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Project 401

The Study of Intra- and Inter-specific Variation in British Woodland Trees
Preliminary Appreciation and Proposals

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1. Introduction

This project is a logical tactical development of the broader research strategy directed towards increasing our knowledge of the between- and within-site variation of the different woodland habitats of Great Britain.

It has arisen from a need to have more accurate information about the pattern and extent of intra- and inter-specific variation in indigenous, and, in a few cases, exotic, broad-leaved and coniferous tree species. It constitutes a preliminary stage in any work that is undertaken to give us a clearer understanding of the genecological history and future development of British woodlands.

In a number of widely distributed species, e.g. the oaks and the birches, a great deal is still unknown about inter-specific relationships and the distribution ranges. It is a popular view, particularly in the two cases cited, that a great deal of the morphological variation is due to inter-specific hybridization and subsequent introgression. A considerable amount of research is envisaged in order to test the validity of this particular belief.

Exotic conifers, in particular Lodgepole pine have been planted on a few Nature Reserves where environmental conditions will support little other tree cover and it is important therefore that some attention should be given to studying the morphological development of the various races of this particular species in order that the plasticity of intra-specific variation may be gauged.

On the technical side the project will be largely concerned with the development of practical computer-based biometrical and possibly chemical techniques for the identification of specimens at the species, racial and if possible individual tree levels. Information of this nature will be of value to other Government Departments, such as the Forestry Commission for planning their tree breeding programmes and seed certification schemes.

In the past and at present most of our woodland trees have been and are being subjected to two types of pressure. On the one hand, generations of timber merchants have doubtlessly removed from our remaining woodlands, by a repeated process of selection felling of increasing intensity where demands have risen, those phenotypes, and by inference certain genotypes, most suited to commerce. This has probably meant a continuous loss from certain populations of the straightest and most finely branched trees. This may have resulted in a modal shift in the phenotypic and genotypic frequencies. On the other hand, the replacement of woodland, in some cases by the introduction of exotic provenances of indigenous species, has probably brought about a migration of foreign genes into other native populations, resulting in possible changes of phenotypic and genotypic frequencies.

These two types of pressure may have had the effects of narrowing or broadening the spectrum of variation in certain large and small morphological features, e.g. stem straightness and leaf or needle form respectively.

2. Species and Genera to be Studied

Arranged in order of priority, the proposed programme embraces the following species and genera: Scots pine, Pinus sylvestris L.; the two common oaks, Quercus robur L. and Q. petraea (Mattuschka) Liebl.; the birches, genus Betula L.; Lodgepole pine, Pinus contorta Dougl.; the species and species aggregates of the genus Sorbus L.; various poplars, genus Populus L.; beech, Fagus sylvatica L.. Other species will be added as resources become available.

2.1 Objects

The project has four main objects, which are applicable, either in full or in part, to the species and genera under consideration:-

1) Obtaining an accurate picture of intra-specific variation and its place in species distribution:

2) Obtaining precise information on inter-specific hybridization and its effects on species evolution:

3) The development of simple biometrical and chemical techniques, which can be used to solve particular problems of identification:

4) The determination of the localities of origin of local and regional introductions whose ancestries are in dispute or unknown.

3. Scots pine: - Synopsis of the current situation

Although its natural range has been reduced doubtlessly by man's activities, Scots pine is widely distributed throughout Britain. In the decades following two World Wars, seed from home and foreign sources has been used to form artificial populations in most parts of the country. In addition several provenance experiments exist, which contain material covering most of the natural range of the distribution of the species. It is possible, therefore, that, in terms of botanical wealth, Scots pine represents our richest species.

Within the native remnants, Steven and Carlisle found an interesting variety of habit types, needle, bark and cone forms, whose frequency distributions did not differ significantly throughout the range. There is little evidence at the moment, therefore, to suggest the development of a number of distinct sub-species in our native pinewoods.

Evidence from I.U.F.R.O. provenance trials however, shows that material, taken from the different geographical regions covering its natural range, exhibits significantly variable patterns of behaviour.

Forestry Commission provenance trials are probably the best starting point for a biometric study of this species.

3.1 Objectives

1) Finding the most suitable set of variables, reasonably simple to measure, which can be used in multivariate analyses for the classification of the various provenances of Scots pine.

2) Carrying out a multivariate analysis of the data from provenance trials, with a view to obtaining a sound basis for the classification of populations and individual specimens from other sources.

The results would provide the soundest basis for comparative examinations of Scots pine growing under similar ecological conditions or of analogous material whose origin is in doubt.

Several files of information on Native Scots pine have been obtained from Dr. A. Carlisle. Unfortunately these contain data which, on the whole, are unsuitable for multivariate analyses. At the outset, examinations will be confined to those characters used successfully by Dr. Black in his classification of the various provenances of Lodgepole pine. Before embarking on field work a search through the literature will be made for more recent information, which might affect the choice of variables and sampling methods.

Close contact will be maintained with other workers such as R. Lines and A. F. Mitchell who are engaged in provenance studies for the Forestry Commission, and also R. Faulkner and C. McLean of the same department who have embarked on a breeding programme for Scots pine.

4. Birch: - Synopsis of the distribution and taxonomy of Great Britain

Most botanists recognise three birch species as indigenous to this country; these are the Silver or Warty birch, Betula pendula Roth (B. verrucosa Ehrh.), the Pubescent birch, B. pubescens Ehrh. and the Dwarf birch B. nana L. Both the major species can be considered to be widely distributed throughout Britain, with the exceptions that the Pubescent birch is the more common species in the north and we[illegible] of Scotland whilst the Silver birch

predominates in the south of England. There are also differences in site preference; B. pubescens, for example, is more tolerant than B. pendula of wet conditions. The Dwarf birch is a more local species found only in certain areas of the Highlands of Scotland, the Southern Uplands and northern England.

In the case of the Silver birch B. pendula, apart from the varieties and forms raised by the nursery trade, no sub-specific rankings have been advanced in Great Britain. Authorities in Scandinavia, notably the late Bertil Lindquist, have divided the species into var. lapponica and var. saxatalis, mainly on bark features. Other sub-divisions have been suggested by botanists in the Balkans and Russia. In the case of B. pubescens, two sub-species are listed in the more recent British floras. These are ssp. pubescens which is confined to England and south Scotland and ssp. odorata which is found in the west and north of Scotland. However, a biometrical analysis of material from two Scottish sources by Professor Jentys-Szaferowa at Cracow in Poland, indicates that birches classified as ssp. odorata may in fact belong to another distinct species complex or aggregate. In European literature, this complex is divided at present into two taxa each of specific rank, B. carpatica, Wald. and Kit. and B. tortuosa Ledeb. Both species are found in mountainous regions of Europe and Scandinavia.

It is a widely held view that much of the wide range in morphological variation is due to hybridization between the Silver and Pubescent birch, a belief which has been fostered by many of the popular handbooks. In experimental circles, hybridization is considered to be a rare occurrence because of genetic differences, and the small numbers of hybrids obtained from artificial crosses. Many research workers on the other hand often find it impossible to classify individual trees and reasonable doubts have been cast on the present low frequency ascribed to hybrids and hybrid swarms.

4.1 Objectives

In planning a taxonomic study of the British birches, there are three objectives:

1) the identification of indigenous species;

2) the establishment of the extent of intra-specific variation and its place in species distribution;

3) obtaining an accurate knowledge of natural inter-specific hybridization and introgression, and their effects on species distribution.

The various aspects of these objectives can now be examined at the species level.

B. pendula — A study of intra-specific variation will be carried out to ascertain if the species displays clinal variation; also to determine the existence of isolated populations,

which may have evolved into distinct sub-species. The existence of hybrids and introgression with B. pubescens will be assumed, and suspect areas falling within the Nature Reserves will be studied. Close contact will be maintained with other interested parties such as W. J. Kinnaird at Banchory and F. J. W. England of the Scottish Plant Breeding Station at Roslin.

B. pubescens ssp. pubescens — This will be treated in a similar fashion to B. pendula, and during the same period, where both species occur together or in the same district.

B. pubescens ssp. odorata — The hypothesis will be maintained until disproved, that this sub-species is conspecific with the carpatica-tortuosa complex. Examinations will also follow a similar pattern to that planned for B. pendula.

B. nana — There appear to be no pressing problems connected with this species. Its distribution may require clearer definition. The occurrence of hybrids with B. pubescens will be studied.

4.2 Preliminary study proposals

Initial examinations will be restricted to dwarf shoot leaves and fruits. Measurements will be made of the parameters selected by Jentys-Szaferowa (leaves) and Biolobrzeska and Truchanowiczowna (fruits), using the sub-sets for both series suggested by Jeffers and Gardiner. Other features may suggest themselves as suitable descriminants and these will also be examined.

An examination of the more recent literature will be made to learn whether alternative features have been used successfully by other workers; also to obtain the latest information on the question of inter-specific hybridization. Measurements have already been made on leaf-rubbings obtained from twenty-one populations of B. pubescens and nine of B. pendula, collected by F. J. W. England of the Scottish plant Breeding Station at Roslin. These will provide a suitable starting point for statistical analyses.

5. Oak: - Synopsis of the current taxonomic situation

The actual number and botanical features of the various oak species growing in Britain appears to be quite distinct and not in dispute. What is not clear, however, is the nature of the relationship between the two dominant

species, namely Quercus robur L. and Q. petraea (Mattuschka) Liebl. Are they separate taxa, whose ranges of variation overlap or have they become, in most localities, so introgressed through hybridization and back-crossing, that they must now be regarded as sub-units of the same species complex?

A cursory survey of the literature points to two lines of argument, either in favour of or against the conspecific hypothesis.

1) The species must be regarded as separate because:-

   a) The frequency of first generation or F_1 hybrids in artificial crossing experiments is reported to be low.

   b) Reports of dissimilarities in specific chromosomal arrangements, which would suggest problematic hybridization.

   c) Both species display considerable intra-specific variation, as shown by recent botanical studies and Continental provenace trials, pointing to possible overlaps in ranges of variability.

   d) The site requirements of both species are different, suggesting that one species would thrive at the expense of the other on a given site.

2) The two taxa must be regarded as parts of the same species complex because:-

   a) Techniques such as hybrid indices and pictorial scatter diagrams produce distributions indicative of introgression.

   b) Half-sib progeny trials in Sweden showed that several progenies contained intermediate individuals as well as specimens typical of the parent species.

   c) Occasional individuals arise bearing the morphological features of both species.

5.1 Objectives

The objectives of the study have been formulated in an attempt to solve the problems of introgression or purity of both species. No work is being planned on other oaks such as the American red oak, Q. borealis Michx. f. and now under trial in Forestry Commission experiments, or the Turkey oak, Q. cerris L. which is found in arboreta and elsewhere.

1) Locating areas of the crown, where the within-tree variation in leaf and fruit characters is at a minimum, in order to obtain a series of parameters

suitable for inclusion in multivariate analyses so that individual trees can be labelled mathematically. Work on this particular objective is already being done by Mr. M. W. Shaw and Dr. R. G. H. Bunce.

2) Building three-dimensional models of pure and putative hybrid populations in order that the inter-relationship of individual trees may be examined.

3) The selection of individuals of both species for inter- and intra-specific crossing experiments followed by long-term progeny trials to observe the pattern of morphological behaviour.

4) If inter-specific crossing can be shown to be a probable natural phenomenon through controlled pollination work, the construction of a mathematical model to simulate the course of introgression in an attempt to trace the history and possible future of oak populations.

5.2 Preliminary proposals

An extensive examination will be made of the literature, particularly on the question of hybridization and introgression, to ascertain the background history and depth of knowledge. The subject will then be reviewed in a short publication.

Numerous measurements have already been made on leaf and fruit characters by Mr. M. W. Shaw from a number of oak populations. These will form a very suitable starting point for future multivariate analyses.

Contact will be made with other workers, who have worked or are working in the same field, so that advice may be obtained or exchanged; this will also avoid duplication.

A series of individuals of both species, whose identities can be verified, will be sought in a suitable locality or localities in order to carry out crossing experiments when conditions of copious flowering are likely to be obtained.

6. Lodgepole pine: - Synopsis of present knowledge in Britain

Because of its known tolerance of the poorest site conditions, Lodgepole pine has become one of the most important exotic conifers in Great Britain. It has been used extensively by the Forestry Commission and to a very

limited extent by the Nature Conservancy. In silviculture, it is the practice to classify this species into three main provenance groups. These are Coastal, Inland and Intermediate, the first two being the most commonly used. Three methods of multivariate analysis were carried out in 1961 by Mr. J. N. R. Jeffers on data submitted by Dr. T. M. Black of Northern Ireland, which revealed a previously unrecognised component of botanical variation, in addition to confirming the broad division into inland and coastal provenances.

6.1 Objectives

These are technically similar to those described for Scots pine.

6.2 Material and Methods of Study

Since its introduction as a forest tree, more than fifty provenance trials have been laid down by the Forestry Commission in an endeavour to find the most suitable seed collection areas for British conditions. These experiments, together with nursery stock representing seventy-two seed origins which are being made available to the Nature Conservancy, will provide the necessary basic material for the extension of multivariate analyses of the types carried out by Mr. Jeffers and Dr. Black.

A particular study will be made of the provenances which have been planted by the Nature Conservancy, such as those on the Island of Rhum.

7. British species of the genus Sorbus L.

Clapham, Tutin and Warburg describe three major species as indigenous to Britain. These are S. aucuparia L., the rowan, S. aria (L.) Crantz, the whitebeam and S. torminalis (L.) Crantz, the wild service. They also hold the view that, by a long process of introgression between these species, three aggregates or species complexes have arisen. All three aggregates contain interesting local species endemic to Britain, e.g. S. arranensis, localised in Arran, and S. bristoliensis, found only in the Avon Gorge. The complete list of currently named species, together with putative evolutionary pathways is given in the appendix.

The twenty-two British species in this genus would appear to be worthy of examination as a whole, rather than in isolation, in order to obtain a clearer picture of their relationships.

7.1 Objectives

1) To find a combination of measureable attributes which will produce components or variates capable of discriminating between the various species and identifying specimens whose origins

are unknown.

2) To build a three-dimensional model of the genus, which will permit critical examinations to be made of species inter-relationships.

7.2 Preliminary proposals

It is possible that a number of leaf attributes or a combination of leaf and fruit attributes will yield the necessary information, but no information is currently available of biometric studies involving these species. There is a suggestion that some work has been done in Czechoslovakia by Kovanda, and his publications will be examined as a starting point for planning new investigations.

8. Beech, Fagus sylvatica L.

Beech is another interesting example of a native species whose natural range of distribution has been enlarged considerably by man's activities. Although this has been achieved most probably by the use of home collected seed, there is no doubt that imported seed has been employed also.

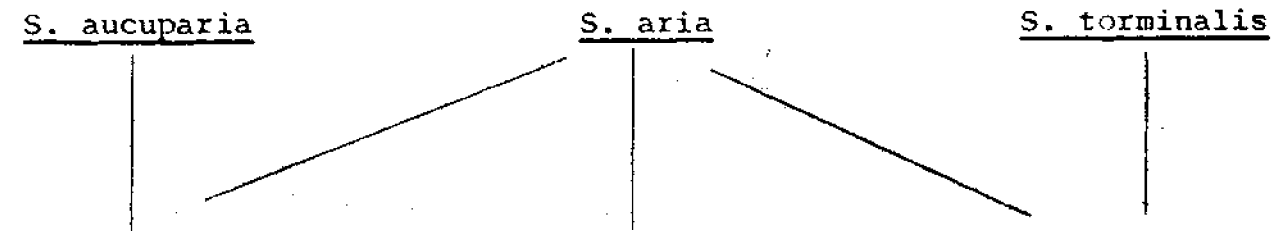
No extensive study is being planned at present within this project; research will be confined to tracing the identity, or place of origin, of such putative introductions as the Chiltern beech. The original seed is reputed to have been collected during the Waterloo Campaign in 1815. In 1951 a small quantity of beech seed was obtained by the Forestry Commission from the Foret de Soignes, an area bordering the original battlefield. Efforts will be made to trace any sowings or plantings which may have resulted from this importation. These would provide an obvious source of comparative material. Another area of possible French origin is the magnificent beech stand at Slindon Park in Sussex.

Initial investigations will be concentrated on finding a suitable biometric, and possible biochemical, technique for differentiating between the various beech provenances

9. Poplar (Populus L.)

This genus has been included because of the existence of a considerable number of leaf measurements from studies initiated by the late T. R. Peace and continued by others. These data will provide an early opportunity for gaining experience with the latest computer techniques.

The genus Sorbus in Britain (Clapham, Tutin and Warburg)



intermedia agg.	aria agg.	latifolia agg.
arranensis	leptophylla	bristoliensis
leyana	willmottiana	subcuneata
minima	eminens	devoniensis
anglica	hibernica	
intermedia	porrigentiformis	
	lancastriensis	
	rupicola	
	vexans	

Listed separately

S. aria x torminalis = S x vagensis

S. domestica (no longer a wild species)

S. pseudofennica