THE ASSESSMENT OF THE TAXONOMIC STATUS OF MIXED OAK (*QUERCUS* spp.) *POPULATIONS*

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Abstract

The oaks (*Quercus* spp.) on slate, limestone and peat sites in Roudsea Wood, North Lancashire, were subjected to a taxonomic analysis using both the Hybrid Index and Pictorial Scatter Diagram methods. Both methods showed that *Quercus petraea* (Mattuschka) Liebl. predominates on the slate site, while the oaks on both the limestone and peat sites are very mixed, with a well-developed *Q. robur* L. component. The Hybrid Index method over-estimated the morphological intermediacy of the trees, while the Pictorial Scatter Diagram method under-estimated the *Q. robur* component. The scatter diagrams suggested that hybridization and introgression had occurred between *Q. petraea* and *Q. robur*.

Introduction

Until recently there has been confusion about the identification of *Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl. in Britain, partly due to contradictions in the literature and partly to the fact that in Britain many of the oaks exhibit intermediate characteristics. Jones' (1959) paper has gone a long way towards clarifying the characteristic morphology of the two species, but even so, apart from the recent work by Cousens (1962a, 1962b, 1963) the descriptions of British oak populations have generally been qualitative. In fundamental work on the autecology and nutrient cycles of oak woodlands, of which this study forms a part, it is essential to have a quantitative description of the individuals and populations if comparisons are to have any real meaning. The present investigation was undertaken to examine two methods of quantitative classification of individual oak (*Quercus* spp.) trees and mixed populations of *Quercus petraea* and *Q. robur*.

Site description

The investigation was carried out in Roudsea Wood in North Lancashire (SD(34)/331828). The woodland, which is owned by Mr. R. E. O. Cavendish, covers 116 hectares (287 acres) of which 45·3 hectares (112 acres) are currently leased by the Nature Conservancy.

The mean annual rainfall is 136 cm (53·5 in), and the mean monthly temperature ranges from 4·2 to 14·8° C (Ordnance Survey 1949; Meteorological Office, 1952).

The woodland includes areas of Upper Silurian slates of the Bannisdale series, carboniferous limestone, and peat, with local glacial and fluvio-glacial deposits. The oak populations were examined on all these sites.

The soils on the slate area are well drained brown earths of low base status, generally > 0·5 m deep, with a pH of 3·6–4·3 at a depth of 5–10 cm, and humus of the moder type (Kubiena 1953). The tree cover on these sites is irregular oak high forest, 70–80 years old, and the ground flora is dominated by *Deschampsia flexuosa*.

The soils of the limestone site are well drained, shallow (< 0·5 m) brown earths of higher base status than the slate soils, and are more variable owing to patches of glacial material containing slate debris. The pH at 5–10 cm depth is 4·3–8·0, and the humus type is similar to a mull. The tree cover on the limestone area consists mainly of dense thickets of oak, ash (*Fraxinus excelsior*), birch (*Betula* spp.), and hazel (*Corylus avellana*) coppice, with scattered standards of the first three. This woodland has a rich ground flora dominated by *Mercurialis perennis* and *Brachypodium sylvaticum*.

The peats are deep (> 1 m), poorly drained, contain 10 per cent of ash (550° C) per unit dry (105° C) weight, and have a pH of 3·2–3·8 at 5–10 cm depth. The woodland on the peats consists of irregular, uneven-aged birch/Scots pine (*Pinus sylvestris*) woodland with scattered oak standards more than 50 years old. The ground flora is dominated by *Calluna vulgaris* and *Vaccinium myrtillus*.

There are no records of planting in Roudsea Wood earlier than 1953, but it is not certain that all the oak is completely natural and indigenous. These woodlands are probably the end product of a number of coppice rotations originating mainly from indigenous, natural maiden trees.

Methods

Two methods were used to assess the taxonomic status of individuals and populations of oak in the present investigation, both of them being what Anderson (1949) terms 'polygraphic analyses':

I The Hybrid Index (HI) Method;
II The Pictorial Scatter Diagram (PSD) Method.

The main survey of the oak populations in Roudsea Wood was carried out using the HI method. Sub-samples (n = 20) of the populations were assessed by both methods.

I. The Hybrid Index method

This method, explained in detail by Anderson (1936, 1949), is useful for describing complex populations where two species have hybridized and backcrossed to produce plants of intermediate morphology (Anderson 1936, Raunkaier 1925, Riley 1938). It consists of calculating for each sample tree a numerical index, which describes the degree to which overall morphology of the individual is typical of one or other of the species.

When frequency distributions of these indices, calculated for a sample of plants from a population, are drawn as histograms, they give a visual description of the extent to which the components of the population are intermediate or typical of the species.

In the present investigation the calculation of the Hybrid Index was modified to permit different numbers of characters being examined in individual sample trees. In the calculation of the ordinary HI for a number of individual plants it is essential to keep the number of characters examined constant, otherwise the indices are not comparable. This is not always possible, and if strictly adhered to could introduce a bias into the sampling. *Q. robur* tends to produce seed more readily than *Q. petraea* (Jones 1959), and if all trees without acorns were rejected from the sample there would be a tendency to sample *Q. robur* more often than *Q. petraea* in a mixed population. In this instance, therefore, a variable number of characters must be accepted, and to overcome this difficulty, the index was calculated as a Percentage Hybrid Index. As many as possible of the selected characters were examined, assigned individually to the three categories *Q. robur*, or intermediate, or *Q. petraea*, and the number of characters in each category summed. These three sums were then calculated as percentages of the total number of characters examined, and the percentages multiplied by the factors 0, $\frac{1}{2}$ and 1 respectively. The summation of these products gave the Percentage Hybrid Index (PHI) which has a range of 0–100 (0 = *Q. robur*, 100 = *Q. petraea*) and is independent of variations in the total number of characters recorded.

The characters used in the estimation of the PHIs of the oaks in Roudsea Wood were based on Jones' definitions (1959). To begin with, 23 characters were examined by two independent workers examining the same set of specimens. Persistent disagreement occurred when attempting to categorize leaf glossiness, colour and texture, and these characters were discarded. The remaining 20 characters are defined in Table 1.

In view of the current lack of knowledge on the relative importance of individual oak characters, no weighting was used in the calculation of the PHI.

Roudsea Wood was divided into three parts, on the basis of the main soil types: slate soils, limestone soils, and peat. A random sample of 118 trees was taken on the slate site, 54 on the limestone, 48 on the peat. More than half the oaks in the wood are on the

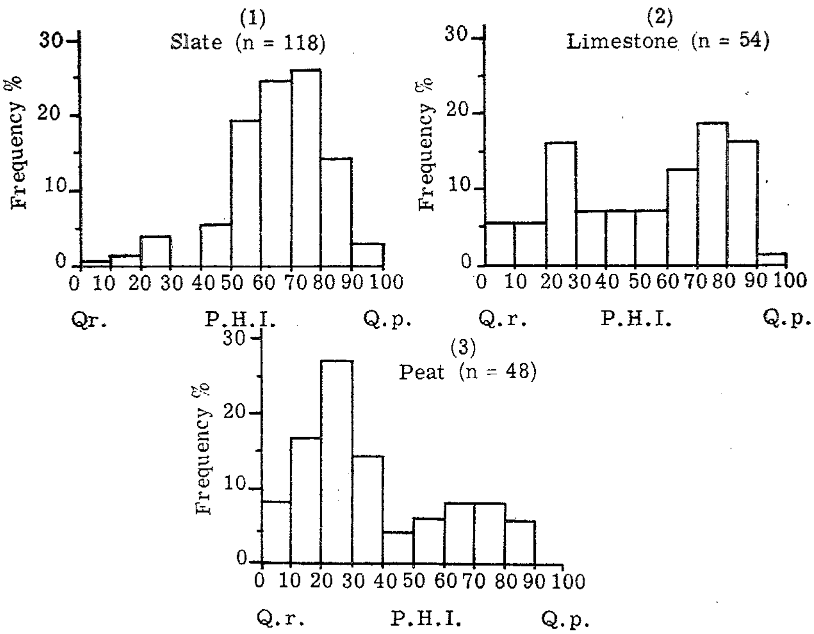
TABLE 1. Morphological characters of *Quercus* spp. used in the assessment of percentage hybrid indices.

Character	*Q. robur*	*Q. petraea*
Stem persistence	Not persistent	Persistent
Angle between branches	> 45°	< 45°
Crown density	Open (foliage in clusters)	Dense (foliage uniformly distributed)
Bark	Thick elongated units	Thin rectangular units
Buds (terminal)		
(a) Size	Small (< 5 mm long)	Large (> 5 mm long)
(b) Form	Obtuse tip	Acute tip
Leaves		
(a) Shape	Obovate, widest in apical third of leaf	Ovate, widest near mid-leaf
(b) Lobe number*	< 5	> 5
(c) Lobe depth	Deep (> 50% of half leaf width)	Shallow (< 50% of half leaf width)
(d) Lobe regularity	Irregular	Regular
(e) Venation	Some veins to the sinuses between lobes	None to the sinuses
(f) Base auricle	Strongly auriculate, with the auricle lobes overlapping the petiole	Cordate, or slightly indented
(g) Petiole	< 7 mm	> 13 mm
(h) Simple hairs on abaxial surface	Few or absent	Abundant
(i) Stellate hairs on abaxial surface	Absent	Present
Acorns		
(a) Colour (when ripe)	Pale fawn	Dark brown
(b) Stripe (when ripe)	Olive green	None
(c) Form	Elongated	Rounded
(d) Peduncle length†	> 30 mm	< 20 mm
(e) Peduncle pubescence	Glabrous	Clustered hairs

* Jones gives the leaf lobe number of *Q. robur* as 3–5 (–6), and for *Q. petraea* as 5–6–8.
† Peduncle length taken as peduncle length to the terminal flower or bract.

slate site, and this area was sampled most intensively. Even so the sample of the trees on the slate site was less than a 10 per cent enumeration. On the limestone and peat more than half the total number of oaks present were sampled. The trees were sampled in the autumns (August to September) of 1961 and 1962. Stem persistence, branch angle, bark form and crown density were all recorded in the field. Ten sample shoots were taken from the upper half of the south side of the crown of each tree, all the shoots being free from shading. Lammas shoots were not included. Acorns were taken where possible, but a tree was not discarded from the sample because acorns were absent. Samples were examined either the same day or the day after collection. Ten leaves were taken at random from the pre-Lammas growth, and as many acorns as possible (up to 10) were examined. Decisions were made as to whether each character was typical of *Q. robur* or *Q. petraea*, or intermediate, and the PHIs calculated (Figs. 1–3).

There was a tendency to regard a character which was only slightly atypical of one or other of the species as intermediate. This was particularly so where a character was defined qualitatively (e.g. leaf lobe regularity, acorn shape). There is therefore a tendency for the PHI method to over-emphasize the intermediate character of a tree.



Figs. 1–3. The frequency distributions of Percentage Hybrid Indices (PHI) of oaks on slate, limestone and peat sites in Roudsea Wood.

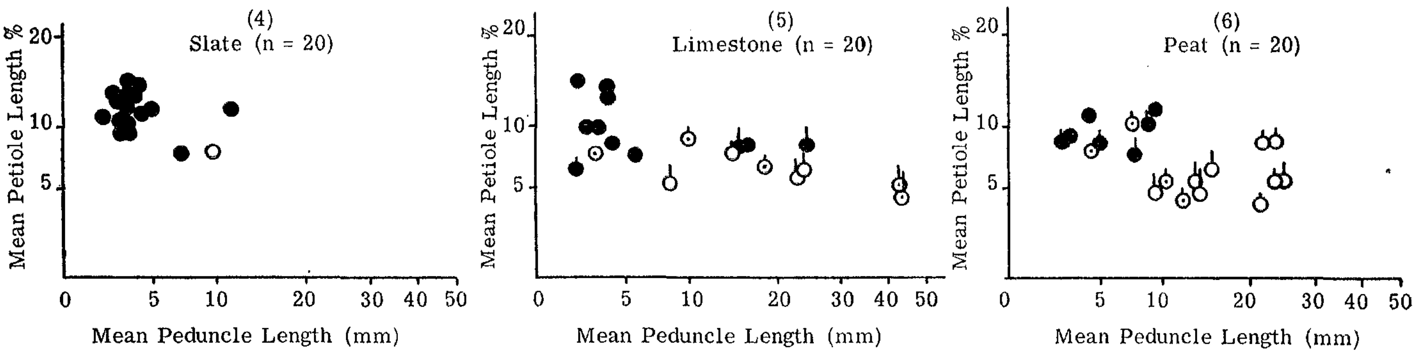
We examined samples from 10 trees twice within a period of a week, and the two PHI estimates differed by a mean of $\pm 2 \cdot 6$ PHI units with a maximum difference of 6·0 units. The method can, therefore, be repeated with an acceptable degree of error.

II. Pictorial scatter diagram

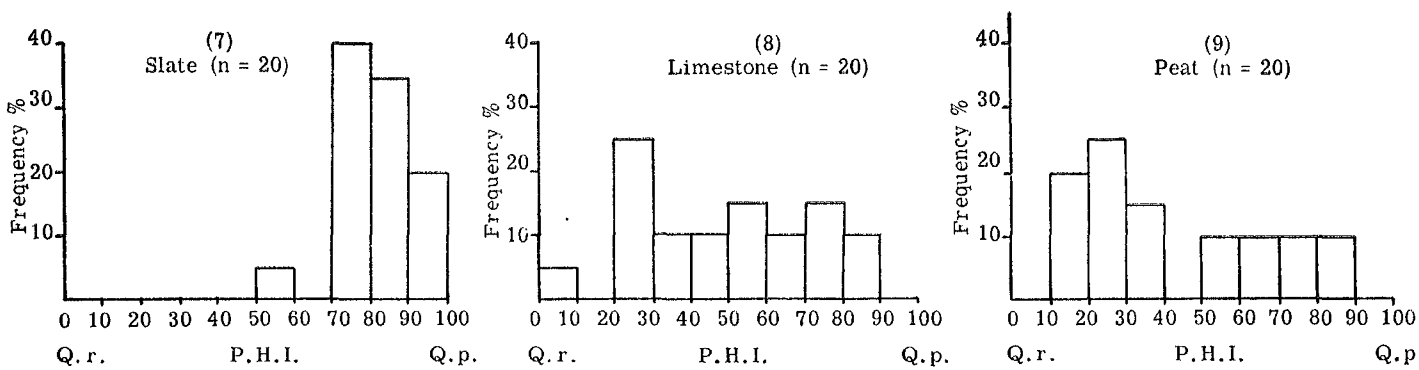
This method, based upon a technique described by Anderson (1949), has been used by Cousens (1962a and b) for surveys of oak populations in Britain. The principle of the method is that when, in a population of two species and their hybrids, two continuously variable morphological attributes by which the species are known to differ are plotted graphically, and each co-ordinate coded for subsidiary characteristics, the resultant scatter diagram gives a visual description of the population. The pattern of the scatter may be interpreted in terms of the degree of hybridization and introgression, and different populations can be compared visually. Points for the two species tend to concentrate in two separate zones, those for individuals with intermediate characteristics lying outside and between these zones.

The Pictorial Scatter Diagram (PSD) method was used on a sample of 20 trees taken at random on each of the slate, limestone, and peat sites. Ten shoots were taken from the upper half of the south side of the crown of each tree. Lammas growth was excluded from the sample. As many acorns as possible (up to 10) were included in each sample. Five leaves were taken from the mid-zone of each of the 10 shoots, mixed, and 10 of these 50 leaves taken at random. The petiole length, total leaf length, leaf auricle type and abaxial stellate pubescence were assessed for these 10 leaves, and the petiole length expressed as a percentage of total leaf length as suggested by Cousens. The acorn peduncle lengths to the first bract or flower were measured and the mean calculated. The mean petiole per cent. and mean peduncle length were plotted on logarithmic paper, and the points coded for leaf auricle type and abaxial stellate pubescence (Figs. 4–6). The same 20 trees were subjected to a PHI analysis (Figs. 7–9).

This PSD procedure differed from that used by Cousens in that 10 leaves per tree



Figs. 4–6. Pictorial Scatter Diagrams for oaks on slate, limestone and peat sites in Roudsea Wood. ●, ⊙, ○ = stellate pubescence on abaxial leaf surface abundant, sparse and absent respectively. ○ with long line, ○ with short line, ○ = leaf auricle well developed, weak and absent respectively.



Figs. 7–9. The frequency distributions of the Percentage Hybrid Indices (PHI) of the oak samples from slate, limestone and peat sites in Roudsea Wood used to construct the Pictorial Scatter Diagrams (Figs. 4–6).

were used instead of two; the mean acorn peduncle length was used instead of maximum peduncle length; and the peduncle stoutness and pubescence were not included in the code on the scatter diagram.

RESULTS

The taxonomic status of the oak populations

The PHI frequency distributions (Figs. 1–3) show differences between the oak populations on the different sites. On the slate site, the oaks are mainly trees with marked *Q. petraea* characteristics, and there are very few *Q. robur*. The oak populations on the limestone and peat are more mixed with modes near both the *Q. robur* and *Q. petraea* ends of the scale. There is a strong *Q. robur* component in the woodlands on the peat site.

The scatter diagrams (Figs. 4–6) also show that the oak populations on the slate, limestone and peat sites are different. On the diagram (Fig. 4) for the slate site, there is a concentration of points in a zone where the mean petiole length per cent. is high and the mean peduncle length low, the leaves having well-developed stellate hairs and no leaf auricles, all of which indicates that most of the trees are *Q. petraea*. There are three intermediate points. This suggests a predominantly *Q. petraea* population containing a few trees with intermediate characteristics. The diagram (Fig. 5) for the limestone site suggests a very mixed population ranging from trees with high mean petiole percentages and low mean peduncle lengths (*Q. petraea*) to trees with low mean petiole percentages and high mean peduncle lengths (*Q. robur*), with many intermediates. The *Q. petraea* trees all have at least a few stellate hairs and no auricle, and all the points in the *Q. robur* zone are associated with trees having well-developed auricles and few or no stellate hairs. The diagram for the peat site shows that while there are a few trees in or near the *Q. petraea* zone on the diagram, and a few more or less in the *Q. robur* zone, most of the trees are intermediate in their petiole and peduncle characteristics. Near the *Q. petraea* zone some of the trees have weakly-developed auricles.

The scatter diagrams reflect the *Q. petraea* component suggested by the PHI frequency distributions, but the former do not suggest as strong a *Q. robur* component as the latter.

As *Q. robur* apparently prefers base-rich fertile soils and *Q. petraea* the more acid, less fertile soils (Jones 1959, Moss 1914), the distribution of the species on the slate and limestone sites in Roudsea Wood, with *Q. petraea* predominating on the slate and a well-represented *Q. robur* component on the limestone, could perhaps be interpreted in terms of these soil preferences. However, it must be remembered that it is possible that some oak has been planted in Roudsea Wood, although there is no evidence of such plantings in the estate records. It seems most unlikely that oak has ever been planted on the peat sites and more likely that the trees have arisen naturally. If any oaks survive at all on these peats, it would be expected that *Q. robur*, with its tolerance of soil waterlogging (Jones 1959) would compete successfully with the *Q. petraea*.

Hybridization and introgression

So far, all the trees with characteristics which are neither markedly those of *Q. petraea* nor *Q. robur* have been termed "intermediates", and no assumptions have been made that they are necessarily due to hybridization. Dengler (1941) suggests that *Q. robur* and *Q. petraea* are able to hybridize to a certain extent, and it is likely that hybridization occurs in field conditions. Cousens (1962a and b) has discussed the possibility of introgression occurring.

The PHI frequency distributions give little information about hybridization and introgression other than showing that the populations are mixed, with many intermediates which may or may not be hybrids. On the other hand, PSDs provide a certain amount of information on this point. The patterns of the scatter diagrams in Figs. 4–6 are similar to those described by Anderson (1949) as being associated with populations of plants where hybridization and introgression have occurred. The scatter diagram for the slate site suggests a population of *Q. petraea* that is almost pure but slightly introgressed. The other scatter diagrams (Figs. 5–6) suggest strongly introgressed populations, possibly with some F1 hybrids.

These data lend support to Cousens' (1962a and b) view that introgression occurs in British oak woodlands.

A comparison of the Hybrid Index and Pictorial Scatter Diagram methods

Although the two methods give similar general pictures of the taxonomic status of the oak populations in Roudsea Wood, these pictures differ in detail. The closest agreement is in the *Q. petraea* component. The marked *Q. petraea* tendencies of the slate population as shown by the PHI frequency distribution histograms (Figs. 1 and 7) are also reflected by the pronounced concentration of points in the long petiole/short peduncle zone on the PSD in Fig. 4. In the PHI histograms in Figs 2–3 and 8–9 there are indications of a strong *Q. robur* component which are not reflected in the corresponding PSDs in Figs. 5–6. Either the PHI method tends to over-estimate the *Q. robur* component or the PSD method under-estimates it. It has already been mentioned that there is a tendency in the PHI method to over-emphasize the intermediacy of a specimen. It seems unlikely, therefore, that this method will over-emphasize the *Q. robur* (or *Q. petraea*) components, and more likely that the PSD is under-estimating the *Q. robur* component. This under-estimation may well be due to the fact that *Q. robur* apparently is much more variable than *Q. petraea* (Weimarck 1947). This greater variability may extend to the petiole and peduncle lengths, so that unless large numbers of trees are examined, there may not be clear evidence of a concentration of points in any particular zone at the small petiole/long peduncle end of the scale, even though a PHI analysis suggests an almost pure population of *Q. robur*. Cousens (1962a and b) designates concentration centres on his scatter diagrams, using petiole length per cent. and maximum peduncle length. He found that none of the many oak woodlands examined by him was pure *Q. robur*, i.e. not all the points came within the limits of the *Q. robur* concentration centres. It is possible that this apparent absence of pure *Q. robur* woodlands may be due to this method under-estimating the *Q. robur* component. On the scatter diagrams, it will probably be necessary to allow more latitude for *Q. robur* than *Q. petraea* if concentration centres are delineated.

The two methods, when used simultaneously in an oak population survey, provide complementary information. The PHI method is based upon more characters; the histograms give an overall picture of the population. The PSD method, on the other hand, provides information about hybridization and introgression. Where extreme purity of a species is needed, as, for example when seed is needed for autecological studies, the PHI method is to be preferred as it is based on more characters and tends to over-estimate the intermediacy and under-estimate the purity of the trees. For a tree to have a PHI of <10 or >90 it has to be very typical of the species indeed.

Modifications of the oak population survey methods

In future surveys using the PHI method, it will be better to use only the characters of bud size and form; leaf shape, lobe number, lobe depth, lobe regularity, venation, auricle, petiole, abaxial stellate pubescence; and acorn colour, stripe, form and peduncle length (Table 1). The petiole length character should be expressed as a percentage of the total leaf length as suggested by Cousens (1962a and b), and defined as $<6\cdot5$ per cent for *Q. robur* and $>9\cdot5$ per cent for *Q. petraea* as suggested by the scatter diagrams in Figs. 4–6. The mean value should be based upon 10 or more leaves taken from the middle of shoots from the south side of the upper half of the crown where possible. The peduncle length should be expressed as the mean length of the peduncle to the first bract or flower, based upon 10 or more peduncles per tree where possible. Tentatively it is suggested that a mean peduncle length of $>$ 20 mm is regarded as a *Q. robur* characteristic and $<$ 6 mm as a *Q. petraea* characteristic.

The main weakness of both the methods is our lack of knowledge about the variations of the individual characters within pure stands of *Q. petraea* and *Q. robur*. Individual morphological characters may have considerable latitude in the pure species types. If this is so, at least some characters which are now regarded as morphologically intermediate may occur in pure types. At the moment, therefore, estimates of the taxonomic status of these oaks probably under-estimate the purity of the trees. The species are at present defined in terms of multiple qualitative data so that more precise statistical methods of discrimination, such as Fisher's discriminant analysis (Fisher 1950), cannot be used.

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