The outlying areas of this species in the Cotswolds and in Berkshire are isolated by present (and former) forests from the main area and were probably colonised from local refugia. Biometric studies on these local populations might yield some data on their degree of genetic isolation and hence on their relative age.

Carex ericetorum is another species of open calcareous grassland with probably a rather similar recent history. It was formerly thought to be confined to Breckland, and to be a good example of a continental species which invaded Britain fairly recently from the east. It is now known, however, in grassland on the Magnesian Limestone in several places from near Bolsover in Derbyshire to near Ripon in Yorks (Lousley, 1950), on the Lincolnshire Oolite, near Ancaster (Miss E. J. Gibbons, personal communication), and in two upland localities, on Widdybank Fell in Teesdale and on Scout Scar in Westmorland. Before the vast limestone "heaths" of Lincolnshire were enclosed and ploughed in the 18th and early 19th centuries, the species may well have had a more or less continuous distribution along the Lincolnshire Oolite (see fig. 2a). In this case one may postulate survival of the species on the sugar-limestone of Teesdale above the tree-line through the period of forest maximum, and subsequent spread down the Magnesian Limestone as this was cleared, followed by spread to East Anglia as suggested for *Anemone pulsatilla*. There is evidence that the Neolithic cultures of the eastern side of England were interconnected and contemporary (Glyn Daniel, 1951).

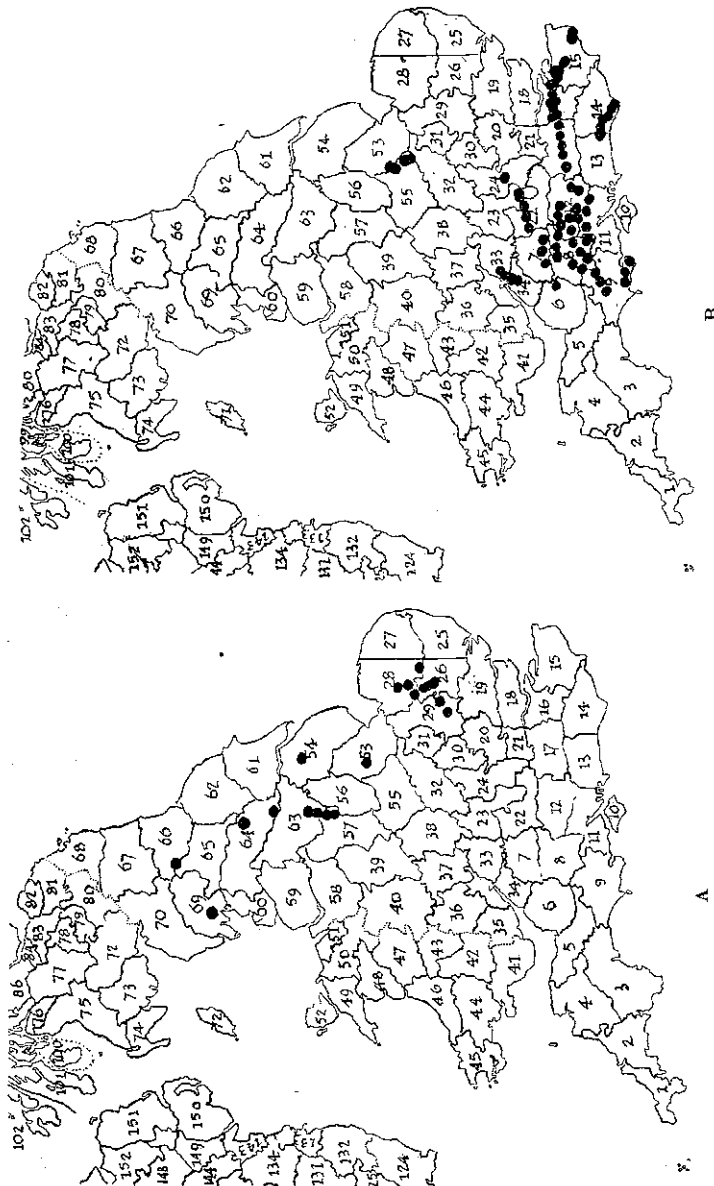


FIG. 2. Distributions in Britain of (a) *Carex ericetorum* (b) *Polygala calcarea*.
With acknowledgment to the "New Naturalist" for the use of part of their base-map.

Astragalus danicus has a similar distribution-pattern to *Anemone pulsatilla*, but extends far to the north along the coast into Scotland; in this northern part of its range it is largely confined to sand-dunes, which could have provided an excellent open and calcareous refugium for it during the forest maximum.

Perhaps the two most interesting and significant features shown by the East Anglian calcicole flora as a whole from the geographical viewpoint are:—

(1) Its close similarity in component species with the Lincolnshire Oolite flora; *Hypochoeris maculata*, *Thalictrum minus*, *Anemone pulsatilla*, *Astragalus danicus*, *Herniaria glabra*, and *Carex ericetorum* are all very local species these areas have in common which are absent in S.E. England, and there are many other more widely distributed species common to the two areas.

(2) The striking way in which many of the more "exacting" calcicoles disappear as one passes south-westwards, all of this group being absent from the Chilterns S.W. of Tring (see fig. 2a). The south-western recorded limits of some of these species on the East Anglian chalk are given below:

Carex ericetorum—Cambridge.
Thesium humifusum—Sandon, Herts.
Thalictrum minus—Royston.
Phleum phleoides—Hitchin.
Hypochoeris maculata—Knockinghoe, Beds.
Seseli libanotis—Knockinghoe (? formerly to Dunstable).
Astragalus danicus—north of Luton.
Carum bulbocastanum—Tring.
Anemone pulsatilla—Tring.
Senecio integrifolius—Tring, and a little beyond.

On "old" chalk grassland near Wendover (S.W. of Tring) none of these species occur, though conditions appear ecologically suitable: historical features would appear responsible for this.

It is perhaps significant that, while all the chalk N.E. of Tring up into Norfolk was covered by an ice sheet, the Chilterns chalk S.W. of this town was not, and unlike the chalk to the N.E., retains a dense plateau cover of clay-with-flints. With this clay cover is associated a dense forest cover, mainly of beech, which, though apparently denser now than in earlier historical times, appears always to have been present to a great extent on the plateau at least. This forested Chilterns area bears little evidence of early man, who may well have found it difficult to clear; and thus the Chilterns forests may have remained as a barrier to the south-western spread of the peculiar East Anglian calcicole flora. As mentioned above, the Cotswolds (heavily settled in Neolithic times) may have provided, on cliffs or screes of the harder Oolite, local refugia for the *Anemone*, the *Astragalus*, *Senecio integrifolius*, and the open-habitat *Carex tomentosa*.

POSSIBLE REFUGIA IN S.E. ENGLAND

In the chalk areas of the south-east, many of the species mentioned above are absent or very local; Neolithic settlement was much more local in this region, and much clay drift with forest cover exists. However, there are a few possible sites where refugia could have existed, and it is notable how the more local open-habitat calcicoles are associated in most cases with the neighbourhood of these possible refugia. I shall now discuss some of these sites.

The Boxhill River Cliff, Surrey. The occurrence of the box (*Buxus sempervirens*), a "Southern Continental" species, on the steep warm S.W.-facing slope here is discussed by Pigott and Walters (1953), who point out that on this slope, constantly undercut by the River Mole, and hence not available for development of closed climax forest of beech, the box may well have found a refuge through the period of forest maximum. One can see today the apparent inability of the beech to spread on to the steep box-dominated area from the more gentle scarp to the south-east. It is perhaps significant also that two mosses, *Isoetecium striatulum* and *Pleurochaete squarrosa*, are confined on the western North Downs to this slope: the former occurs on ash roots in the open woodland, the latter in small areas of very open chalk turf: both are southern species, the latter Mediterranean. A similar steep river-cut slope in the Arun gap through the South Downs also has abundant box (R. A. Boniface *in litt.*).

The Medway Gap in the Kent North Downs. Neolithic settlement in Kent, according to the Kent Archaeological Society, centred about the Medway Gap (Kit's Coty and Coldrum settlements) from 1800 B.C. onwards, and so was very late and unconnected with the Neolithic settlements of Wessex in time. The Neolithic settlers may have already found by this river gap small open areas on the steep slopes, and no doubt extended them. It is noteworthy that here we find the box again in its only other native-seeming locality on the North Downs (near Boxley), that *Senecio integrifolius* is only known from the eastern North Downs in grassland here, and that *Helleborus foetidus*, *Filipendula vulgaris*, *Campanula glomerata*, *Polygala calcarea*, and the mosses *Thuidium hystricosum* and *Pleurochaete squarrosa*, have their main centres of concentration on the eastern North Downs here, and diminish or disappear east and west from the river gap.

The Coastal Chalk Cliffs of East Kent. The chalk cliffs of East Kent may well have provided a treeless open habitat for calcicole grassland species during the forest maximum, until Bronze Age clearances in the country north of Dover enabled re-spread to occur. In the chalk country north and east of Dover, and behind Folkestone, there occur on downland or cliff-tops to-day *Galium pumilum* (an octoploid form, closer to the central European form than to the other British races of the species-

aggregate—Goodway (1955)), *Falcaria vulgaris*†, *Euphorbia cyparissias*†, *Silene nutans* var. *smithiana*†, *Thesium humifusum*, and *Cirsium eriophorum*†. These species are absent as native plants elsewhere on the eastern North Downs, or (marked “†”) elsewhere in S.E. England. In the Dover area also occurs a small pale-flowered form of *Polygala calcarea*, which preliminary studies suggest is significantly different from the mid-Kent populations; there is indeed a gap in the otherwise continuous range of this species along the North Downs, of 17 miles between Westwell on the west and Lydden on the east, although suitable habitats occur abundantly in between (see fig. 3). Some or all of these plants may have used the clifftop downs near Dover, where most of them occur now, as a refugium.

The orchids and broomrapes of East Kent probably had a different history. In East Kent have occurred 33 species of *Orchidaceae* (69% of the species of Great Britain) and 8 species of *Orobanche* (80% of the species of Great Britain), a remarkable total, considering the numerous calcicole species mentioned above missing from S.E. England compared with East Anglia. But orchids and broomrapes all produce large amounts of light minute seeds, readily wind-borne. These species are mostly of Continental-Southern type, and conditions for their successful colonisation of Britain may not have existed until after the separation of this island from the Continent, which appears to have taken place in the Boreal Period, about 6-7,000 B.C. (Godwin). They may have colonised East Kent after the separation, by means of seeds blown across the Straits of Dover. The flora of the Pas de Calais is similarly rich in orchids and broomrapes (Good, 1925). This hypothesis seems to be the most satisfactory one to explain the large orchid-broomrape population in extreme east Kent, which contrasts with its lack of many other calcicole species. It is worth noting in this connection that the chalk scarp which must once have existed between the present sites of Abbotscliff and Cape Blanc Nez was almost certainly breached in the glacial period (Wooldridge & Goldring, 1953), so that in the Post-glacial there is no reason to suppose that a land-bridge persisted here any longer than anywhere else.

The Beachy Head Area. In East Sussex, open conditions probably existed on the chalk slopes adjoining the cliffs of Beachy Head through the forest maximum; Neolithic colonisation of the South Downs would have resulted in an extension of open habitats far inland. Again, just as in East Kent, we find a group of calcicoles centred on Beachy Head, and either confined in S.E. England to its neighbourhood (*Seseli libanotis*, *Bupleurum opacum*), or at least tailing off very markedly westwards (*Polygala calcarea*, *Senecio integrifolius*, *Thesium humifusum*). The East Sussex population of *P. calcarea* shows differences from both the East Kent and the mid-North Downs ones; mauve-white flowers are here most common and not blue ones. Again, careful

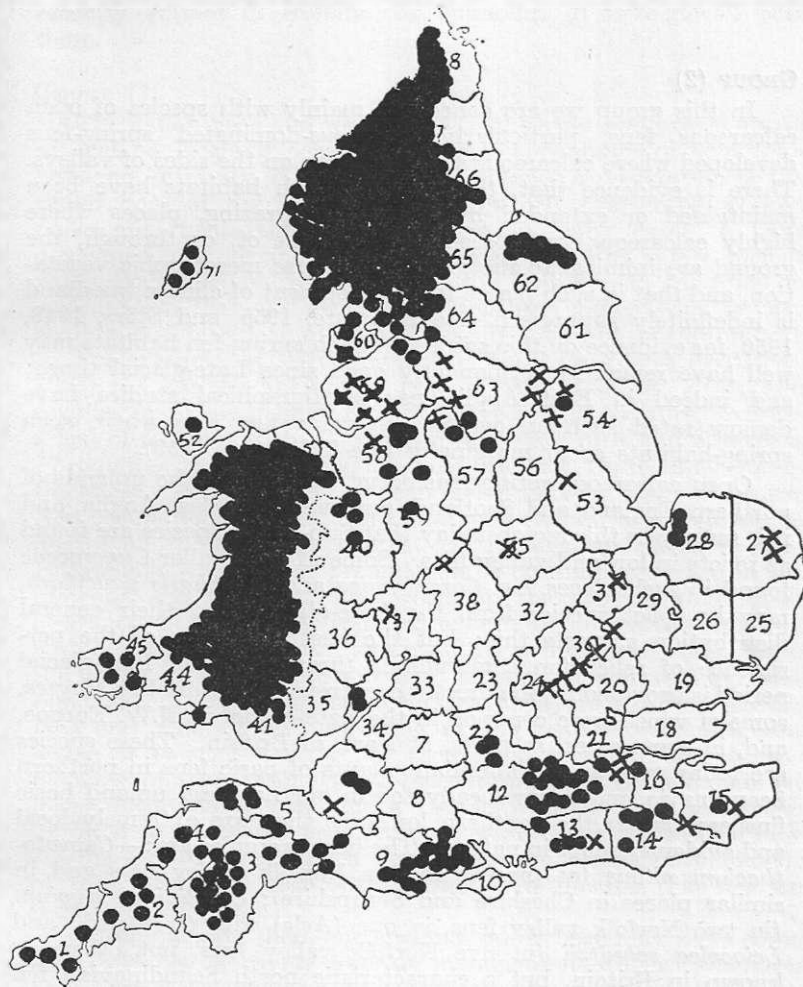


Fig. 3.

Distribution in England and Wales of *Narthecium ossifragum*.
 ● = Localities recently authenticated.
 X = Localities now destroyed.
 Continuous black indicates areas where the species is generally common.
 With acknowledgment to the "New Naturalist" for the use of part of their
 base-map.

biometric studies on these isolated populations might be very useful in giving some idea of the actual degree of differentiation and hence of the relative lengths of time of isolation.

GROUP (2)

In this group we are concerned mainly with species of open calcareous fens, particularly *Schoenus*-dominated spring-fens developed where calcareous strata outcrop on the sides of valleys. There is evidence that, though some such habitats have been maintained or extended by mowing or grazing, places where highly calcareous water seeps steadily out of, or through, the ground are inimical to the growth of coarse mesotrophic vegetation, and that in such places the development of climax woodland is indefinitely suppressed (see Holdgate, 1955, and Sjörs, 1948, 1950, for evidence on this subject). Such spring-fen habitats may well have remained permanently open since Late-glacial times; and indeed in East Anglia peat-stratigraphical studies have demonstrated such an age for several valley fens where such spring-habitats occur marginally (see Tallantire, 1953).

Open calcareous spring-fens occur, not only in the uplands of northern England and Scotland, but widely in East Anglia, and it is mainly in this region today that Sub-Arctic species are found as relicts in lowland valley fens. Some of the smaller *Cyperaceae* found in such places, e.g. *Carex dioica* and *Eleocharis pauciflora*, may be relict species from the Late-glacial, and their general distribution suggests this; but the best indication of the persistence of relict fen communities throughout the Post-glacial period is provided by the present occurrence of certain bryophytes, some of which were common in the Late-glacial in N.W. Europe, and, in some cases, in parts, at least, of Britain. These species are today typical and abundant plants of basic fens in northern Scandinavia and occur locally too in our northern upland basic flushes; but in the southern lowlands they are extremely local and evidently relict in nature. The best examples are: —*Camptothecium nitens* (at present in five Norfolk valley fens and in similar places in Cheshire and Shropshire); *Cinclidium stygium* (in two Norfolk valley fens, in one (Acle) with *C. nitens*); and *Leiocolea schultzei* (in five Norfolk valley fens, not otherwise known in Britain, but a characteristic north Scandinavian fen species). Several other mosses of the same Arctic type (e.g. *Paludella squarrosa*, *Helodium blandowii*, *Calliergon trifarium*) have recently become extinct in lowland English fens, though the last survives in Wales and Scotland. Godwin and Richards (1946) discuss the present and fossil occurrence of such bryophytes in the British Isles, and also record the extinct *Meesia triquetra* in Neolithic peat in Somerset.

Similar relict bryophyte communities in valley fens have been described for lowland areas in Denmark by Thomsen (1944), where *Paludella squarrosa* has persisted in spring fens since the

Late-glacial, and in Holland by Landwehr (1952), who describes the persistence of the Sub-Arctic moss *Mnium cinclidioides* in fen at Bergeijk; Landwehr (1949) also refers to *Helodium blandowii*, recently extinct in Holland, as abundant in Late-glacial peat there.

GROUP (3)

The valley bogs and wet heaths of the sand and gravel strata of lowland England have a superficial appearance of primitiveness and antiquity, due to their resemblance in vegetation to the raised bogs of the north and west, which stratigraphical and pollen-analytical studies have shown in many cases to have developed over glacial lakes. However, excepting a few ancient valley bogs such as Cranes Moor in the New Forest, one finds on examination that the peat in our southern valley bogs is very shallow (1-3 feet deep only) and usually fluid and uncompressed.

For example, at Wilverley Bog in the New Forest (see Rose, 1953) the surface *Sphagnum* peat is only 20-30 cm. deep, and overlies in places a layer of flint gravel. This, in turn, overlies a bed of fen peat with *Alnus* wood abundant in it and numerous *Phragmites* rhizomes, this fen peat varying from 15-60 cm. in thickness. Beneath this is a deep bed of gravel. Signs of Bronze Age occupation, in the form of round barrows, are frequent on nearly all the southern heaths. It is suggested that, in pre-Bronze Age times, these present heaths bore mixed forest on the plateaux and fens with alderwoods in the valleys; that forest clearance on these light soils led eventually to heath formation with consequent podsolisation, resulting in increased run-off into the valleys of acid drainage water; and that erosion due to forest removal led to the deposition of gravel layers locally over the fens and alderwoods. Flooding of the valleys with stagnant water, it is suggested, would then have occurred, due to the blocking of their drainage by the deposition of eroded material lower down the valleys; and a new hydrosere would have been initiated in which the acid drainage water from the heaths now existing around the valleys would have led to the development of the *Sphagnum* bogs with marginal wet-heaths that we see today.

In such a way, then, our lowland valley bogs may have come into existence relatively recently in regions in which *Sphagnum* bogs cannot be regarded as a climatic climax formation owing to the low rainfall. On this theory, they must, in many cases, be regarded as owing their origin to indirect human intervention, and not as relics, like the basic fens, of the Late-glacial times.

The seeds of bog plants to colonise these valley bogs may well have come from the few ancient raised bogs that existed in the south of England in Bronze Age and later times, as at Amberley in Sussex, Shapwick in Somerset, and Whittlesey in Hunts, all of which are now derelict. In this way, species such as *Eriophorum vaginatum*, *Drosera* spp., *Erica tetralix* and *Narthecium*

ossifragum may have come to have the fairly continuous distributions along the Greensand and Bagshot Sand outcrops that they apparently had until about two hundred years ago, to judge from early records and specimens (see fig. 3). Their present more scattered distributions are a reflection of a second phase of more intense human interference, involving drainage and enclosure, just as with the chalk grassland species ploughing has led to restriction to secondary refugia.

GROUP (4)

Just as the open conditions of the Late-glacial, and the clearances of the Neolithic and Bronze Ages, have left, it is suggested, their relicts behind, so the period of maximum forest cover has apparently left its relicts too. In one sense every bit of old woodland which has never been completely cleared is a potential refugium for species of the forest maximum: but here we must confine ourselves to those species which were apparently more at home in the warmer, moister climate of the "climatic optimum", to use Godwin's term, in the mid-Atlantic period, about 4,000 B.C. There are a number of species which now show very disjunct distributions which had probably a more continuous distribution then. In this category come such plants as *Dryopteris aemula*, *Hymenophyllum tunbridgense*, *Festuca altissima*, *Wahlenbergia hederacea*, *Sibthorpia europaea*, and many bryophytes. These forest species, besides showing a more continuous distribution of the type one would expect of such humidity-demanding plants, i.e., along our western and south-western coastal areas, also occur in the Weald of Sussex and, in some cases, of Kent and Surrey. Markedly disjunct distribution patterns result.

Dryopteris aemula, for instance, (fig. 4a) is known today in 28 localities in the High Weald of Sussex and Kent, but is not known again westwards until the Devon-Dorset border and the Quantocks are reached. In the Weald it occurs on steep shaded banks in sheltered valley woods, both on sandy peaty mildly acid soil and on sandstone rocks. In south-east England today, only the Weald appears to provide suitable localities, but I would suggest that in mid-Atlantic times the existence of both more continuous forest cover, and a warmer more humid climate, may have enabled it to have had a much more continuous distribution than now. Then, the shelter of deep valleys may have been less necessary to it than today. *Hymenophyllum tunbridgense* shows a similar distribution; it is more confined to rocks in the Weald than is *D. aemula*, but may, in a moister climate, have grown more widely on trees, as it does on the west coast today. *Festuca altissima*, recently refound in the Sussex Weald in a rocky oak-wood, occurs today no nearer than the Wye Valley, and may also have had in Atlantic times a wider distribution.

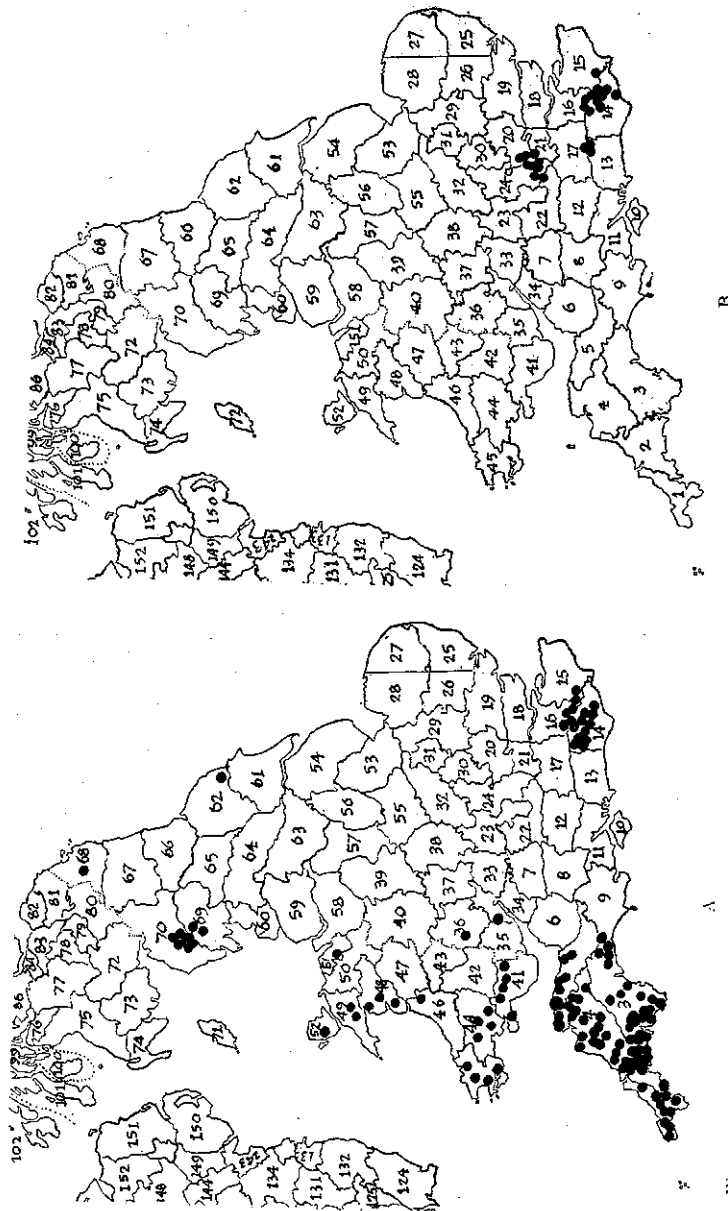


Fig. 4. Distributions in England and Wales of (a) *Dryopteris acmula* and (b) *Dentaria bulbifera* (Native localities only).
With acknowledgment to the "New Naturalist" for the use of part of their base-map.

GROUP (5)

Beside the species of the type discussed in the last group, which appear to be associated with forest because of their high air-humidity requirements, there are other forest species of more "Continental" distribution abroad. Such are the well-known *Primula elatior*, discussed by Miller Christy (1922), confined to two separate areas on the East Anglian Chalky Boulder Clay, and *Dentaria bulbifera*, confined, for no obvious reason, to three quite isolated areas in S.E. England. This latter plant is, according to Clapham, Tutin and Warburg (1952), a characteristic species of base-rich beechwoods in central Europe. In Britain, however, it occurs on damp loamy neutral soils in the Weald, on more acid (pH 5.5-6.0) sandy soils with bracken in oakwoods on Hastings Sands in the same area, and in the Chiltern region both on sandy soils and in beechwoods on the chalk (pH 7-8). Thus in Britain it shows no evident ecological preference. Its markedly south-eastern distribution in Britain (fig. 4b) suggests relatively late arrival in this country, as it flourishes, where naturalised, further north-west (as in Staffordshire). Its peculiar mode of reproduction (almost entirely by bulbils, seed being very rarely set in England) may well account for its highly isolated areas of distribution in this country, for, within these areas, it is often abundant and more or less continuous in woodland, especially along the courses of streams in which the large bulbils could float and so spread the plant. Its apparently wide ecological tolerance would suggest that with a more efficient means of dispersal it might have by now achieved a more continuous spread. Its distribution is disjunct but not, it is suggested, relict.

GROUP (6)

The last category, of possible relicts of the Boreal Coniferous Forest Period, includes perhaps only two species in lowland England, *Goodyera repens* and *Trientalis europaea*. Both occur in East Anglia. Pollen-diagrams (Godwin and Tallantire, 1951, etc.) indicate the persistence of small amounts of pine in East Anglia throughout the Post-glacial; it is in such relict pine-woods that *Goodyera* may have survived until planting of pine-woods gave it an opportunity for stronger re-establishment. There are several recent records for this orchid in Norfolk and at least one place (Holt) where it is still plentiful.

Trientalis europaea was found by me in 1955 in a boggy birch-alder wood in N.E. Suffolk; its nearest other localities are in the uplands of N.E. Yorkshire.

Goodyera and *Trientalis* may be introductions with planted trees (pine plantations exist near each), and *Trientalis* may have been brought by birds (a lake visited by waterfowl is nearby), But Duiven (1952) and Andreas (1953), who discuss the occurrence of *Trientalis* and other typical northern coniferous forest species in the lowland country of N.E. Holland, believe such

species to be true relicts there, for such species need not have been constant as to their exact localities in an area all the time.

It is of interest to note that Holt Lowes in Norfolk contains possible relicts of four of the groups mentioned:

- (a) *Leiocolea schultzei* and *Cinclidium stygium* in basic valley fen (? Late-glacial relicts);
- (b) *Goodyera repens* in pinewood (? Boreal Forest relic);
- (c) *Hookeria lucens* (a moss) in a sheltered boggy alderwood (? Atlantic Deciduous Forest relic); and
- (d) *Trichophorum caespitosum* in nearby open wet-heath (? relic of Bronze Age clearance).

CONCLUSION

The hypotheses put forward in this paper can be summarised by saying that several periods of Late- and Post-glacial history may have left their relicts behind in disjunct species-distribution patterns over our lowland English countryside:—

- (1) The Late-glacial Period, with its widespread, both wet and dry, open base-rich habitats;
- (2) The Boreal Period, with its pine-birch forest and warmer dry climate;
- (3) The Atlantic Period, with its deciduous forest and still warmer, and wetter, climate;
- (4) The period of Neolithic clearances, mostly on the calcareous soils of the English lowlands;
- (5) The period of Bronze Age clearances, on both calcareous and sandy soils; and
- (6) The enclosures, cultivations, and drainages of the recent historical period.

I am well aware that further ecological study *may* in time show that some of these distribution-phenomena can be satisfactorily explained on purely ecological grounds; but that time is not here yet. Meanwhile, if I have been able to stimulate anyone at all to undertake detailed autecological studies of any of the groups of species mentioned, I shall feel that the preparation of this paper has been worth while.

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Mr. F. PERRING suggested that Dr. Rose may well be right about the barrier to distribution caused by the Chilterns, but in the case of *Anemone pulsatilla* it would be equally reasonable to correlate its distribution with that of the present-day climate. A map giving Precipitation/Evaporation ratio values of Britain shows that a line enclosing values below 150 coincides remarkably closely with the limits of distribution of *Anemone pulsatilla* and of *Astragalus danicus* on the chalk and limestone. Values in the Chilterns are above 150, those in the Cotswolds below. To what extent does Dr. Rose consider that present climate should also be studied to explain present distribution? Dr. ROSE replied that in addition to general climate, consideration must also be given to the importance of micro-climates in determining the flora of an area.

Mr. J. E. LOUSLEY congratulated Dr. Rose on the way he had presented his hypotheses, but suggested that it was important to remember that they were only hypotheses and supported by very little valid scientific evidence. There was a vast gap between the relatively few facts available about past distribution from fossil botany and our detailed knowledge of present distribution. It is dangerous to assume that because intervening areas seem to us ecologically suitable that plants with disjunct distributions could in fact grow there. Dr. Whitehead's paper (see pp. 56-60) was a reminder that there is still much to be learned about the ecological requirements of plants and further autecological studies might well show that some, at least, of the disjunct distributions could be explained in terms of present conditions. We also need more information about seed dispersal and rate of spread. Recent introductions have shown how rapidly plants can spread if they find the right ecological niche and the period since the Post-glacial seems sufficiently long to cover, perhaps many times over, the time needed for a species arriving afresh from the continent to

extend to its present distribution. For example, it could be that the feathery plumed achenes of *Anemone pulsatilla* played some part in facilitating long distance dispersal in the past, that ecological requirements explained its restriction to remarkably limited areas of apparently uniform downland to-day, and that it was entirely unnecessary to postulate "refuges" in the north or elsewhere. Mr. Lousley suggested that the most profitable long-term approach to the problems of distribution over relatively small areas like southern Britain would be to stimulate research on the ecology and biology of the species concerned. Dr. Rose replied that this was his object. He set up the hypotheses as an "Aunt Sally" and he hoped his paper would stimulate interest in all the aspects involved.

**DEVELOPMENT OF KNOWLEDGE OF THE BRITISH FLORA IN
RELATION TO NORTH TEMPERATE FLORAS**

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The British flora is a small one, possessing, at a rough estimate about 15% of the species of the European flora; and the great majority of its species have a geographical range which extends far beyond the British Isles. Thus, in order to understand its nature and composition, it has to be viewed against the background of the north temperate flora as a whole. To do this adequately in a short paper is practically impossible, and much has to be omitted or taken for granted; but I shall try to deal with some general points of evolutionary and taxonomic interest which arise in the flowering plants. I shall have to leave on one side any attempt at a comparison between British plant communities and their analogues elsewhere.

In order to make the account as concise and coherent as possible, I propose to restrict the discussion, at least to begin with, to a single family which can be regarded as fairly representative, and to use this family to illustrate some general points. The family I have selected is the Primulaceae, and Table 1 gives a list of the genera, together with a brief note on their geographical distribution and the number of species they contain; for various reasons, it is difficult to ensure that the latter figure is accurate, but there are probably no major errors. There are also differences of opinion about the delimitation of the genera, some of which will be discussed later.

The family is of moderate size, with 22 genera and about 800 species. Its distribution, like that of a good many other families, is mainly in the north temperate regions of the world, though there are some species (especially in the Lysimachieae) in the southern hemisphere. Such tropical species as there are occur mainly in cool mountain climates, as for example in *Ardisiandra*, from the mountains of tropical Africa. It will be noted that about one-third of the genera occur in Britain, and that these are all genera with a very wide distribution; thus they are all found in North America as well as in Europe. These facts illustrate two points. First, it is legitimate to speak of a north temperate flora; for there are many genera which have a circumpolar distribution; and not only the genera but sometimes the species too (e.g. *Glaux maritima*) may be common to Eurasia and North America. Secondly, the number of genera and species which are represented in Britain is rather small; thus, there are only seven genera of Primulaceae in Britain, as compared with fourteen in

TABLE 1. GENERA OF THE PRIMULACEAE

	<i>No. of Species</i>	<i>Distribution</i>
ANDROSACEAE		
* <i>Primula</i>	about 400	N. Hemisphere, [1 sp. S.]
<i>Omphalogramma</i>	11	Himalayas, W. China
<i>Dionysia</i>	20	Persia, Afghanistan
<i>Douglasia</i>	6	Alps, Pyrenees, N. America
<i>Androsace</i>	about 85	Eurasia, N.W. America
<i>Cortusa</i>	2	C. Europe, Asia
<i>Stimpsonia</i>	1	Japan, China
<i>Ardisiandra</i>	3	Africa
<i>Soldanella</i>	6	Alps
<i>Pomatosace</i>	1	China
<i>Bryocarpum</i>	1	Sikkim
* <i>Hottonia</i>	2	Eurasia, N. America
<i>Dodecatheon</i>	30	N. America, N.E. Asia
CYCLAMINEAE		
<i>Cyclamen</i>	18	C. Europe, Mediterranean
LYSIMACHIEAE		
* <i>Lysimachia</i>	about 150	N. & S. Hemisphere
* <i>Trientalis</i>	3	N. Hemisphere
<i>Asterolinum</i>	2	Mediterranean, East Africa
<i>Pelletiera</i>	1	S. America
* <i>Glaux</i>	1	N. Hemisphere
* <i>Anagallis</i>	24	N. & S. Hemisphere
SAMOLEAE		
* <i>Samolus</i>	10	N. & S. Hemisphere
CORIDEAE		
<i>Coris</i>	2	Mediterranean, Somaliland

Genera native in Britain are marked with an asterisk.

Europe as a whole. The reasons for this are well known and can be stated briefly. The British Isles have been subjected to repeated glaciations during the last million years. During the glacial periods much of the vegetation was destroyed; and it was replaced by immigration, in the inter- and post-glacial periods, from continental areas to the south and east. Plant migration is a slow and chancy affair; and the result is that the British flora has come to consist of only a fraction of its potential inhabitants. Many other genera and species which could survive in the British Isles, or have lived there in the past, even as recently as in interglacial times, are no longer found in the wild state. To some extent, of course, the whole of the north

European flora has been impoverished by glaciation; but this is emphasised in Britain because of its marginal position and also because it is an island. It may be added that its vegetation, on the whole, is very similar to that of western Europe. The five main formations represented are the deciduous forest, coniferous forest, heath, bog and arctic-alpine formations. Of these, it is probably true to say that only the bog communities, which are particularly favoured by the mild and damp climate, especially of Ireland, are sufficiently distinctive to make them of special interest to the ecologist with a wide knowledge of European plant communities.

I want next to use the list of the genera of the Primulaceae to illustrate a general taxonomic point. It will be seen that two of the genera which appear in Clapham, Tutin and Warburg's British Flora are omitted from the list, viz. *Naumburgia* and *Centunculus*; and the reasons for this are, I think, relevant to the subject of this paper. No two taxonomists have quite the same ideas about the scope of a genus; one will favour few large genera, another numerous small genera. In any particular case, the person best fitted to decide is the man who has monographed the genus in question; for if he has done his work properly he will have studied his group over the whole of its range. The examples I have mentioned illustrate the point. *Naumburgia* and *Lysimachia* can be readily distinguished in Europe; but in eastern Asia, transitional species occur, and Handel-Mazzetti (1928) who has most recently revised the genus, decided that a generic distinction between the two could not be sustained. The case of *Centunculus* is similar. Taylor (1955), in the course of work on the Flora of Tropical East Africa, has had to revise the genus *Anagallis*; and it is clear from his revision, in which he deals with a considerable number of African species, that *Centunculus* falls into place as a species of *Anagallis* and can no longer be maintained as a separate genus.

It is thus unsafe to form an opinion of the scope of a genus merely from a knowledge of its British or even its European representatives. This point can be illustrated in another way by reference to *Primula*, a very large genus represented in Britain by only 5 species which belong to 2 sections, the Vernales and the Farinosae. About 30 sections are generally recognized; and a high proportion both of the sections and the species are confined to the area which includes the Himalayas, Tibet and western China. If our knowledge of *Primula* were limited to the British species, we should have a very inadequate idea of the range of form and habit in the genus. Fortunately this is not so, in this particular case, because frequent expeditions to the mountains of Asia have produced a diversity of plants which are now grown in our gardens. Naturalists are greatly indebted to both explorers and horticulturalists for these and other plants which they have made known to us. It is well to remember that a study of the plants which have been introduced into

Britain may be just as instructive as a study of native plants, and we do well not to concentrate our attention too closely on the natives. This point was well made by Warburg in his paper on British trees and shrubs given at the 1952 Conference. By getting to know plants grown in gardens, we can take a step towards viewing the British flora in its proper perspective; and when we are familiar with such common species as *Primula sinensis*, *P. japonica*, *P. auricula* and *P. kewensis*, each in a different section, we begin to form a juster idea of the scope of the genus. If, in addition, the plant concerned becomes naturalised (as has happened, for example, with *Cyclamen neapolitanum*), the fact that it is tolerant of British climatic conditions tells us something of its ecology and physiology, which is frequently of scientific value.

I want next to speak about some of the problems of the delimitation of species, because here too a wide view is essential. The three British species of *Primula* of the section *Vernales* provide a good illustration. Of these, two (*P. veris* L. and *P. vulgaris* Huds.) are common and widespread in Britain, while the third (*P. elatior* (L.) Schreb.) is confined to East Anglia, where it is locally abundant. The fact that these species form natural hybrids was one of the reasons why early taxonomists were doubtful about their proper treatment. In particular, the Oxlip (*P. elatior*) was confused with the hybrid *P. veris* × *vulgaris* which is widespread in Britain; anyone who cares to read about the controversy can find the papers in the *Phytologist*, a journal which flourished from 1844 to 1863. The trouble was partly due to the unfamiliarity of British botanists with the Oxlip, which is only found in rather remote rural areas in Cambridgeshire, Essex and the neighbouring counties; and partly due to their ignorance, natural at the time, of the distribution of the species over the whole of their range. But it was soon shown that British and west European plants of *P. elatior* were practically identical, and that the latter often occurred in regions from which *P. vulgaris* was absent. For these and other reasons, the erroneous hypothesis of the hybrid nature of *P. elatior* was soon disposed of.

Further work has not only emphasised the distinctions between these three taxa, but has shown that each must be regarded as an aggregate species or a species complex, comprising numerous taxa which are provisionally given subspecific rank. Thus *P. vulgaris* agg. consists of the western subsp. *vulgaris* with which we are familiar, a Turkish subsp. *sibthorpii*, and a subsp. *heterochroma* found further east as far as the shores of the Caspian sea; in addition, there are a number of local races or subspecies on the Mediterranean islands. *P. elatior* agg. is even more complex, and is still imperfectly known. Among the taxa which belong to the circle of affinity of *P. elatior* are the western subsp. *elatior*, the southern Spanish subsp. *lofthousei*, the Mediterranean subsp.

intricata and the Caucasian and Asiatic subsp. *pallasii*; and this by no means completes the list. Further work will probably show that some of these subspecies should be given specific status, though there is little doubt that they are closer to *P. elatior* than to either *P. veris* or *P. vulgaris*. But the point I want to make here will, I think, be fairly obvious. We see Primrose, Cowslip and Oxlip in Britain at the extreme western edge of their distribution, and we cannot regard either their form or behaviour, as we know them, as typical; they must be studied over their whole range. Still less can we be certain, from mere local knowledge, of the evolutionary history of the species, which, in the Vernales, is clearly rather complex. It is worth adding that the habitat of *P. elatior* subsp. *elatior* in Britain contrasts with that in Central Europe; here it is practically confined to woodlands on calcareous clay, there it is frequently a meadow plant and by no means confined to calcareous soil. The factor which seems to be common to all the *P. elatior* habitats is their wetness, particularly in winter and spring; but, in other respects, it looks as though the British habitat is not very typical of that of the species in general. Differences in ecological tolerance and in other physiological characters between species at the centre and the margin of their range are quite well known in other plants and in some animals as well.

This leads us to a consideration of the many studies, which have been made in the last thirty years, of the evolution and differentiation of plant populations in relation to habitat and climate; these studies were first extensively developed by Turesson, who introduced the concept of the ecotype. Considering groups at and below the level of subspecies, which were quite homogeneous taxonomically, evidence for considerable differentiation was found. To give only one example of many, Turesson (1930) showed that there were genotypic differences in physiological behaviour between populations of *Primula vulgaris* from southern and northern Europe; the main difference noted was in time of flowering; it is probable that there are also differences in the behaviour of the seeds in respect of their cold requirement for germination. Such differences are, in many cases, best described in terms of clines. Another example from the work of a number of Danish botanists, who are making extensive population studies of European species, may be mentioned here. They have recently published an account (Böcher *et al.*, 1955) of *Plantago coronopus*, which ranges from northern Europe to the Mediterranean. In one of the subspecies (the one which occurs in Britain), broad and gradual changes in the form of the plant, associated with geographical location, can be detected, as well as ecotypic or ecoclinical differences associated with habitat. Thus, they conclude that in *P. coronopus*, populations of southern origin differ from northern in being of greater size, in having more ascending leaves and scapes, in having longer spikes, and in their greater resistance to drought.

I think it is relevant to insert here a short discussion on endemism in the British flora. Although the British Isles are isolated by sea from the mainland of Europe, this isolation has existed for only a relatively short time. It is, therefore, to be expected that British plants will be substantially identical with their European neighbours, and that no major evolutionary divergence will have occurred. This is, in fact, found to be the case; in a number of groups that have been examined (e.g. *Primula elatior*, *Plantago coronopus*) it has been found that the British plants are taxonomically the same (i.e. in the same subspecies) as their nearest European neighbours; and it can be said, with some confidence, that there are very few endemic species in the British flora. This contrasts markedly, of course, with the situation in many other island floras, such as that of New Zealand, a pair of islands roughly comparable in size and number of species with the British Isles. New Zealand is a thousand miles distant from the nearest mainland, and has been thus isolated for a very long time; and though it has few endemic genera, more than half of its flora consists of endemic species.

Such endemic taxa as have been described in Britain are, as might be expected, mainly to be found in groups which are either regularly inbreeding or apomictic. Populations of such plants consist of numbers of pure or nearly pure lines; and when such populations are examined by taxonomists, they can distinguish forms which are more or less constant and can be named. Whether the 'microspecies' so distinguished have any general value depends on a number of factors. Where the microspecies are relatively few and differ markedly in ecology and geographical distribution, as in the apomict *Alchemilla vulgaris* agg., they are obviously important. Where they are many, and difficult to distinguish in this way, they may be of little value; new microspecies in such an aggregate as *Rubus fruticosus*, which is a facultative apomict, are constantly arising, and it is unlikely that more than a small proportion will be of ecological or geographical importance, though they are, of course, of evolutionary interest. A number of endemic microspecies of *Rubus*, *Hieracium* and other apomicts have been described from Britain; and there are doubtless endemic microspecies of *Erophila verna*, *Capsella bursa-pastoris* and other regularly inbreeding groups.

Amongst other recorded endemics are a species of *Fumaria* and a species of *Arabis*; these are not known to be apomictic, but may well be inbreeders. Another interesting endemic is *Primula scotica*, which is confined to north Scotland and Orkney. This is an inbreeding species, and a hexaploid ($n=54$), doubtless derived from the more widespread *P. farinosa*, which is a diploid ($2n = 18$); its closest relative is *P. scandinavica*, which is octoploid. Ritchie (1955) has recently discussed the ecology and distribution of this species, and has pointed out that there is evidence that it was once more widespread, as it has been identified from glacial deposits near Cambridge. It is probable

that some of the endemics in the apomictic groups have arisen *in situ* and are of very recent origin; but this is not necessarily the case with all endemics. Thus *P. scotica* may have originated far from its present area of distribution, to which it has migrated in post-glacial times, having become extinct everywhere else. The movement of plants in interglacial and post-glacial times may well have been responsible for the origin of a number of polyploid species such as *P. scotica* which have now a rather restricted distribution. *Cochlearia micacea*, a polyploid species with $2n = 36$, and practically restricted to Britain (possibly also found in Norway) is perhaps another example. The classic example of a polyploid endemic species of recent origin is, of course, *Spartina townsendii*, though it has since spread from its locality of origin, in the south of England, to northern France.

This discussion of the endemic element of the British flora is necessarily very incomplete; but it serves here to emphasise the need, in detailed taxonomic studies, of comparing British plants very carefully with their relatives in the countries surrounding the British Isles, and in particular, in investigating both their breeding mechanism and genetical constitution. This has been well shown by Young (1953) in his studies of inbreeding species of *Epipactis* in Britain and Scandinavia; the degree of endemism in the group and the connections between British and European taxa have both been made much clearer by his work.

Finally, it is very important to take account of work which is aimed at the study of species groups with an extremely wide range, either Eurasiatic or circumpolar. The number of arctic and boreal plants with such ranges is quite large. I might refer here to two workers in other countries who are studying this problem. Hara (1952) in Japan, is making extensive comparative studies using both taxonomic and cytological methods of Japanese plants which are related to those in Europe or N. America; and his results show well how complex the situation may be, and how it varies from group to group. Thus, in some species, such as *Drosera rotundifolia* and *Oxyria digyna*, the Japanese and European plants seem to be substantially the same; in some, such as *Ranunculus repens*, the Japanese plants are thought to be only varietally different; in some, such as *Chelidonium majus*, the Japanese and E. Asiatic plants differ in both morphology, chromosome number and fertility from the European, and are given subspecific status; and in some, such as *Sanicula europaea* agg., the Japanese members of the group are given specific rank. In many cases, Hara points out the necessarily tentative nature of his treatment; and very often the intermediate forms connecting the E. Asiatic with the European forms are imperfectly known.

In all work of this kind it is, of course, essential to combine cytological and taxonomic studies. This point is well illustrated by my second example, taken from the work of Löve and Löve

(1954) on *Galium boreale*. This is a species which occurs in northern Britain and which has an extremely wide geographical distribution throughout Eurasia and north America. The authors made a careful comparison of European and American material, and found a number of constant and associated differences in hairiness, shape of bract and panicle, width and colour of corolla, and length of fruits and anthers. They further found that the European material was tetraploid ($2n=44$) and the American material hexaploid ($2n=66$). Examination of herbarium specimens over the whole range of the taxon showed that the two types of plant could always be readily distinguished; the tetraploid extended from Iceland to Western Asia and the hexaploid from Central Asia across N. America to Nova Scotia. There are thus good grounds for separating the two forms as distinct species; the European form is then *G. boreale* of Linnaeus; the American form is *G. septentrionale* of Roemer and Schultes, who described it under this name in 1818.

These two species of *Galium* are at different levels of polyploidy; this phenomenon is very common. The point was well made by Manton, at the 1954 Conference, that the investigation of the origin and evolution of these polyploids presents fascinating problems. There is no need here to go into the question in detail; I may merely mention one example in which I am interested, in the genus *Viola*. *V. riviniana* is a tetraploid species, almost certainly an allotetraploid, and the diploid species *V. reichenbachiana* is very probably one of its parents. As in so many other cases, the other parent is as yet unknown; and it has to be sought over the whole of the northern hemisphere, which is the range of this group of rosulate violets. The other British species of this group, *V. rupestris*, is a possible parent, although there is now some evidence against this view; the Japanese species, on morphological grounds, seem unlikely; and it is most probable that the other parent, if not extinct, may be one of the North American species, of which there are three or four—possibly *V. conspersa*.

I hope that these rather miscellaneous notes will have sufficiently demonstrated the importance of looking at the British flora as a constituent part of the boreal flora as a whole. I have deliberately emphasised the importance of combining cytogenetical and taxonomic investigations because it is clear that further advances in knowledge can often only be made in this way. For various reasons I have said very little on the subject of floristic plant geography; first, the subject has been discussed at a previous Conference, and secondly a geographical analysis of the British flora, using modern European systems of classification, is not yet available. Such an analysis, when it comes, will have to take into account the critical taxonomic work of the kind I have mentioned, which is now being produced, on an increasing scale, in countries all round the northern hemisphere. For although much of our knowledge of the British flora has been,

and must continue to be, gained by British botanists, exchange of information with botanists in other lands is more important than ever. Co-operation is effective in various ways; but perhaps I might be permitted to suggest that occasional contacts between this Society, and similar Societies in Europe, though doubtless difficult to organise, would be invaluable, particularly if joint field meetings could be arranged; and I hope the Society will consider the suggestion.

I have, in conclusion, one further general point. The development of modern taxonomy has made it both more difficult and more important to produce floristic works which cover a wide area. While not detracting from the value of local or national floras, I think there is no doubt that a local view can often be misleading, and that large floristic works are required. For North America, the 8th edition of Gray's *Manual*, revised by Fernald, covers a large part of the United States and Canada; and for the east, there is the *Flora of the U.R.S.S.*, which is rapidly nearing completion. A European Flora does not yet exist; the nearest approach to it is Hegi's Flora of Central Europe; and invaluable as this is, it does not cover the whole continent. The production of a European Flora, if it could be achieved, would be a big step forward towards our understanding of the floras both of Britain and of the whole north temperate region.

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Dr. E. F. WARBURG said that it was very evident that British botanists had treated our flora in isolation for far too long. Thus the *Flora of the British Isles*, of which he was one of the authors, had been criticised for using names unfamiliar to English workers although in fact most of these "new" names were those widely used on the continent. He was a little puzzled by Professor Valentine's insistence that endemic microspecies were of importance only if their distribution showed geographical significance. What was meant by this and would he, for example, dismiss an endemic *Sorbus* species because it was confined to a single hill? Prof. VALENTINE replied that he put the emphasis on ecological rather than geographical significance. He thought the test should be whether it was possible to draw conclusions of value—it seemed to him that mere scattered data of minor variants had no value at all.

Dr. D. P. YOUNG said that no species of *Epipactis* in this country was endemic.

Dr. S. M. WALTERS said that although a good many species of *Hieracium* had been described from this country and regarded as endemic this had often resulted from failure to consult European herbaria. Mr. Scell and Dr. West in the course of their work had found that many so-called endemics in this group are plants already known on the continent.

Dr. F. ROSE asked if *Oenothera fluvialis*, which was at one time regarded as a British endemic, was still known from only a few places on the continent. Prof. VALENTINE replied that he believed this was still the case.

DISTRIBUTION MAPS OF PLANTS—AN HISTORICAL SURVEY

S. M. WALTERS (University of Cambridge)

I will begin with an apology and a confession. The apology is for inadequacy of preparation, which may well reveal itself to you in the course of this paper when I have to say 'I have not consulted the original work' or 'I have been unable to trace any earlier use of this or that method'. Research into the diffuse literature relevant to the construction of plant distribution maps is a very fascinating, but equally a very time-consuming occupation, and one in which one can never hope to have explored all the possible by-ways. The confession is that there is little original in what I have to offer. Nearly all the works to which I shall refer can be traced *via* that remarkably useful book, Herman Meusel's *Vergleichende Arealkunde*, which was published in Berlin in 1943, and is, therefore, understandably and regrettably difficult to obtain. Meusel's introductory chapters, dealing with general principles and historical aspects of the study of plant distribution, I have found particularly helpful.

I do not intend to limit myself to workers with the British flora in this survey of the history of mapping plant distributions. Such a limitation would fail to bring out what has proved, to me at any rate, one of the most interesting points of the historical survey, namely, the degree to which workers in one country or region may have influenced or been influenced by work published elsewhere. I have, however, confined myself to Europe, partly because there is every reason to believe that the pioneer work in this field was done by European botanists, who had, of course, the advantage of several hundred years' start over, for example, their North American colleagues, and partly for reasons of available time and available literature.

There is no evidence known to me of any plant distribution map earlier than the nineteenth century. Exactly which, however, of the early nineteenth century writers on plant geography should be acknowledged the pioneer in publishing such maps I have not been able to decide. Schouw (1823) has a very good claim with a coloured area outline map of the world distribution of Beech (*Fagus sylvatica*), and at least one Englishman had published before 1830 a map giving an outline N. limit for a number of European species. This was Barton (1827). Note that these early maps gave, at the best, area outlines only.

Such early work was familiar to Watson at the outset of his botanical career. We find him already in 1836 discussing 'the best manner of constructing . . . maps (illustrating the distribution of plants), or any diagrams in substitution'. 'To represent

the distribution of individual forms or species' Watson says, 'let us first imagine a common geographical map, in outline, of such dimensions as would render it possible to mark every locality for any given species, by some sign, or spot of colour, covering a corresponding space on the map. This would give an exact picture of the topographical distribution; but, as it would require to be made on the scale of at least a yard to the mile, it is obviously out of the question. With less precision . . . we might greatly reduce the scale by indicating all localities within certain distances of each other as single ones Another mode of representing the distribution of species would be by an outline map, in which the only places named should be those where the species was known to grow, larger or smaller topographical dimensions (townships, parishes, counties, etc.) being adopted according as the species was more or less generally diffused'. From this passage it is clear that Watson appreciated the different possible methods to be adopted—area outline, vice-county, and dot maps as they later developed—and suggested that the method chosen should depend upon 'the different matters which it may be wished to represent, and the degree of precision to be sought in such representation'.

Why then, if Watson appreciated so clearly and at such an early stage the possible types of cartographic representation, did he not develop this side of his interest in plant distribution in step with his great work which laid the foundation, in the *Cybele* and *Topographical Botany*, for all subsequent botanical recording in this country? The answer is simple, if we are to take his published statements on the subject at their face value. In 1843, Watson published the first (and only) volume of what he called the 'third edition' of *The Geographical Distribution of British Plants*. In this we find what we may call 'provincial distribution maps' for 39 native British species, together with the data on which the maps are based. Britain, on these maps—or, as Watson himself calls them in the 'Preliminary Explanations', diagrams—is divided into the 18 provinces which were later, in *Topographical Botany*, to be subdivided into the familiar 112 vice-counties. For each species Watson has a diagram in which 'by omitting the figures from those squares which correspond to districts within which the species has not been ascertained to grow, a tolerably exact notion of its topographical area may be instantly conveyed to the eye of the reader. Those botanists who are sufficiently interested in such investigations, may give greater precision to the diagram by colouring the spaces in accordance with the details of distribution given in the text for each species In each copy of the work, one or more of the diagrams will be so coloured by way of example, but the manual labour of applying colour to all of them would be far too great; while the cost of engraving equally prevented the substitution of printed shades or markings in the diagram, the introduction of which would have necessitated the cutting of a separate block for each of twelve hundred species'.

In other words, Watson says 'Make your own maps; I will supply you with the outline and the raw material in the form of reliable data'. It was a sensible decision based on considerations of economy in expenditure of time and money (fig. 5).

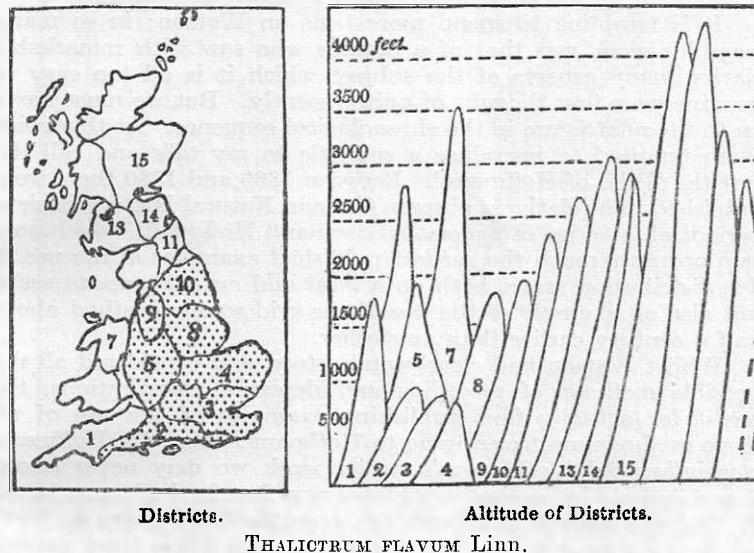


Fig. 5.

Hand-coloured Map from Watson's 'Geographical Distribution of British Plants' (1843). The area hand-coloured is indicated by stippling.

To appreciate how completely Watson had grasped the essential points to be borne in mind in recording and mapping plant distributions, one should, however, turn to the introduction to the *Cybele* published in 1847. Here he distinguishes two so-called 'circumstances of distribution'—'first the extent of geographical surface, over which the plant is spread', for which he suggests the term *Area* should be used, 'and secondly the greater or less frequency of the species within that space', which he suggests might be called *Census*. He sees clearly that, by making the recording units sufficiently small, some sort of measure of the second attribute of distribution can be obtained. To quote: '*Tormentilla officinalis* (i.e. *Potentilla erecta*) and *Hypericum pulchrum* are found in every province; and it is not improbable that they would equally be found in every county, if looked for. But if we could subdivide all the counties into sections of a square mile each, the *Tormentilla* would assumedly be found in many more of these square mile sections, than would the *Hypericum*'. Over a hundred years later, we are at last within sight of completing Watson's example, if, for 'county' we read 'vice-county',

and for 'a square mile' we read 'a 10-kilometre square'. Watson was not quite right about the vice-counties; *Hypericum pulchrum* is apparently absent from Hunts.; but there is no doubt that the Maps Scheme will abundantly bear out his general contention with regard to the relative frequency of these two plants.

It is tempting to spend more time on Watson; in so many ways his work was that of a pioneer who saw with remarkable clarity many aspects of the subject which it is all too easy to imagine were first thought of quite recently. But we must move on to the next figure in the chronological sequence. At this point I am tempted to introduce a sub-title to my talk and call the rest the 'Tales of Hoffmann'. Between 1860 and 1880 there were published in a relatively obscure German Natural History Society periodical, a series of papers by Hermann Hoffmann, which contain not only much the earliest published examples of the use of dot distribution maps, both on a local and on a European scale, but also an example of the use of the grid square method about half a century earlier than any other.

Whilst Watson had clearly understood and considered all the possible methods of recording and depicting distributions, the credit for actually first publishing examples of the use of all these methods must clearly go to Hoffmann. How far Hoffmann was influenced by Watson's earlier work we may never know. I can find no indication in his writings that he had even heard of Watson; indeed, in discussing his methods of mapping Hoffmann gives no hint that he has derived his ideas from anyone else, and there is, of course, no reason at all why he should not have developed them in complete isolation. It is, however, worth remembering that Watson's work was widely known to Continental plant-geographers by the middle of the nineteenth century, and there is nothing improbable in Hoffmann having read, for example, the Introduction to the *Cybele*.

Hoffmann was Professor at Giessen, north of Frankfurt in the province of Upper Hesse. His interest in mapping, unlike that of Watson, seems to have been throughout subsidiary and auxiliary to his main study, that of the different soil preferences of different species. He must, incidentally, have been one of the first men to investigate by means of controlled transplant experiments the so-called 'calcicole' species of his local flora. The first of his published works of interest from our point of view was a paper in 1860 on this theme, in which he dealt particularly with the two calcicolous species *Prunella grandiflora* and *Dianthus carthusianorum*. The two maps which accompany this paper have a good claim to be the earliest published example of dot distribution maps (Plate 2). In this paper he explains the advantage of dot-mapping over the previously used area outline methods. To quote (a free translation): 'If one would consider the distribution as more or less continuous . . . and therefore colour or shade in whole areas, one would, as things stand at present, not only allow too much scope for interpolation, but at the same time



No 21. GENTIANA VERNA L.

Plate 3.

The first 'European Dot Map'? (Hoffmann, 1867).

obscure the expression of the actual observations which should remain (valid and) independent of all hypotheses The isolated occurrences, far removed from the main distribution, stand out all the clearer, and it is precisely these . . . which are of particular importance. In these cases, any attempt to delineate subsidiary distribution-areas instead of separate dots to represent faithfully the occurrence in nature obviously contains an arbitrary element.' In his next paper on the theme (1865) he has many interesting things to say in defence of his detailed dot-mapping. Time will only permit me two short extracts. On the habit of drawing area outline maps on insufficient or unknown data, he has this to say: 'It has always seemed to me irresponsible 'poetic license' for the geologists not only to cover whole surfaces of their maps with different colours when they . . . can never have covered the ground completely, but also to neglect to record the routes which they really have covered. In this way everything remains dubious, uncertain, and everyone who follows must start again from the beginning I have wanted to avoid this; my dots can be increased in number, but it is unlikely that they can be altered'. And on local floras and their generalisations on species distributions: '—although special (local) floras exist . . . their remarks are almost always much too general and imprecise to be useful for the present purpose, even when they are correct. With a statement like 'common in Obenwalde' we can do nothing here; and when it says, for *Erucastrum pollichii* 'everywhere common', a glance at the dot-map will reveal that this is false, for it is absent from most of the region, though in plenty where it does occur.'

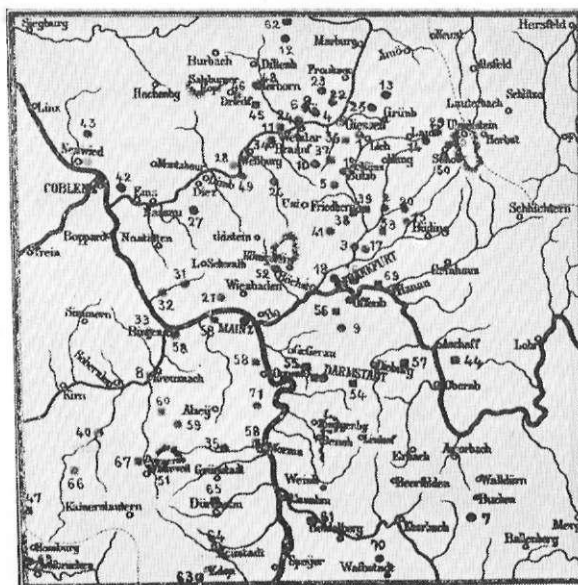
Two main papers (1867 and 1869) provide many examples of Hoffmann's local mapping, but also, quite unexpectedly, what must be the first European dot-map, that of *Gentiana verna*, based on data from De Candolle's *Prodromus* (Plate 3). Even more unexpectedly, Hoffmann makes no special comment on the map, although it is unique in an otherwise uniform set. Finally (1879), Hoffmann invents a simple grid method of recording and uses it throughout his *Flora of the Middle Rhine* (Plate 4). His main arguments for adopting it sound curiously like Watson—convenience and financial (printing) economy. His published maps are mere diagrams in which the numbers of the squares are given where the plant in question has been recorded.

As with Watson, we could profitably linger over Hoffmann. Perhaps we have already spent too long. The rest of the story does not need such detail, however, for the development of dot-mapping in Europe now looks like a more or less continuously-expanding activity. Already by 1879, Ihne (who on internal evidence was probably a pupil of Hoffmann) had published a dot-map using several symbols to distinguish records made in different years and therefore to indicate change of range. In Germany, as Meusel suggests, others followed the established methods. I cannot agree with Hultén, who suggests in a recent

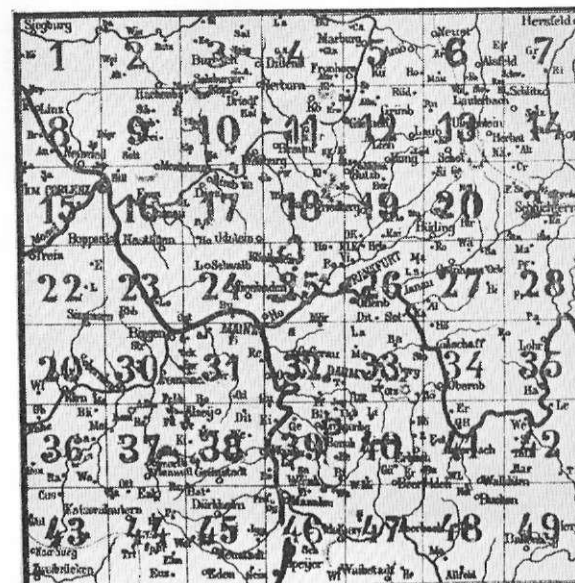
note (1954) that Hoffmann was an isolated pioneer whose 'method was not generally adopted before about 1909, first in Scandinavia and Finland'. The credit for developing the dot-method ought clearly to go to the German workers, of whom Hoffmann was the first; but in any case dot-mapping was quite well-established, I should have thought, in the Scandinavian literature before the turn of the century. As an outstanding early example we may quote the maps of Murbeck (1892) of *Gentianella* species in Europe.

How does the British work fit into this picture? So far as I have been able to ascertain, the answer is simply that there isn't any! Watson's invitation extended to British botanists to 'make their own maps' seemed to fall on deaf ears. The data were there, of course—Watson had seen to that—but I can find no published distribution map of any British plant in the nineteenth century after Watson's originals, except the classic of Miller Christy on the oxlip (*Primula elatior*), first published in 1884. No doubt some people had made themselves vice-county maps from *Topographical Botany* data; F. A. Lees had certainly done so, for we have a hand-coloured map of his in a pamphlet in the Cambridge Botany School; but we must go into the present century to find examples of published maps—and then we find that the 'pioneer' was Praeger (1902) for the Irish flora only! Even Stapf (1914, 1916) who prepared an excellent base-map for his studies of the distribution of the British flora in relation to that of the Continent, did not apparently publish this map for any individual species. Our search for the first published vice-county maps for the whole of the British Isles then takes us well into the modern period, and to Sir Edward Salisbury's deservedly famous study of the East Anglian Flora (1932).^{*} It would be true to say, I think, that until very recently—in fact I suspect until the advent of the Biological Flora—British botanists have been content on the whole with the enumeration of vice-comital distribution and felt very little need for visual presentation of the data. This might be an expression of national character—perhaps we could refer it to Dr. Nikolaus Pevsner to decide! At any rate, since 1950 we have, so to speak, mended our ways, and allowed the excellence of the work in other European countries, notably Professor Hultén's *Atlas* (1950) to influence our work and our methods. If, however, we are late starters in the field, we have two very considerable advantages; firstly a body of codified data on the Watsonian system and a tradition of field botany accustomed to this system; and secondly the varied experience of others to select from and on which to build. The careful deliberations since 1950 which have laid the foundations for the Maps Scheme took account of German, Dutch and

^{*}It has been pointed out to me that C. E. Moss, *Cambridge British Flora* (1914), has numerous distribution maps. Strictly speaking, these are comital and not vice-comital; but obviously the credit for the first use of such maps on any scale in the British literature should go to Moss.



№5. Sambucus Ebulus.



№6. Orientirungs-Karte.

Plate 4.

The first use of the Grid Method for Recording? (Hoffmann, 1879).

No. 5 is a species dot map with the localities numbered for reference to data given in full.

No. 6 is the basic grid of 7x7 squares covering the area; in the text diagrams are given for each species showing those squares (by reference number) in which it is recorded.

Scandinavian work in particular, and finally produced a plan of which, I feel sure, both Watson and Hoffmann would have approved. And what higher commendation do we need? If we read carefully the works of these two pioneers, we shall find all the important arguments in favour of the method or combination of methods we are now adopting—excepting solely the use of mechanical aids. And this last would surely have pleased them more than anything, for economy of time, labour and expense were to them, as to us, important considerations.

A final word. Sooner or later, a sufficient number of people will be interested in a co-operative project to map the European flora. Perhaps here we can repay our debt to European phytogeography by suggesting a practicable, standardised method for doing it. I have ventured to outline such a method as part of our Maps Exhibit at this Conference.

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Dr. E. F. WARBURG said that he was interested to see that on one of the maps shown on the screen the name of the tree (*Pinus sylvestris*) which nearly everyone referred to as "Scots Pine" was correctly given as "Scotch Fir". He was also interested in the very clear cut distribution for *Gentianella campestris* and *G. baltica* shown on Murbeck's map. Recently N. M. Pritchard had been working on these and had found the supposed differences between these taxa entirely elusive. It seemed that Murbeck had in effect drawn his outlines first and allowed his ideas of geographical distribution to influence his judgment on the value of the characters.

Dr. WALTERS then said that he would value comments on his statement that it was necessary to go right into the modern period to find vice-county maps published. His search had not been exhaustive and there might well be published examples in, for example, the publications of local natural history societies. It seemed remarkable if the first successors to Watson's early efforts did not appear until recent years. Prof. D. H. VALENTINE observed that vegetation maps appeared earlier than distribution maps, and Dr. Walters agreed that foreign examples of generalised vegetation maps did, in fact, antedate them by about 30 years.

Prof. VALENTINE then enquired whether Dr. Walters had studied the development of methods used for mapping the geographical distribution of animals, and, if so, whether the development has been contemporaneous with that in flowering plants. Dr. Walters replied that he had no information on this.

Dr. E. F. WARBURG suggested that in the past we have been too obsessed with the use of vice-counties as our standard units and this was encouraged by the cheapness of expressing distribution in print by a series of numbers, as compared with the greater expense of maps. He suggested that we had also relied too much on the wealth of detail available in our local floras which might seem to reduce the need for maps. Dr. WALTERS, in reply, said that perhaps a more important reason explaining the absence of published maps was that until recently there had been little real interest in correlating distribution in this country with distribution in Europe.

Mr. N. M. PRITCHARD referred again to Murbeck's map showing the distribution of *Gentianellas* in Europe. He suggested that Murbeck had found it tempting to assume that where his lines as plotted came to an end on the European coast they should be continued into Britain to round off what might seem the obvious distribution. There was more justification for the contrary assumption that a plant was absent from Britain because no records were available, but this had also led to some inaccurate distribution patterns.

Dr. WARBURG added that Love's recent distribution map of *Rumex angiocarpus*, in which the whole of south-east England was marked in for this species, was another example of how workers abroad delimited distribution in Britain on little evidence.

THE STATUS OF VIOLA LACTEA

(Exhibit)

D. M. MOORE (The Durham Colleges, University of Durham)

Viola lactea was described by J. E. Smith in Sowerby's *English Botany* (1790) and even the author did not seem entirely convinced that it justified specific rank. He opens his account with the comment:—"We are extremely doubtful of the permanence of this species, and now publish it as distinct from *V. canina* rather in conformity to the opinions of others, and in the hope of having the point cleared up by investigation and culture, than as willing to decide upon it ourselves".

There has been considerable diversity of opinion amongst later authors as to the grade of this plant. For example, while Babington in his *Manual*, Gregory in *British Violets*, and Warburg in the *Flora of the British Isles*, treat it as a species; in J. D. Hooker's *Students' Flora*, Hegi's *Illustrierte Flora von Mittel-Europa*, and Rouy and Foucaud's *Flore de France* it is included as a subspecies of *V. canina* L. Considerable difficulties arise in the identification of hybrids in populations including *V. lactea*, *V. canina* and *V. riviniana*, and these hybrid populations are probably frequent.

V. lactea is placed, together with *V. canina* L., *V. stagnina* Kit., and *V. elatior* Fries, in the sub-section Arosulatae of the section Uncinatae. It is most closely related to *V. canina*, of which the principal characters are set out for comparison in the following table:—

<i>V. lactea</i>	<i>V. canina</i>
Habit.	
Perennial.	Perennial.
No central non-flowering rosette.	No central non-flowering rosette.
Sub-glabrous.	Glabrous or sparingly pubescent.
Stems ascending.	Stems decumbent to erect.
Leaves.	
Lanceolate to ovate-lanceolate, subacute, shallowly crenate-serrate, cuneate at the base, broadest about the middle. Foliage sometimes purplish.	Ovate to ovate-lanceolate, obtuse or subacute, crenate or crenate-serrate, truncate or shallowly and widely cordate at the base.

Stipules.

Large (except the lower), lanceolate to ovate-lanceolate, coarsely and irregularly fimbriate-serrate or dentate, equalling or somewhat longer than the petiole.

Rather small, \pm lanceolate, distantly serrate-dentate, with few short and stout teeth, about half as long as the petiole.

Corolla.

Petals narrow (3-4 times as long as broad), creamy to pale lilac.

Petals obovate ($1\frac{1}{2}$ -2 times as long as broad), blue with little or no violet tint.

Flowering period.

May to June.

April to June.

Viola canina has a wide Eurasiatic distribution (reports from North America refer to *V. adunca*, which is allied to our *V. rupestris* Schmidt) but *V. lactea* is much more restricted. It reaches its northernmost limit in the south and west of the British Isles and has been recognised (under a variety of specific names, including *V. lusitanica* Thore) in S. France, Portugal and Spain. It therefore belongs to Matthews' Oceanic West European Element.

Broadly speaking, *V. canina* in Britain is a plant of downs and dunes, and *V. lactea* a plant of heaths, especially near the sea.

I have found that *V. lactea* has 58-60 chromosomes (counts on 5 plants from four localities) in contrast to *V. canina* which normally has 40, both British and foreign material having been examined. Artificial hybrids have been made by Prof. D. H. Valentine between *V. lactea* and *V. canina* and with *V. riviniana*, and both, as expected, are pentaploid with about 50 chromosomes. It may be added that *V. canina* \times *riviniana* is practically sterile, while the hybrid *V. canina* \times *lactea*, though of reduced fertility, is able to produce some viable seed.

The data on morphology, geographical distribution and cytology, taken together, support the view that *V. lactea* is worthy of specific status, and this conclusion clears the way for a study of variation in *V. lactea* and for an investigation into the extent and importance of hybridisation in natural populations.

In the summer of 1955 I examined a number of field populations in S.W. England, collecting samples of 30 specimens from each in order to carry out a biometrical analysis. Since violet flowers are notorious for their deterioration when dried, the flower colour was scored in the field, and the diagnostically valuable lower petals were preserved by sticking them on cards with strips of cello tape; this method was used by Heslop Harrison (1949) for wild populations of the Dactylorchids. The remainder of each flower was preserved in alcohol while the stem and leaves were pressed and numbered to correlate with the petals.

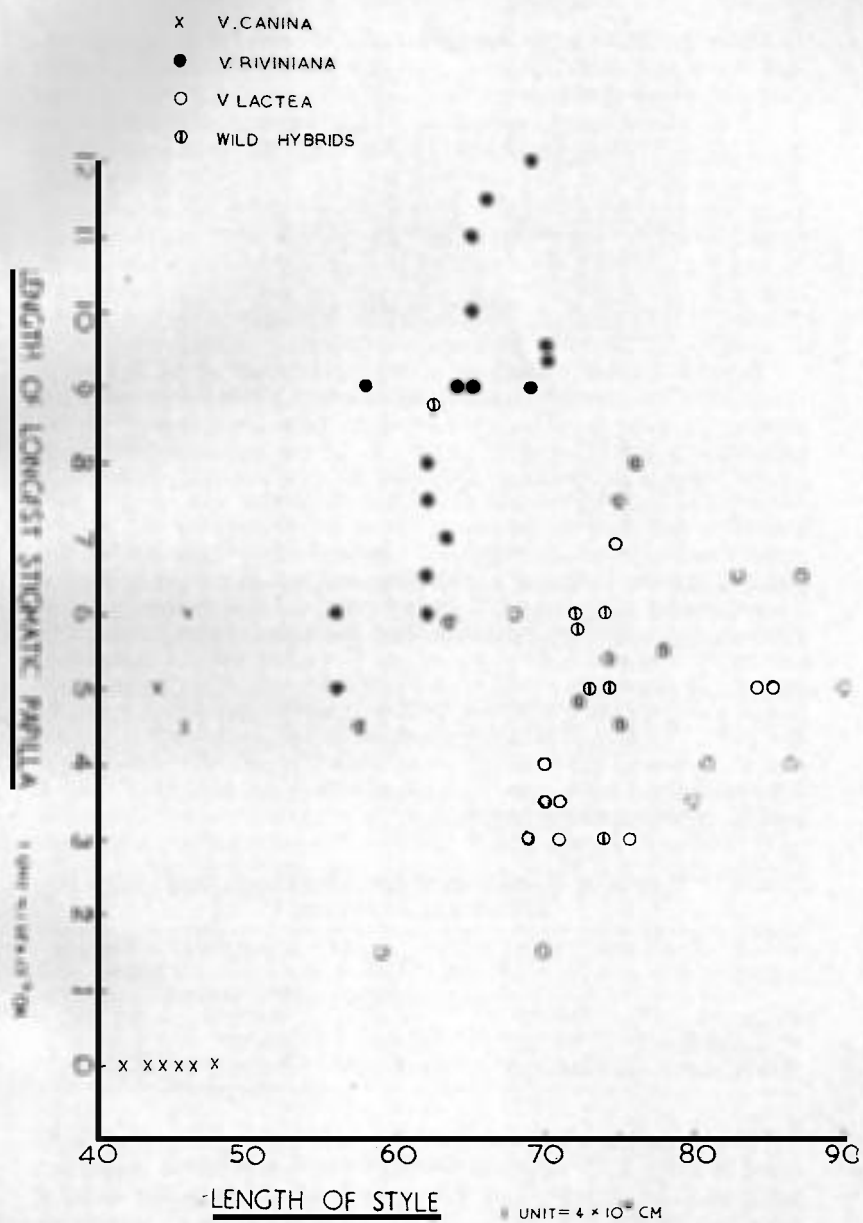


Fig. 4

Scatter diagram based on the length of the longest stigmatic papilla and length of style of *V. canina*, *V. riviniana*, *V. lactea*, and wild hybrids. In vegetative characters, *V. canina* is intermediate between *V. lactea* and *V. riviniana*, so that hybrids involving these species may be difficult to distinguish in dried or fruiting specimens. The wild hybrids scored closely resembled *V. canina* in vegetative characters, but it is evident that on the floral characters used *V. canina* is not involved.

Subsequent investigations showed that the following characters were biometrically most suitable for delimiting *V. lactea* from the other species:—

1. Leaf shape, scored as length/greatest breadth.
2. Basal angle of leaf, i.e. the angle between midrib and blade to give degree of cordate- or truncate-ness.
3. Length/greatest breadth of the lower petal.
4. Angle formed at apex of lower petal.
5. Petal colour.
6. Style length.
7. Length of longest stigmatic papilla.
8. Pollen fertility.

In a preliminary analysis of the data obtained in this way, the method of radiate indicators (Fassett, 1941) was used on characters 1 to 5. The conclusion at this stage was that the populations consisted of *V. lactea*, *V. riviniana*, and hybrids between these two species. In order to confirm this conclusion, further analysis by means of scatter diagrams was carried out, this time including characters 6, 7 and 8 (compare fig. 6). All the results agree in indicating that the hybrids concerned in the populations are *V. lactea* × *riviniana* and not *V. canina* × *lactea*. These results are somewhat unexpected, as the impression had been gained from the literature, and from herbarium notes, that the most frequent hybrid including *V. lactea* was *V. canina* × *lactea*. It should be noted that the conclusions from these population analyses are confirmed by the observations so far made in the field. In the hybrid populations so far examined *V. lactea* and *V. riviniana* are both present, while *V. canina* is absent, and I have not yet been able, in spite of searching, to find *V. lactea* and *V. canina* growing together.

TABLE 1. RANGE OF VARIATION IN SPECIFIC CHARACTERS USED FOR BIOMETRIC ANALYSIS.

	Leaf	length	Petal	length
	Basal Angle	Leaf breadth	Apical Angle	Petal breadth
<i>V. lactea</i>	40-90°	1.4-2.5	39-76°	1.6-2.05
<i>V. canina</i>	90-139°	1.0-1.5	75-80°	1.0-1.6
<i>V. riviniana</i>	118-160°	0.7-1.2	78-90°	1.2-1.43

These results have one further consequence since, as indicated in Table 1, *V. canina* is intermediate in vegetative characters between *V. lactea* and *V. riviniana*; so that, although the *lactea* × *riviniana* hybrid can safely be distinguished from *V. canina* on floral characters, it is difficult to make the distinction on herbarium or fruiting specimens. Thus, if populations containing all three species are encountered, it may be difficult to analyse them. Clearly Anderson's hybrid index, which is very suitable

for certain groups, is of little use here; and it will probably be more satisfactory to describe hybrid populations either graphically, in terms of cyclic polygons, or numerically, by making use of discriminant analysis.

In conclusion, it must be pointed out that these observations need to be extended much further, but they do suggest very strongly some of the causes for the doubt concerning the taxonomic status of *V. lactea*, and its delimitation. The ecological tolerances of this species and of *V. canina* are at present under investigation and this, together with experimental breeding now in progress, and further analysis of field populations, should provide an understanding of the evolutionary position of the species.

Summarising the preceding notes one may say that:—

1. Smith's recognition of *V. lactea* in *English Botany*, as a species distinct from *V. canina* L., has been shown to hold good on morphological, cytological and geographical grounds.

2. *V. lactea* is found to be hexaploid, $2n=58-60$; compared with the tetraploid *V. canina* with $2n=40$.

3. Much of the indecision as to the status of *V. lactea* seems to have been due to the confusion between its hybrids with *V. canina* and *V. riviniana*. Several reasons for this difficulty are suggested.

4. Preliminary notes on biometrical analysis of wild populations containing hybridising *V. lactea* show that, in all cases examined, these hybrids are *V. lactea* \times *riviniana*.

5. In this country, *V. lactea* and *V. canina* generally seem to occupy different habitats and, so far, I have been unable to find them growing together in the field. Further work is to be undertaken in this direction and information on this is badly needed and would be gratefully accepted if anyone can help.

I should like to express my thanks to Professor D. H. Valentine both for suggesting this problem and for his constant invaluable advice and encouragement.

I also wish to acknowledge the aid given by the Department of Scientific and Industrial Research whose grant enables this work to be carried out.

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Mr. J. E. LOUSLEY said that his experiences of *Viola lactea* in localities in the west of England and Wales confirmed Mr. Moore's observation that it hybridised freely with *V. riviniana*. He thought it important to analyse also populations further east where habitat requirements might be somewhat different, and instanced the puzzling plants on Chailey Common, East Sussex, which some botanists had regarded as including hybrids with *V. canina*, as well as with *V. riviniana*, and some had been regarded as involving all three species.

NATURAL HYBRIDIZATION OF AGROSTIS STOLONIFERA AND A. TENUIS

(Exhibit)

A. D. BRADSHAW (Dept. of Agricultural Botany, Bangor)

Agrostis tenuis Sibth. and *Agrostis stolonifera* L. are two very common plants and in their own particular habitats are very distinct, and easily separated by the following contrasting characters:—

	<i>Agrostis stolonifera</i>	<i>Agrostis tenuis</i>
Growth habitat	Stoloniferous, never rhizomatous.	Rhizomatous, sometimes slightly stoloniferous.
Ligule	Longer than broad, pointed.	Not more than half as long as broad, square.
Panicle	Cylindrical, closing in fruit.	Pyramidal, open in fruit.
Lemma	5-nerved.	3-nerved.
Pedicels	Scabrid.	Scarcely scabrid.
Habitat	Base rich soils, usually damp.	Base poor soils, usually dry.

Yet in many regions it is difficult to distinguish the two species and in the past there has been taxonomic confusion. We might well ask why is there this difficulty? Is it possible that the two species hybridize?

Fouillade (1932) reported in France the considerable occurrence of hybrids, but the possibility seems to have been overlooked in this country by Philipson (1937) in his excellent account of the genus. Recently interest in the genus has grown, and Davies (1953) carried out a complete series of artificial hybridizations between various *Agrostis* species. He showed that the formation of artificial hybrids between *Agrostis tenuis* and *A. stolonifera* was easy: seed setting in the crosses was 25% of that of normal. He grew the hybrids and found them to be intermediate in all characters between the parents. They were very sterile with about 1% seed set. Jones (1953) showed that this was due to poor chromosome pairing and univalent formation, though both the parent species are of the same chromosome number, $2n=28$.

In the course of a general investigation of the genecology of *Agrostis tenuis*, a very old pasture, Port Meadow, near Oxford, was sampled. About 60 tillers of the *Agrostis* plants which were growing there were taken at random over a wide area, and were grown as spaced plants in an experimental garden. The composition of this sample, on a morphological basis, was found to be:

(i) Plants of <i>Agrostis tenuis</i>	11%
(ii) Plants of <i>Agrostis stolonifera</i>	31%
(iii) Plants of F_1 type	70%
(iv) Plants not easily ascribable to any of the above categories (presumably F_2 s or backcrosses)	25%

(Total number of plants = 60)

The diagnosis of these plants has been confirmed by their pollen fertilities. The fertilities of a few are given below:

Type	% fertility
(i) <i>Agrostis tenuis</i>	96, 94
(ii) <i>Agrostis stolonifera</i>	94 $\frac{1}{2}$, 93
(iii) F_1 type	7, 3, 8, 4
(iv) Plants not easily ascribable to any of the above	2, 7, 5, 9 $\frac{1}{2}$

Further confirmation has been given by Jones (unpublished) who has examined the meiosis of a number of the sterile plants, and found that their behaviour was similar to that of the synthetic hybrids.

This population is therefore remarkable in that it is composed almost entirely of sterile hybrid plants. This can only mean that the hybrid can compete successfully with its parents despite its sterility. In heavily grazed grassland, such as Port Meadow (there is documentary evidence that Port Meadow has been common grazing since Domesday times), reproduction by seed would be of negligible importance in comparison with vegetative spread.

Some preliminary evidence of the superiority of the vegetative growth of the hybrids is available. Under cultivation the natural hybrid plants appear to have a growth habit better adapted to grazing conditions than either parent.

	General habit	Density of tillers	Height of tillers	Vigour
<i>Agrostis tenuis</i>	Tufted	Medium	Medium	Average
<i>Agrostis stolonifera</i>	Diffusely spreading	Low	Medium	Below average
Hybrid types	Densely spreading	High	Short	Above average

The F_1 of *Agrostis stolonifera* \times *tenuis* is not completely sterile, as already pointed out. Thus *Agrostis stolonifera* \times *tenuis* will form a hybrid swarm, i.e. give rise to a population with a multitude of backcross and F_2 types, etc., besides the F_1 types. But the Port Meadow population does not show this to any degree. Only 25% of the plants do not appear to be pure species or F_1 types, and the fertilities of these suggest that they are not far removed from F_1 types. This gives the idea, though further proof is necessary, that selection is discriminating not just in favour of the hybrids in general, but in favour of the F_1 type.

If we recognise the possibility of finding similar extensive areas of this hybrid elsewhere, it may help us to solve taxonomic difficulties in these two species. This seems to be similar to other cases of sterile F_1 hybrids known in the *Gramineae* such as \times *Agropogon littoralis*, \times *Ammocalamagrostis baltica* and *Glyceria* \times *pedicellata* which survive by vegetative growth. But it is unlike most of them in that the hybrid is occupying a closed habitat, and by this shows that the hybrid is able to withstand severe competition.

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Mr. K. GOODWAY enquired whether Mr. Bradshaw had any idea of how long individual plants could exist in a vegetative condition. Mr. BRADSHAW replied that if a plant was able to keep growing into new soil conditions it could grow on indefinitely in the case of some hybrids. At the Welsh Plant Breeding Station they have various hybrid grasses which have been grown for many years—for example, *Lolium* plants which they have had since 1925. He saw no reason why the *Agrostis* hybrids in Port Meadow should not be very old, but it must be remembered that the population was not due to one old hybrid plant having spread throughout the meadow since many different forms of the hybrid could be found.

Mr. A. W. WESTRUP pointed out that lawns which are regularly mown offer an example of grasses which perennate for very long periods.

ALCHEMILLA VULGARIS L. AGG. IN BRITAIN**(Exhibit)**

Miss M. E. BRADSHAW (University of Durham)

The Common Lady's Mantle, *Alchemilla vulgaris* L., is an obligate apomict, widespread in the Northern Hemisphere; it is an aggregate consisting of a number of species differing markedly in geographical range; there are few, if any, endemic species.

Following the great work of Buser in the Alps (1891+), and Lindberg (1909) in Sweden, Salmon studied the British species and described five in the *Journal of Botany* in 1914. In 1922, Wilmott included seven species in an Appendix to the 10th edition of Babington's *Manual of British Botany*; and in view of the confusion which followed, it is noteworthy that these species are all recognised to-day. After this promising beginning it is regrettable that so much material submitted to Jaquet (Buser's pupil) was inaccurately named, resulting in nineteen species being recorded by Druce in the *Comital Flora*. Salmon, Wilmott and Druce struggled with the aggregate, and records are scattered through the *Journal of Botany* and the *Reports of the Botanical Society and Exchange Club* between 1920 and 1939. Wilmott added *A. minor* Huds. in 1939, and identified *A. acutiloba* from herbarium material in 1946. Samuelsson's monograph, and several papers by Rothmaler, on Scandinavian and Central European species respectively, had been published by the time Walters revised Jaquet's determinations and reduced the total of species in this country from nineteen to eleven, thus producing in 1949 some order out of the chaos and a firm basis on which to study the group.

Sufficient work has now been done to get a fairly clear picture of the range of each species in this country. As found by Samuelsson in Sweden, there is a marked difference between species in geographical range. Each is best considered in relation to its type of distribution in the Northern Hemisphere. Samuelsson found no endemics, a notable contrast to the situation in *Hieracium* and *Taraxacum*, which contain a number of local endemics.

The species may be arranged as follows:—

1. European-Atlantic
A. xanthochlora Rothm. (*A. pratensis* auct. non Schmidt)
2. Central European
A. minor Huds. (*A. glaucescens* Wallroth)
A. monticola Opiz (*A. pastoralis* Bus.)
A. acutiloba Opiz (*A. acutangula* Bus.)
A. subcrenata Bus.

3. Amphi-Atlantic, Arctic-montane
A. glomerulans Bus.
A. wichurae (Bus.) Stef.
4. Amphi-Atlantic, Boreal
A. glabra Neyg. (*A. alpestris* auct. vix Schmidt)
A. filicaulis Bus.
A. vestita (Bus.) Raunk.
5. Endemic
A. minima Walters.

The distribution of most of these was given in maps in the Exhibit. They may be considered as follows:—

1. *European-Atlantic*. *A. xanthochlora* is rather strictly oceanic in Europe from Spain to South Scandinavia and is one of the three common species in Britain.

2. *Central European*. *A. minor* Huds. (more correctly *A. glaucescens* Wallroth) is widespread on the continent; its isolated records on limestone in Craven, Scotland and Ireland may be relicts of a wider distribution.

A. monticola, *A. acutiloba* and *A. subcrenata*. Walters found the first two to be common in Upper Teesdale; another feature of the floristic uniqueness of this district. In 1951, *A. acutiloba* was found in some quantity in Weardale, and, shortly afterwards, a third Central European species, *A. subcrenata*, was discovered in Teesdale; though, even after intensive searching, *A. gracilis* (*A. micans*), widely associated with the first two species in Europe, has not been found. Further work in the area has revealed a striking difference in the detailed distribution of these three species, which initially appeared to be similar since all are components of hay-meadows, pastures and roadside verges. *A. monticola* is concentrated in Upper Teesdale over a large area and is most abundant in meadows, especially about Middleton-in-Teesdale. The many records along roads leading from the valley suggest that active spread is taking place, presumably much helped by modern traffic. *A. acutiloba*, in contrast, is most common along road and railway verges, especially in Weardale. Though many of the records in meadows are associated with field paths, there are striking concentrations in fields and along the roads in some areas in Upper Weardale, as at Westgate, north of Wolsingham and Bedburn. *A. subcrenata* is known only from meadows in two small areas in Teesdale and one in Weardale. This association with man-maintained habitats was also noticed by Samuelsson in Sweden and has given rise to discussion about the status of these three species as natives of Britain.

3. *Amphi-Atlantic, Arctic-montane*. *A. glomerulans* and *A. wichurae* were known by Wilmott from Scotland. Walters found both in Teesdale, where they are now known to be more common; their distribution contrasts sharply with that of the

Central European species by their occurrence mainly in natural or semi-natural habitats. *A. wichurae* occurs in N. England and Scotland and is associated with calcareous rocks. *A. glomerulans* has a disjunct distribution; it is more widespread in Scotland than *A. wichurae*, but in England is only found in Teesdale and Weardale. There is some evidence that the Scottish and Teesdale plants are ecotypically different and it is important to know if their distribution is really disjunct. There is only one record from Weardale (made in 1954) but the whole Cheviot, and Southern Uplands area urgently needs exploring.

4. *Amphi-Atlantic, Boreal.* *A. glabra* is the common species of the northern and montane areas of Britain. *A. filicaulis* and *A. vestita* differ only on a character of hair cover and are regarded as one species by many workers. The more hairy *A. vestita* is the most widespread over the country and is the common *Alchemilla* of southern England; the scarcity of records in Scotland may, in part, be due to lack of botanists; or the species may really be replaced by *A. filicaulis*, the more glabrous, montane form. Hultén includes it with *A. wichurae* and the British distribution fits this, but it is doubtful whether the taxonomic position is clear since *A. vestita* shows great variation in hair density. A study is being made to determine the taxonomic status of the pair.

5. *Endemic.* *A. minima* is still only recorded from one locality (Simon Fell, Ingleborough), which is not surprising since the plant is only distinguished with difficulty from the hairy dwarf plants with which it grows. Cultivation of *A. vestita* from a range of habitats has shown the existence of other dwarf ecotypes. A large number of dwarf plants from montane areas are now being grown at Durham; the results of these experiments should help to decide the status of *A. minima*.

Though the majority of British plants belong to these segregates, a small residue remains of individuals which do not clearly belong to these species. There are some plants from Scotland allied to *A. acutidens* (which group contains *A. wichurae*) which is a group studied in Sweden but not clearly understood; and there are plants from N. England which appear to constitute a new taxon which awaits comparison with European material.

I wish to thank Prof. D. H. Valentine and Dr. S. M. Walters for helpful discussions and the Nature Conservancy and Durham Colleges Research Fund Committee for financial assistance.

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A COMPARISON OF THE SPREAD OF *GALINSOGA PARVIFLORA* AND *G. CILIATA* IN BRITAIN

(Exhibit)

W. S. LACEY (University College of North Wales, Bangor)

Two species of the genus *Galinsoga* are now widely distributed in Britain. The distinction between them has been given by various authors (for example, Brenan, 1939; Lousley, 1950; Lacey, 1951; Clapham, 1952) and need not be repeated here.

Up to the present time *G. parviflora* Cav. has been recorded from 39 vice-counties and the more recently recognised *G. ciliata* (Raf.) Blake from 35 vice-counties, mainly in England but also extending into south and north Wales and into Scotland. So far neither species has been recorded from Northern Ireland or Eire.

Although *G. parviflora* was first introduced to this country more than a century and a half ago, and nearly 100 years have elapsed since it was first recorded as an escape from the Royal Botanic Gardens at Kew, its spread during the greater part of this time has been very slow. It has been calculated that for the first 80 years or so the spread in the London area was at the rate of about one mile in ten years (Salisbury, 1943). By contrast, *G. ciliata*, which probably arrived in Britain at about the turn of the century, has spread very rapidly indeed, especially during and since the Second World War. As a result, it has achieved almost the same distribution as *G. parviflora* in about one-third of the time and, indeed, in some districts is now the more abundant species. Calculations made by the present writer, based on records from three different parts of the country, suggest a pre-war average rate of spread of about one mile in two to five years.

The exhibit attempted to compare the spread of the two species in two ways; (a) by distribution maps showing increase by vice-counties for each species during the same selected periods of years (fig. 7, A to C, and fig. 8, A and B) and (b) by a graph showing the total number of records for each species plotted against time (fig. 9). It is realised that both these methods have their limitations. In the distribution maps, vice-counties have been given line shading where the record or records are *unconfirmed* (almost confined to early records of *G. parviflora*), but they are shown solid black on the basis of one or more *confirmed* records. This does not, of course, give any information about the relative abundance of the two species in

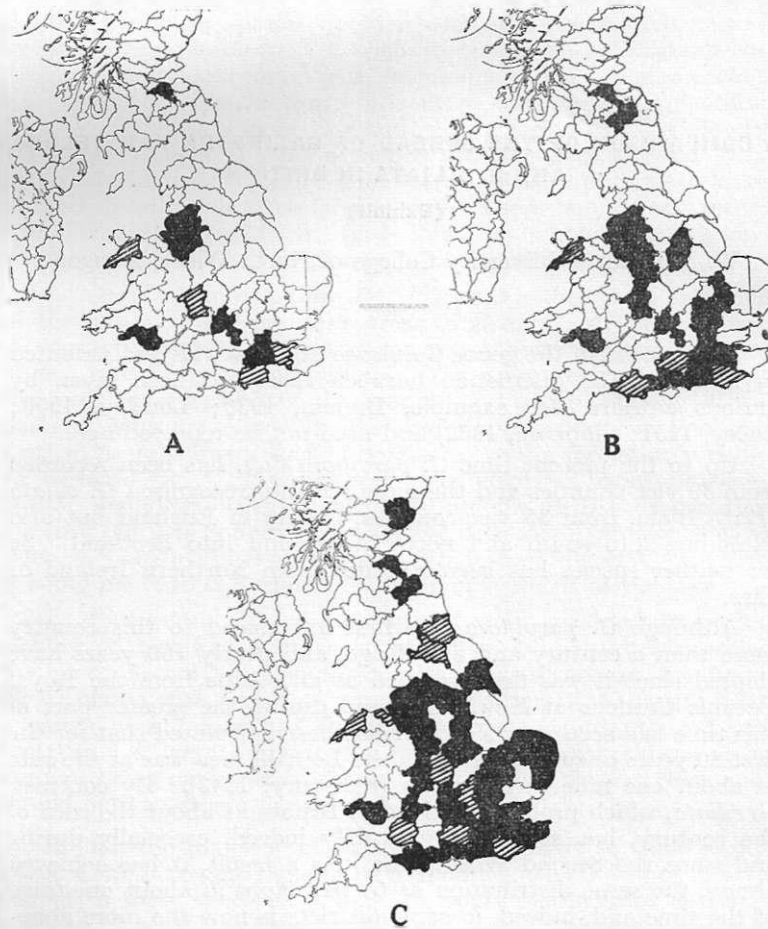


Fig. 7.

A to C. Spread of *Galinsoga parviflora* Cav. in Britain. A, 1908. B, 1939. C, 1955. Vice-counties with unconfirmed records shown by line shading. Further explanation in the text.

With acknowledgment to the "New Naturalist" for use of part of their base-map.

different parts of the distribution area, and may give a false impression that they are common throughout a large part of the country. They are, in fact, most frequently found in south-east England, and in the vicinity of docks, especially in southern England, south Wales, and on Merseyside, with a comparatively thin scatter throughout the rest of the country. Distribution maps showing the actual localities for each species were also exhibited in order to correct any misleading impression from the vice-county maps.

The graphical method of representing the spread depends for its reliability in part on the recording of the correct year for the first appearance in a particular locality, and this information is not always available. Both methods, vice-county maps and graphical representation alike, fail to make allowance for different intensity of botanical activity in different parts of the country, or in the same part at different times. In this case, however, in spite of the difficulties, both methods have given results which are distinct enough to show a striking difference in the rate of spread of the two species.

MAPPING METHOD

Figure 10, A to C, gives the distribution of *G. parviflora* by vice-counties; (a) for the period 1860-1908, that is from the first recorded occurrence outside Kew Gardens until the first recorded appearance of *G. ciliata* in 1909, (b) with additional records from 1909-1939, that is up to the outbreak of the Second World War, and (c) with additional records from 1940-1955. The three maps thus show the distribution of *G. parviflora* in 1908, 1939, and 1955.

The first map (fig. 7, A) includes six probable main centres of introduction, namely London (Kew, 1860), Manchester area (cotton mills at Micklehurst, 1874), Cardiff (Penarth Ferry, on ballast, 1876), Merseyside (1892), Hewell, Wores. (1901, said to be introduced with American wheat), and Edinburgh (Botanic Gardens, 1902, actually known there as far back as 1815). The second and third maps (Figs. 7, B and C) show that the subsequent spread is mainly into Central and Southern England.

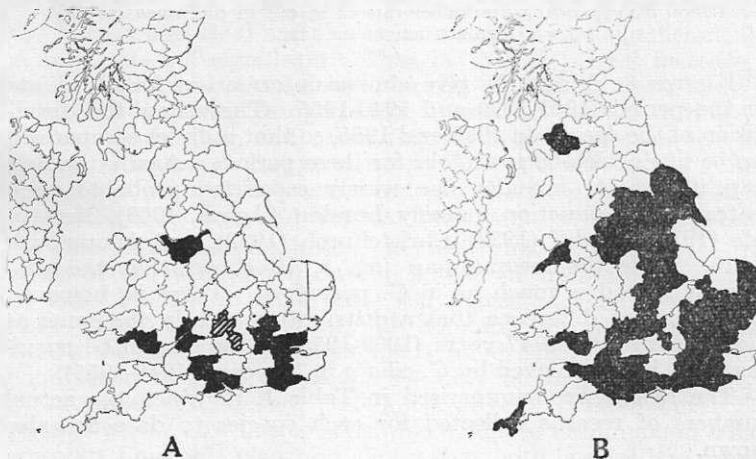


Fig. 8.

A and B. Spread of *Galinsoga ciliata* (Raf.) Blake in Britain. A, 1939. B, 1955. Vice-county with unconfirmed records shown by line shading. Further explanation in the text.

With acknowledgment to the "New Naturalist" for use of part of their base-map.

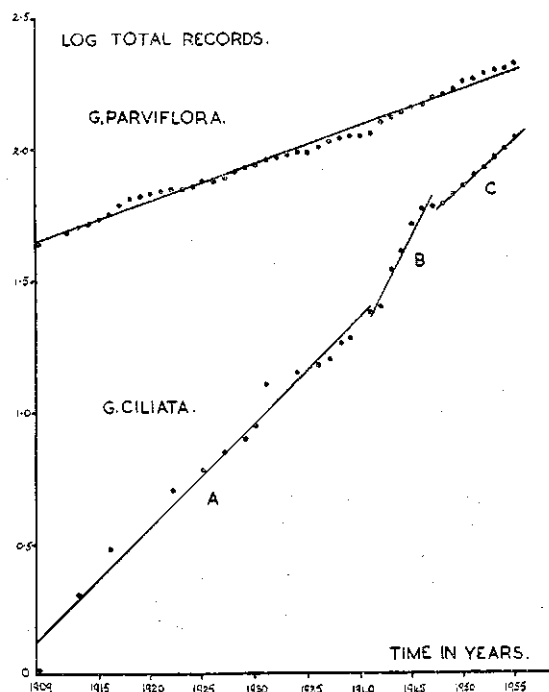


Fig. 9.

Graph demonstrating the higher rate of spread in *Galinsoga ciliata*.
Explanation in the text.

Figures 8, A and B, give similar information for *G. ciliata* for the periods 1909-1939 and 1940-1955. They show the distribution of the species in 1939 and 1955, so that a direct comparison can be made with *G. parviflora* for these periods. Again, the first map (fig. 8, A) includes five widely separated probable main centres of introduction, namely London (Acton, 1909), Merseyside (1913), Cardiff (1922), Christchurch (1922), and Avonmouth (1926), while the second map (fig. 8, B) shows that the subsequent spread is much as in *G. parviflora*. There is, however, the important difference that a distribution, nearly the same as that which required 47 years (1909-1955) in the case of *G. parviflora*, has been achieved by *G. ciliata* in 16 years (1940-1955).

The results are summarised in Table 1, in which the actual numbers of records collected for each species to date are also shown.

It can be seen from the data in Table I, that during the last 16 years, *G. ciliata* has increased in terms of vice-counties by about 200%, and in terms of actual records by nearly 500%, while the corresponding figures for *G. parviflora* for the same period are 86% and 93%.

TABLE 1.

Species	Period	1860-1908	1909-1939	1940-1955	Totals
<i>G. parviflora</i>	Time in Years	49	31	16	
	No. of v.-cs	11	+10	+18	39
	No. of records	42	+71	+105	218
<i>G. ciliata</i>	No. of v.-cs	—	11	+24	35
	No. of records	—	20	+95	115

GRAPH METHOD

In figure 9 the total number of records for each species (using new localities only) is plotted against time. It should be noted that the straight line for *G. parviflora* and the three straight lines A, B, and C for *G. ciliata* are the calculated "lines of best fit", i.e. regression lines of y (log/no. records) on x (time). Further, the slopes of all four lines have been compared and their significance determined statistically.

Two interesting points have emerged:—

(1) The differences in slope between the *G. parviflora* line on the one hand, and the *G. ciliata* lines taken separately or as a whole on the other, are highly significant. That is, *G. ciliata* shows a higher intrinsic rate of spread than *G. parviflora*.

(2) For *G. ciliata*, the differences in slope between the lines A and B, B and C were also found to be significant, but A to C was not significant. That is, there is a real increase in the rate of spread from about the end of 1942 to 1947, more or less coinciding with the period of intensive bombing during the Second World War, and continuing for some time after the war before returning to approximately the pre-war level. There appears to be a slightly increased rate for *G. parviflora* also, at about the same time, but this could not be proved with certainty.

This clear demonstration, at least for *G. ciliata*, of the effect of the war period on the spread of *Galinsoga* species is of some interest in confirming the suggestions made by Salisbury (1953) on the effects of bombing on plant dispersal. But, although it is doubtless made more effective by bombing, wind dispersal is by no means the only factor in the spread of these plants, as Lousley (1953) has already pointed out. The present writer now has considerable evidence accumulated which supports Lousley's view and shows that both species have probably been distributed to a very large extent with horticultural produce, both plants and materials (for example, potted plants, topiary tubs, bedding plants, shrubs, root-stocks, bulbs, seeds, soil, and peat).

In a recent paper on chromosomes and plant ecology, Haskell (1954) states that *G. ciliata* "has not made headway" and that it "will maintain itself only by continual reintroduction". These views are not supported, however, either by the present demonstration of a higher rate of spread in *G. ciliata*, which has enabled the species to achieve practically the same distribution as *G. parviflora* in much less time, or by the continuous presence of *G. ciliata* in several inland localities over periods ranging from six to twelve years. These points will be discussed in more detail in an account of the genus *Galinsoga* in Britain which is in preparation. In this connection, I would welcome any information relating to vice-counties for which no records are as yet available.

I would here express my thanks to the many correspondents who have already kindly responded to my requests for confirmed records, specimens and information. I am especially indebted to Messrs. E. B. Bangerter, J. P. M. Brenan, and J. E. Lousley. I should also like to thank my colleague, Mr. P. Greig-Smith, for statistical assistance with the graph forming figure 9.

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Dr. S. M. WALTERS enquired to what extent the taxonomic error factor had been taken into account in interpreting the statistics. If some of the early records of *G. parviflora* really referred to *G. ciliata*, which was not then recognised, the relative rate of spread of the two species could be quite different. Dr. LACEY replied that during the last few years there had been renewed interest and records of both species had been much more numerous, which, of course, had an influence on the statistics. Reviewing the records over the whole of their history he had the impression that the rapid increase of *G. ciliata* was very real, but it was appreciated that there could be quite a big margin of error.

Mr. A. W. WESTRUP pointed out the importance of continuing to collect records as fully as possible. If *G. ciliata* had now caught up with *G. parviflora*, it was to be expected that the present rate of increase would enable it to outstrip the other species during the next few years. Now that the distinction is clearly recognised, it should not be difficult to keep accurate records.

Mr. N. Y. SANDWITH asked whether the different shapes of the pappus squamellae might have any conceivable influence on the relative powers of dispersal of the two species; whether, for instance, the acuminate-aristate squamellae of the pappus of *G. ciliata* could aid its dispersal by animals or other mobile objects. Dr. LACEY replied that he thought animals as well as man might play a part in the dispersal of the two species, and it might be significant that some of the early records were connected with wool. He had no information about the reproductive capacity of *G. ciliata* or the possible biological significance of differences between the pappus of the two species.

THE SPECIES PROBLEM IN *GALIUM PUMILUM*

(Exhibit)

K. M. GOODWAY (University College of North Staffordshire)

The group of taxa which are collectively referred to *Galium pumilum* has been divided up in various ways, and many names have been given to the segregates, both in this country and on the Continent. Some order was brought to this confusion by Sterner (1944), when he showed that there were two main groups in N.W. Europe, which are readily distinguishable from one another morphologically. One group has a southern, more or less continuous distribution; while the other is more northern, and exists in a number of disjunct populations each of which differs slightly from the others morphologically. The situation in the British Isles is not clear, since Sterner could only use the records in the *Comital Flora*.

Further work has shown that both morphological types occur in this country, with a geographical separation as would be expected. In the south and east is Sterner's southern form, *G. pumilum* Murr. *sensu stricto*, while in the north and west is Sterner's northern form, *G. sternerii* Ehrendorfer. This morphological and geographical separation is quite clear and distinct.

It was thought at first that the cytological picture was going to be as clear, for all the plants of *G. pumilum* from British populations which have been examined have been octoploid, and at first all the plants of *G. sternerii* were tetraploid. It was then found that plants of *G. sternerii* from the Burren (Co. Clare) were diploid, and it has since been found that all the plants examined from Ben Bulbin (Sligo), Inchnadamph (W. Sutherland) and Snowdonia (Carnarvon) have also been diploid. On the other hand all the plants from Breconshire, Derbyshire, Yorkshire, Central Scotland and Ben Hope (W. Sutherland) have been tetraploid. The boundary between these two forms is not clear because living plants from N.E. Ireland, the Hebrides and the Orkneys are still needed. It is not clear because these two types can only be distinguished by their chromosome numbers; morphologically they are indistinguishable. It is also impracticable to separate them on characters such as pollen-size, stomatal size, stomatal index, etc., because, although there is a small difference in the average values, the overlap is so great that it would be impossible to assign a single plant, and difficult to assign a population, to one of these groups using these criteria. This is due largely to the great variability of the tetraploid.

This pattern of distribution raises a number of interesting points concerning the history of these groups in the British Isles.

particularly the reason for the restriction of the diploid to the western fringe, but the main problem I want to discuss here is that of the classification of this group. For this I must mention another group of plants which come from the chalk cliffs of the Seine in France. These are the normal *G. pumilum sensu stricto*, identical in appearance with the British plants, but they are tetraploid.

It is difficult, and I have found it impossible, to hybridise plants in this aggregate which are on different chromosome levels. Thus the diploid and tetraploid forms of *G. sternerii* cannot be crossed, and the tetraploid and octoploid forms of *G. pumilum* cannot be crossed. However, I have found that the two tetraploid forms, although morphologically different will cross fairly readily.

This is only one example of a fairly common feature of this genus. The same thing happens in the field in Denmark, where two morphologically different types come into contact. Ehrendorfer has found the same thing in several Austrian species (Ehrendorfer, 1954, 1955), and Fagerlind (1937) showed the same thing with *G. verum* and *G. mollugo*. In each case, the different morphological types have several different levels of polyploidy. The different levels are genetically isolated from one another, but the different morphological types on the same chromosome level can hybridize.

The problem now is that there are two distinct classifications, morphological and cytogenetical, which run directly counter to one another. Which one should be used generally? I suggest that the breeding group or hologamodeme does not provide the basis of the most natural classification. The tetraploid *G. sternerii* has far more in common, ecologically, geographically and historically with its diploid form with which it cannot hybridize than with the tetraploid *G. pumilum* with which it can hybridize.

This, I would suggest, is a case in which the gross morphology of the plant provides a more natural and a more useful classification than does its cytogenetical behaviour.

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Prof. D. H. VALENTINE asked whether self-incompatibility was found in the polyploids as well as in the diploid and whether all the higher polyploids were autopoloids or if some of them might not be allopoloids of the lower chromosome levels. Mr. GOODWAY replied that self-incompatibility was as pronounced in the octoploids and tetraploids as in the diploids, and that, although there was no direct evidence since it was not possible to cross the different chromosome types, it seemed most probable that these were autopoloids, because of their morphological similarity and because one or two quadrivalents were usually present at meiosis in the tetraploids and octoploids.

Mr. A. D. BRADSHAW asked if there was any explanation of the fact that it was impossible to cross the different chromosome races here, pointing out that sterility did not usually appear until the next generation. Mr. GOODWAY replied that he had no explanation to offer. Prof. VALENTINE added that a number of cases were known in which it was difficult to hybridize a diploid with its own autopoloid, while it could be hybridized with its allopoloid quite readily.

DISTRIBUTION AND VARIATION OF ERICA MACKAIANA
(Exhibit)

PETER A. GAY (University College of Wales, Aberystwyth)

Since its discovery in 1835, *Erica mackaiana* Bab. has claimed the attention of botanists for two main reasons. Firstly, of the species present in the flora of the British Isles it affords one of the most striking examples of major discontinuity of distribution: and secondly, its true taxonomic status has always been in some doubt.

E. mackaiana is known only from Ireland and Spain and has been included by various authors of phytogeographical classifications as belonging to the Lusitanian element in their schemes. This element, as Stapf (1914) showed, is merely one end of a graded series. This series shows progressive increase in the degree of disjunction of distribution, and *E. mackaiana* is best considered as at the extreme end. While Good (1931) has suggested in his "Theory of Tolerance" that climatic control is primary, and has shown that sometimes a close parallel between distribution and some climatic factor may be found, it appears unlikely that the distribution of *E. mackaiana* could be explained by reference to climatology except in the most general fashion. In the west European area, the relationship of species and climate has undoubtedly been greatly modified by the great movements of species and floras which have taken place in the past and are apparently still continuing. The relationship of any one species to others which have biological association with it is an essential part of the problem. Applying these principles to *E. mackaiana* an attempt will be made to show the relationship of this taxon to *E. ciliaris* and *E. tetralix*.

In Europe, *E. ciliaris* is predominantly south-western in its distribution, reaching only the south-west fringe of the British Isles. Accepting for the moment the former presence of this species in Connemara, where it has been recorded, the Irish stations for *E. mackaiana* are roughly at the northern boundary of the area occupied by *E. ciliaris*. The distribution of *E. tetralix* in Europe is more north-easterly than that of *E. ciliaris*. At the southern boundary of its area, there are a few isolated records beyond the general range which extends to the coastal region of north Spain and Portugal, and it is near this southern boundary that *E. mackaiana* again occurs. According to Webb (1955) *E. tetralix* and *E. mackaiana* behave as vicariads in this region, and perhaps *E. ciliaris* and *E. mackaiana* in the British Isles may be considered in a comparable way.

Turning now to the morphology of *E. mackaiana* it is observed that in certain respects it possesses features intermediate between *E. ciliaris* and *E. tetralix*. This is shown by leaf shape (as measured by leaf length/width): *E. ciliaris* falls at leaf $L/W=2$; *E. tetralix*=4; and *E. mackaiana*=3. There is considerable variation within samples and it is impossible to allot on this character every specimen to either *E. mackaiana* or *E. tetralix*—in random samples of these two species considered together, the two taxa grade into one another, but the modes corresponding to the central type of each taxon are distinct. A non-morphological character in which this intermediacy is shown is the flowering time. *E. mackaiana* falls between *E. tetralix* and *E. ciliaris* in this respect as also do hybrids of these latter two species.

In some features, *E. mackaiana* collected from Craigga More, near Roundstone, differs significantly from that collected at Lough Nacung, near Gweedore. The two most significant characters which demonstrate this are flower number per umbel and pedicel length. Leaf size and colour also differ between the two localities but the leaf shape is identical. The differences are sufficiently marked for there to be a noticeable difference in the appearance of the plants from the two stations, although it is doubtful if every specimen could be allotted to its source through such considerations.

From the time it was first discovered *E. mackaiana* has been assigned to various taxonomic ranks, among them being that of hybrid between *E. ciliaris* and *E. tetralix*, and despite the current feeling against this, the possibility should be seriously examined. An apparent grave objection to this hypothesis is that the hybrids between these species are known—these hybrids have been named *E. × watsonii*. However, in this situation where segregation of the F_1 and later generations and back-crossing of these hybrids and segregates to both parents takes place, it is most unlikely that every biotype will be known and still less, described. Indeed, it is possible to find, in the range of hybrids between *E. ciliaris* and *E. tetralix*, specimens which strongly resemble *E. mackaiana*.

Using a hybrid index scheme which was devised for the study of hybridization between *E. ciliaris* and *E. tetralix*, a comparison of F_1 *E. × watsonii* and *E. mackaiana* can be made. Most of the individual characters scored for F_1 *E. × watsonii* fall half way between the score awarded to *E. ciliaris* at 0 and *E. tetralix* at 1, yet, for *E. mackaiana*, each score tends to fall at the *E. ciliaris* or *E. tetralix* value; nevertheless, the total of the nine scores for both (i.e. the hybrid indices) are approximately equal at $4\frac{1}{2}$. The means (or totals) of the individual character scores are more or less identical but the variances are very different.

A useful guide to the taxonomic status of plants is their fertility. There is strong evidence that *E. mackaiana* is sterile or almost so; certainly seed set in this taxon is unrecorded and

data from the study of pollen grains can be satisfactorily interpreted in the same way. It will be asked, that if *E. mackaiana* is sterile, how then can *E. praegeri*—a supposed hybrid of *E. mackaiana* and *E. tetralix*—be accounted for? This hypothesis is unnecessary when it is realised that *E. mackaiana* is a collection of biotypes and that the 'type' is probably the result of human selection during collection, of something sufficiently different from *E. tetralix* to warrant attention, regard having been taken of one or two characters only. *E. praegeri* seems to be one of the biotypes more closely resembling *E. tetralix* than does the 'type' of *E. mackaiana*.

The relationship of the distribution of *E. mackaiana* to the status of the other two species and to hybridization between this pair can now be considered. From other lines of approach it is clear that *E. ciliaris* has reduced its range in the British Isles. The disjunction in the distribution of *E. tetralix* at the south of its range suggests that it too is migrating, leaving relict areas. In France, hybridization between *E. ciliaris* and *E. tetralix* is an exceedingly rare phenomenon, whereas in Britain it is of common occurrence. Unfortunately, I am not personally familiar with the state of affairs in north Spain.

It appears therefore that *E. mackaiana* is present only where the phytogeographical status of one of its 'parents' is falling, a phenomenon significantly associated with a high incidence of hybridization. It seems that *E. mackaiana* has arisen possibly as a product of hybridization between *E. ciliaris* and *tetralix*, and if this hypothesis is true it can give a more satisfactory explanation of the following facts than has been possible hitherto:—

1. It accounts for the morphological intermediacy of *E. mackaiana* between *E. ciliaris* and *E. tetralix*
2. Similarly for phenological intermediacy.
3. The local distribution can be explained as being the result of vegetative spread only, seed dispersal being discounted owing to the sterility factor.
4. The major and minor disjunctions are explicable through polytopic origin within the former common areas of *E. ciliaris* and *E. tetralix*, an origin which can be legitimately cited here.
5. Polytopic origin explains why plants from different stations show differences in their morphology.
6. It gives added weight to the former records for *E. ciliaris* in West Ireland.

No attempt has been made to say exactly what *E. mackaiana* is, except that it seems to have arisen somehow as a product of hybridization between *E. ciliaris* and *E. tetralix*. If this initial step is accepted, it helps to explain in a comparatively simple way many facts which are apparently otherwise unrelated. By approaching the species not as part of a phytogeographic element but as an individual taxon with biological affinities, a much more comprehensive pattern than previously recognised is shown to exist even if the explanation offered is not final.

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Mr. A. W. WESTRUP asked if there was any cytological evidence to distinguish between *E. mackaiana* and *E. × watsoni*. Mr. GAY replied that there was no cytological evidence and that cytological work on these plants presented exceptional difficulties.

Prof. D. H. VALENTINE asked if *E. mackaiana* propagates itself vegetatively in the field, and if so, what is the means of propagation. Mr. GAY replied that it does propagate vegetatively in the field and this seems to be extensive.

Mr. R. D. MEIKLE said that *E. ciliaris* had been reported near Roundstone on three occasions and specimens had been collected and yet it had not been accepted as part of the Irish flora. The area is difficult to search and *E. ciliaris* may well persist on the extensive heathlands. Mr. GAY said he had seen the Roundstone specimen of *E. ciliaris* in the British Museum collection and it is correctly named.

CONCLUDING REMARKS

PROF. T. G. TUTIN in bringing the conference to a close said that the various speakers had given a first-class bird's-eye view of the study of the British flora. By considering all the major methods in turn, with examples of their application, it had been possible to see them in their proper relationship to each other. Many ideas of lines on which we can progress had been given, and these should be a valuable stimulus to future work. In his introductory remarks he had drawn attention to the importance of increased collaboration with continental workers and the study by us in habitats abroad of species which grow in this country. He thought the papers read during the two days of the conference showed clearly that the old insularity of workers here was breaking down and indicated the profitable field which a wider view of our flora opened up. This was one of the most promising ways in which the work of the Society could develop.

Prof. Tutin then proposed votes of thanks to all those who had read papers or contributed to the discussion, and to the Principal and Council of Bedford College and Professor Audus for letting us have the use of the hall and other facilities of the college for the meetings. These proposals were carried with acclamation.

MR. P. J. WANSTALL then proposed a vote of thanks to the members who had acted as Chairmen during the two days and to those responsible for the organisation of the conference. He said that he was sorry that this was the last conference for which Dr. Dony will be directly responsible and that all present would wish to offer him their best wishes in his even more arduous new duties as Honorary General Secretary.

CONCLUSION

The theme of this Conference was a review and comparison of methods used for the study of the British flora with the object of suggesting the most profitable lines for future developments. A number of valuable suggestions were made and readers of the preceding pages will have noticed the remarkable way in which repeated emphasis was laid on two broad lines as offering the most promising avenues for progress. Although no formal resolutions were put to the Conference it was evident from the enthusiasm with which these proposals were received that they met with the general support of those present.

The first of these proposals was that British botanists should take a broader geographical view and learn to regard our flora as part of that of Europe and of the world. This was the theme of Professor Tutin's introductory remarks and of Professor Valentine's concluding paper. Practical measures for implementing the proposal included greater collaboration with continental botanists, and particularly the encouragement of visits to European countries to study our species as represented abroad, invitations to foreign botanists to join our field meetings, collaboration in the project for a European flora, and Dr. S. M. Walters' plan to extend the system of the B.S.B.I. Maps Scheme to Europe. It is hoped that the Society will take active steps to implement some, at least, of these suggestions.

The second broad proposal covered yet greater collaboration between field and indoor workers. This was brought out very early in the Conference in the discussion following Canon Raven's paper, and was particularly well demonstrated in the papers read by Mr. K. Jones and Dr. F. H. Whitehead which showed very clearly indeed to what great advantage field and laboratory approaches can be combined. Professor Richards showed how much the Biological Flora owed to teamwork of this kind, and, in the discussion which followed his paper, J. E. Lousley suggested setting up an organisation to collect published and unpublished information to facilitate such studies. The importance of collaboration between field and laboratory, and between amateur and professional, was illustrated many times during the two days. Although this is already the well established policy of the Society as stressed at earlier Conferences, it is evident that there is scope for even greater efforts to bring together workers whose research cannot be put to maximum advantage in isolation.

EDITOR.

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