The distribution of *Quercus robur* L., *Q. petraea* (Matt.) Leibl. and their hybrids in south-western England

1. The assessment of the taxonomic status of populations from leaf characters

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ABSTRACT

In the absence of diagnostic characters for the circumscription of *Quercus robur* L. (*Q. pedunculata* Ehrh.) and *Q. petraea* (Matt.) Leibl. (*Q. sessiliflora* Salisb.), it is necessary to assess the taxonomic status of British oak populations using techniques which consider a range of independent characters in combination. Pictorialised scatter diagrams and discriminatory analysis of two quantitative and five qualitative leaf characters show that oak populations can be ascribed to aff. *robur*, aff. *petraea*, mixed or intermediate status using leaf characters alone. Leaf-shape is objectively defined as a quantitative character by the calculation of a leaf-shape index, but the need for a computer programme for the procedure precludes its general application. For field analysis a simple but less sensitive formula for the description of leaf-shape may be substituted. It is established that leaf litter as well as fresh material is suitable for assessment, providing relatively rapid identification of oak populations at all times of the year.

INTRODUCTION

The two indigenous species of oak, *Quercus robur* L. (*Q. pedunculata* Ehrh.) and *Q. petraea* (Matt.) Leibl. (*Q. sessiliflora* Salisb.) have consistently presented problems of nomenclature and identification (see Gardiner 1974). They are notoriously difficult to separate and intermediate individuals, presumed hybrids (*Q.* × *rosacea* Bechst.), have often been reported.

These two papers examine the taxonomic status of oak populations in Devon and eastern Cornwall. Part 1 discusses the allocation of oak populations to either species, mixed or intermediate category on the basis of leaf characters derived from fresh material or leaf litter. Assessment of taxonomic status is made from pictorialised scatter diagrams (Anderson 1949) and discriminatory analysis (Fisher 1936) of the character scores of individual leaves. Part 2 will examine the nature of intermediate taxonomic status, and describe the composition of some 100 oak populations in the south-west peninsula.

THE IDENTIFICATION OF *Q. ROBUR* AND *Q. PETRAEA*

There are no truly diagnostic characters of pedunculate and sessile oak that can, in isolation, be used to reliably assign an individual tree or a population to either species or hybrid category. Such 'good' characters should have a narrow range of expression and be easily recognisable (see Davis & Heywood 1963). The morphological characters of *Q. robur* and *Q. petraea* are highly variable

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and the ranges of the characters for the species overlap. Table 1 summarises the ranges of morphological characters of the two species. The absence of diagnostic characters has led to different authorities placing varying emphasis on the importance of particular characters.

Cousens (1962, 1963, 1965) and Carlisle & Brown (1965) place particular importance on the following characters:—

a) petiole percentage (length of petiole expressed as a percentage of lamina length),
b) peduncle length,
c) abaxial stellate pubescence,
d) auricle type,
e) peduncle diameter,
f) peduncle pubescence.

The first two characters are quantitative and can be used as axes in bivariate scatter diagrams; the remaining four characters are expressed in a qualitative manner and can be coded on the points of a scatter diagram forming a 'pictorialised scatter diagram' (Anderson 1949). Three of these characters depend on obtaining fertile material during a limited period of the year, using restricted sampling methods. Cousens (1963) restricted collection to the period mid-July/ early October, sampling from the south-eastern aspect of accessible parts of the crown. This aspect was chosen because it appeared that the difference in petiole length for *Q. robur* and *Q. petraea* would be greatest here. Carlisle & Brown (1965) used a similar collecting strategy, and excluded lammas growth from the analysis as leaves flushing in mid-summer appear to be different from those of spring growth. Such samples allow reliable comparison between trees of different populations as they largely eliminate variability due to position on the tree, phenology, and environmental conditions.

The use of fruiting characters for the taxonomic assessment of oak populations results in a limited sampling period from year to year. (It is also not without significance that postgraduate research investigations are usually initiated at the end of this critical sampling period!) In addition, many oaks, particularly those of high-level oakwoods, such as the Dartmoor oak copses and Keskadale and Birkrigg in the English Lake District, may not flower or set any seed in one or more consecutive years. Whatever the causes of possible paucity of fruiting characters, in any extensive investigation of the taxonomy of pedunculate and sessile oaks and oakwoods it is worth examining alternative approaches to the assessment of taxonomic status.

A preliminary investigation (Wigston 1965) suggested that oak populations might be identified on the basis of leaf characters alone, including those derived from leaf-litter, so that taxonomic assessment of an oak population could effectively be made at any time of the year. The identification of an individual tree, however, would be limited to the period of leaf production.

SITES AND SAMPLING METHODS

To examine the possibility of assessing the taxonomic status of oak populations from leaf characters, two reference populations were selected:—

1. Wistmans Wood, an aff. *robur* wood (Tansley 1949), v.c. 3, growing among granite clitter at an altitude of 1,250–1,450 ft on the south-west-facing slope of the West Dart River, Dartmoor, GR 20/612.773.

2. Steps Bridge, an aff. *petraea* wood (Harvey & St Leger-Gordon 1953), v.c. 3, growing on the Carboniferous Culm-measures of the south-facing slope of the River Teign, east of Dartmoor, at an altitude of 350–500 ft, GR 20/802.885.

For both populations, samples were obtained of spring and lammas growth from the south-eastern aspect of the crown, and compared with leaf-litter samples. The latter were composed of sub-samples collected at intervals over a wide area (about 200 yards square) within the populations. Restricted sampling of leaf-litter is not desirable as it may produce samples composed of leaves from few trees and possibly atypical specimens; leaf litter is used for assessing the taxonomic status of the *population*, not of *individuals*, and widespread sampling will include specimens of most growth phases. Very small juvenile leaves were eliminated from the samples owing to their extreme variability and differences from adult leaves (Jones 1959).

CHARACTERS

Table 1 indicates that there are eight leaf characters which may be considered. If the representation of populations by pictorialised scatter diagrams (PSD analysis) is used, two (primary) quantitative and a number of (secondary) qualitative characters need to be selected. In practice five qualitative character-states is the maximum that can be satisfactorily coded on a PSD.

QUANTITATIVE CHARACTERS

From Table 1 it can be seen that the only leaf character which is clearly a continuous variable is petiole length. However, if used as a direct measure, an individual value will be dependent on leaf size, which is highly variable (Cousens 1962). If the petiole length is expressed as a percentage of total leaf length the variability due to leaf size is minimised. This character was used by Cousens (1962, 1963, 1965) and by Carlisle & Brown (1965). It is not clear from their papers whether leaf length is considered as lamina length only, or as total leaf length which includes the length of the petiole and lamina. In this investigation petiole percentage implies the length of the petiole expressed as a percentage of total leaf length. However, provided consistency is maintained, either method of calculation is acceptable.

Although lobe-pair number is expressed as an integer variable, the range involved for the two species is insufficient for use as an axis of a PSD. It is therefore necessary to examine the possibility of quantifying alternative characters. Cousens (1962) examined the expression of lobe depth as a percentage of leaf width, calculated as illustrated in Fig. 1. He found the range of *Q. petraea* to be (22–)28–*38*–47(–60)% and of *Q. robur* 40–*55*–75%. However, cultivars of *Q. petraea*, such as var. *mespilifolia* (Wallr.) Schwarz and var. *laciniata* (Lam.) Schwarz, were found to span the whole range for both species. There is a considerable overlap in the ranges of the two species, and the modal values are rather close; for these reasons it is desirable to examine any alternative to percentage lobe depth as a second quantitative variable.

TABLE 1. MORPHOLOGICAL CHARACTERS OF *Q. ROBUR* AND *Q. PETRAEA*[1]

Character	*Q. robur*	*Q. petraea*
1. Leaves		
a) Shape	Obovate; widest in apical third of leaf	Elliptical; widest near mid-leaf
b) Lobe regularity	Irregular	Regular
c) Lobe depth	Deep	Shallow
d) Lobe pair number	3–5 (–6)	5–6 (–8)
e) Venation	Some veins to sinuses between lobes	No veins to sinuses
f) Base of leaf	Narrow; cordate, with margins strongly inflexed to form auricles	Cordate to cuneate, weakly auricled
g) Petiole	Short; (0–) 2–3 (–7) mm	Long; 13–25 mm
h) Pubescence of abaxial surface[2]	Normally glabrous, occasional simple hairs	Simple hairs abundant along midrib and axils of lower veins; always some stellate hairs on lamina
2. Fruiting characters		
a) Peduncle length	2–9 cm	0–3 (–4) cm
b) Peduncle diameter	Slender	Stout
c) Peduncle pubescence	Glabrous	Clustered hairs
d) Acorn form	Elongated	Rounded
e) Stripe on ripe acorn	Olive-green stripes (lost on drying)	Absent
f) Background colour of ripe acorn	Fawn	Dark brown
g) Cupule	Scales closely imbricated, flat	Scales looser, somewhat tumid
3. Axis and canopy		
a) Stem persistence	Tendency for main trunk to disappear in crown	Tendency for main trunk to persist in crown
b) Angle between branches	Wide	Narrow
c) Branch regularity	Irregular	Regular and straighter
d) Twig form	Short, slender	Longer and stouter
e) Crown density	Open (foliage in clusters)	Dense (foliage uniformly distributed)
f) Bark of mature tree	Thick, firm; deeply fissured elongate blocks, usually not scaling	Thinner, with fissures forming more or less rectangular blocks which often tend to excorticate
g) Size of terminal buds	Small	Large
h) Form of terminal buds	Obtuse tip	Acute tip

1. The characters and their states are taken from Jones (1959, 1968), Warburg (1962), Cousens (1963) and Carlisle & Brown (1965).
2. Jones (1959) suggests that many Continental Floras are misleading in describing *Q. petraea* as possessing a glabrous lamina, but this view persists in recent Continental publications on the genus *Quercus* (e.g. Dizerbo 1965).
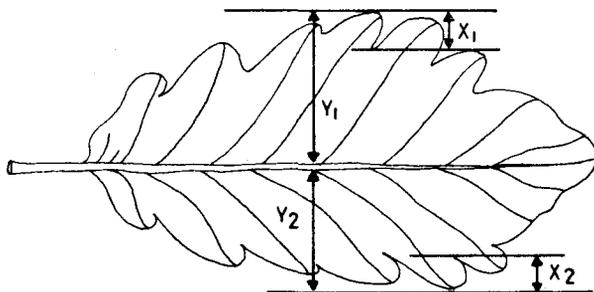
FIGURE 1. Lobe depth percentage (after Cousens 1962).

$$\text{Lobe depth } \% = \frac{(X_1 + X_2)}{(Y_1 + Y_2)} \cdot 100$$

Analysis of leaf-shape

Most authorities cite the *Q. robur* leaf as obovate (widest in the apical third of the lamina). The *Q. petraea* leaf is usually compared with that of *Q. robur* for differences only (see Warburg 1962) and the description of shape is often misleading. For example the description by Warburg (1962) of *Q. petraea* leaves as 'wedge-shaped to cordate' refers to the leaf base (see below) and not the overall shape of the lamina. When described, most authorities say the *Q. petraea* leaf is ovate, implying that the lamina is widest in the basal third of the leaf. However, some descriptions use ovate to mean 'widest near mid-leaf', implying an elliptical shape. In my opinion the leaves of *Q. petraea* are usually elliptical, and distinct from the obovate ones of *Q. robur*.

Representation of leaf-shape has been a vexed problem in botanical studies. Melville (1937) utilised a rectangular co-ordinate system to accurately define the asymmetric leaf of *Ulmus*. However, his system is unwieldy as each leaf has to be independently expressed as a graph. Dale *et alii* (1971) introduced a computer-aided description of the rosette leaves of *Chondrilla juncea* which they believe to be generally applicable to the problem of describing complex leaf-shapes. Their method appears effective, but it does not provide a single measure of leaf-shape suitable for an axis of a PSD. Ashby (1948) represented the cordate leaf of *Ipomoea* by a formula expressing the relationships of various measurements of the leaf. The advantage of deriving such a formula is that for each leaf a single value, the leaf-shape index, can be calculated and used as a co-ordinate on a PSD.

A suitable formula giving an expression of leaf-shape for ovate-elliptical-obovate leaves may be expressed as the ratio between the difference in apical and basal third lamina widths (numerator) and the mid-leaf width (denominator):—

$$I = \frac{(W_3 - W_1)}{W_2}$$

where I is the leaf-shape index and W_1, W_2 and W_3 are the widths to the outline of the lamina respectively of the leaf at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ intervals along the leaf axis (Fig. 2). For an elliptical leaf W_1 and W_3 should be equal and the index will have a value of zero. For an obovate leaf W_3 will be greater than W_1 and the index will have a positive value, and for an ovate leaf W_1 will be greater than W_3
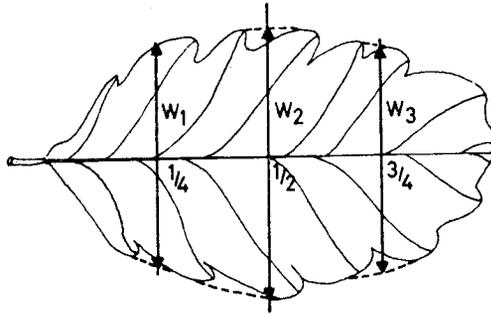
FIGURE 2. Leaf-shape formula.

$$\text{Leaf-shape index} = \frac{W_3 - W_1}{W_2}$$

giving a negative index value. The formula does not give clear separation of the two oak species when used as a co-ordinate on a scatter diagram (Fig. 3);
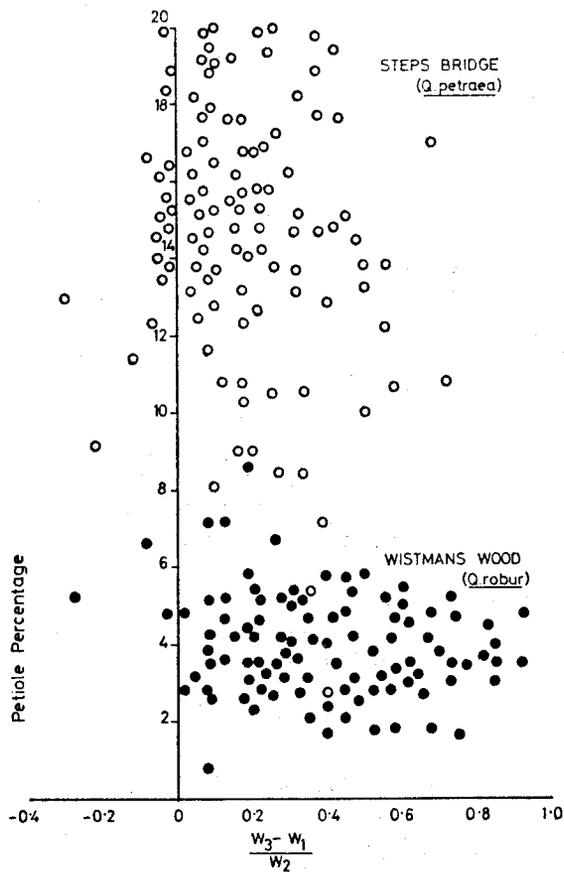

FIGURE 3. Scatter diagram of petiole percentage and leaf-shape index.

Q. robur values are centred around 0·4 and *Q. petraea* values at around 0·18, but there is a considerable overlap. The scatter of *Q. petraea* points shows few negative (ovate) index values and confirms that elliptical is a more accurate description of the *Q. petraea* leaf outline. It should be noted that the formula does not efficiently utilise the available information of shape, the boundary of the outline of the lamina not being defined by the measured values. Nevertheless, calculation of the formula has been found useful in fairly rapid processing of material in the field (Wigston 1974).

Co-ordinate expression of leaf-shape

The boundary outline of a lobed leaf can be expressed from the co-ordinate definition of the apices of the lobes. Two approaches to such a definition are:—

1. A 'statistical' approach utilising a *least-squares* technique to express the difference between the co-ordinate values and those theoretically defined from a perfect ellipse.
2. A 'geometrical approach' utilising a co-ordinate formula for obovateness which encompasses the standard formula for an ellipse.

Method 1—two-dimensional 'best-fit'

L. Muir has written an Algol computer programme which finds the best-fit of one two-dimensional diagram relative to another. A modification of the programme was devised which expresses the overall difference in the co-ordinate diagram for a leaf from that of the corresponding perfect ellipse as a single index d_h. The computational steps are outlined in Appendix 1.

Method 2—elliptical/obovateness formula

The co-ordinate formula for an ellipse with the intersection of the semi-axes a and b (Fig. 4) at the origin is:

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1$$

Consider the equation modified as:

$$\frac{x^2}{(a-c.x)^2} + \frac{y^2}{b^2} = 1 \text{ where } c \text{ is a variable.}$$

For c set at zero the equation simplifies to that of an ellipse; for values of c between zero and unity, increasing values of c create increasing distortion of the ellipse into an obovate shape (Fig. 5). Thus, if, for the co-ordinate diagram of a leaf, a value of c can be calculated relative to the perfect ellipse with the same semi-axes, c can be used as a leaf-shape index. A programme for the calculation of c was written in 1967 in Elliott 803 autocode. The computational steps are outlined in Appendix 2. The determination of c, by minimising chi-squared, results in the occasional *Q. petraea* ovate leaf having an approximately zero index value.
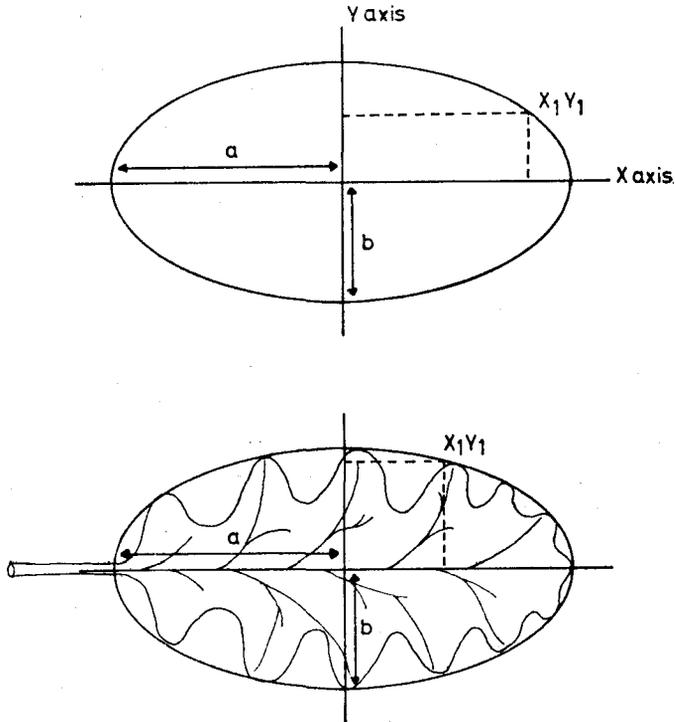
FIGURE 4. The geometry of an ellipse and an elliptical leaf (*Q. petraea*).

$$\frac{X^2}{a^2} + \frac{Y^2}{b^2} = 1$$

The calculation of d_h is computationally much faster than that of c, owing to the large number of iterations involved before a final value of c is obtained. Theoretically, however, c is a more justifiable index of leaf-shape in the study of *Q. robur* and *Q. petraea* as it is a real measure of shape, whereas d_h is an index of difference from a defined reference shape. It is possible that two or more variations from a specified shape could have the same value of d_h although the leaf-shapes are different. A given value of c, however, uniquely defines a degree of obovateness and leaves with the same value of c, although possibly differing in size, have the same shape. For this investigation the use of method 2 is theoretically justified and $c \times 100$ (to avoid non-integer values) is used as a quantitative variable, together with petiole percentage.

The use of c is, however, limited to studies in which the leaves are elliptical-obovate in shape. Provided the range of shapes being studied is not large, the calculation of d_h may provide a more general solution to assigning a numerical index to leaf-shape.

QUALITATIVE CHARACTERS

From Table 1 it may be seen that, if leaf-shape and petiole percentage are used as quantitative characters, six remaining leaf characters are available for consideration as coded qualitative characters. This number may be increased if different types of abaxial pubescence are recognised. Coding of characters
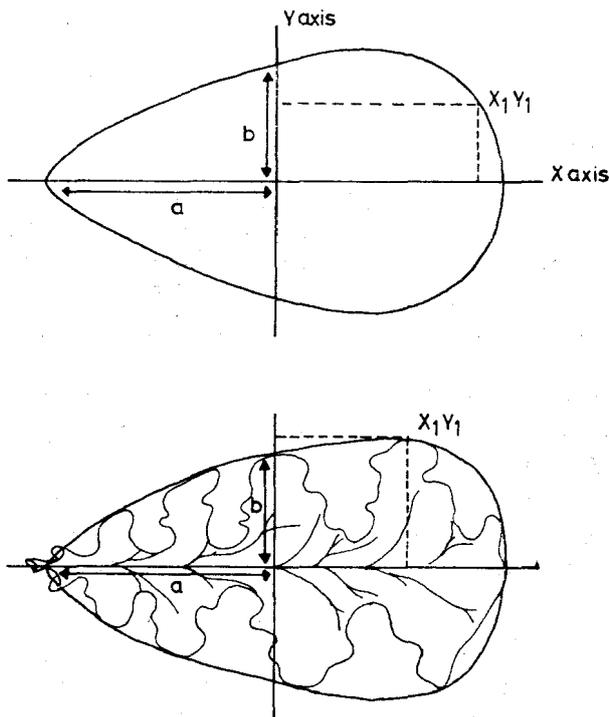
FIGURE 5. The geometry of a distorted ellipse and an obovate leaf (*Q. robur*).

$$\frac{X^2}{(a-c.x)^2} + \frac{Y^2}{b^2} = 1 \text{ (provided } 0 < c > 1)$$

$c = 0$ gives an ellipse, all other values give a cuspid curve

inevitably involves subjective assessment of status, and some characters may be more easily allocated to a category than others (see Carlisle & Brown 1965). Initially samples were coded as 1. (aff. *petraea*); 2. (intermediate); and 3. (aff. *robur*) for all possible qualitative characters. Each leaf was coded on five separate occasions in order to assess the ease and variability of assigning qualitative status to any character, and each character in turn considered for use as a secondary character for PSD representation.

Lobe regularity and lobe depth

For both characters, difficulty was experienced in assigning an intermediate coding. For lobe depth, arbitrary limits must be set for percentage lobe depth (see Fig. 1). Initially lobe depth less than 33% leaf width was coded as 1, greater than 66% as 3, and 33–66% as 2. Although these limits appeared reasonable, it was found that they over-emphasised the intermediate component in a population. All leaves of both species show some lobing, so that values of lobe depth near to zero are most unlikely. Similarly as the leaves are not pinnate, values near to 100% are unlikely. Thus the apparent theoretical range for intermediate status should be narrower than for aff. *robur* and aff. *petraea* coding. However it is difficult to establish any reliable criterion by which the

intermediate range may be delimited. By contrast, lobe regularity presented difficulty because of the absence of any numerical assessment which could be split into coded ranges. Regularly lobed (aff. *petraea*) specimens and irregularly lobed (aff. *robur*) leaves were clearly recognisable, but assigning a leaf to the intermediate category was rather arbitrary. There was a tendency to regard any irregularity as being aff. *robur*; the human eye and mind appreciate regularity, whereas irregularity is appreciated by the absence of pattern. Defining visual criteria for assessing degree of irregularity is virtually impossible.

Because of these difficulties, there were two alternative approaches to the use of lobe regularity and depth as secondary characters:—

a) independent use of the characters scoring only 1 (aff. *petraea*) or 3 (aff. *robur*),

b) use of the characters in combination, including an intermediate category with one character scoring for *Q. robur* and the other character scoring for *Q. petraea*.

The latter solution reduces the number of secondary characters for PSD representation without totally discarding the information from either character, but it assumes a degree of correlation between the two variables. It would seem reasonable to assume that highly variable characters such as leaf-shape and lobing are under polygenic control (e.g. Hutchinson 1934, Silow 1939, Hammond 1941, Cousens 1965), so that in relatively pure stands of either species both lobe depth and lobe regularity may be in the accepted range for a species, whereas in an intermediate their variation may be sufficient for either character to extend within the range of either species. Stephens (1945), found that, in *Gossypium*, lobe formation is governed by the formation of a 'sinus field' of restricted cell division which is, at least partially, under polygenic control. If a similar mechanism operates in *Quercus*, the differences in lobe depth and lobe regularity between *Q. robur* and *Q. petraea* may reflect genetic differences in the control of cell division during leaf formation and growth, and the use of the characters in combination is reasonable.

In this investigation the character 'lobing' is scored as

1. if the lobe depth is less than 50% leaf width and lobing is regular,
3. if greater than 50% with irregular lobing,
2. if (a) lobe depth is less than 50% but irregular or (b) greater than 50% with regular lobing.

Using this assessment little variation was obtained between each occasion on which the reference samples were scored.

Lobe pair number

The number of lobe pairs on a leaf was counted from the base of the lamina to the tip. Occasionally, particularly in *Q. robur*, the number of lobes on one side of a leaf is greater than on the other. This disparity is rarely greater than one lobe. For convenience the lobe pair number was assessed as half the total number of lobes and if the value was a fraction, the integer value was used. Values below 5 scored as 1, above 5 as 3, and 5 as 2. No variation occurred between each sample re-assessment.

Venation

Initially venation was scored as 1: less than 33% of sinuses with veins, 2: 33–66% sinuses with veins, 3: greater than 66% sinuses with veins. This method of scoring proved unsuitable for two reasons:

1. The number of sinuses was too few to give a sufficient range of values to justify the use of percentages.
2. The aff. *petraea* component was over-emphasised; within the normal range for *Q. robur* only some sinuses, not all, will have veins, whereas *Q. petraea* usually has none. Positive scores were only obtained if the veins reached the sinuses; veins failing to reach the sinuses would score as no veins.

Re-scoring using a subjective assessment of status, including scoring short veins as intermediate, proved so variable at each sample re-assessment that this character was rejected.

Leaf base

Cousens (1962) regards the structure of the leaf base as being the most important single diagnostic character for distinguishing between *Q. robur* and *Q. petraea*. His analysis of a range of leaf bases from Scottish populations (Fig. 6) suggests that three types of leaf base can be recognised:

1. aff. *robur*—'strong auricles'—lamina margins strongly reflexed producing characteristic 'points' where the lamina joins the petiole and also at the ends of the sinus (points A and B in Fig. 6); the latter reach and often overlap the petiole on the adaxial surface.
2. intermediate—'medium auricles'—(a) lamina margins strongly reflexed but point B is 'above' A and/or does not reach or overlap the petiole; (b) margins weakly reflexed but points produced.
3. aff. *petraea*—auricles 'weak' or none—the leaf base may be cordate with some reflexion of the lamina, but points are never produced.

Using these categories scoring produced little variation with each re-assessment of a sample.

Abaxial pubescence

Cousens (1962) recognised four types of abaxial pubescence:

a) large stellate hairs with ascending rays along the midrib and the axial portion of the large lateral veins (Fig. 7a),
b) small stellate hairs with rays appressed to the lamina (Fig. 7b),
c) long unicellular hairs on the midrib,
d) minute multicellular hairs with a swollen basal cell; these are sometimes abundant and may be clustered, appearing here and there like stellate hairs.

A further type has been recognised but is usually neglected in taxonomic descriptions (Jones 1974) probably because of the small size of the hairs. These were described by Jones as small, somewhat scarious-looking, simple hairs, normally present on the abaxial surface of both *Q. robur* and *Q. petraea*. They

A. Aff. robur

A1.   A2.   A3.

B. Aff. petraea

B1.   B2.   B3.

C. Intermediate Forms

C1.   C2.   C3.
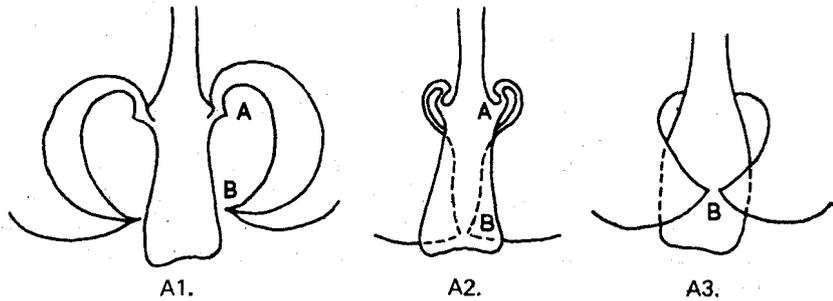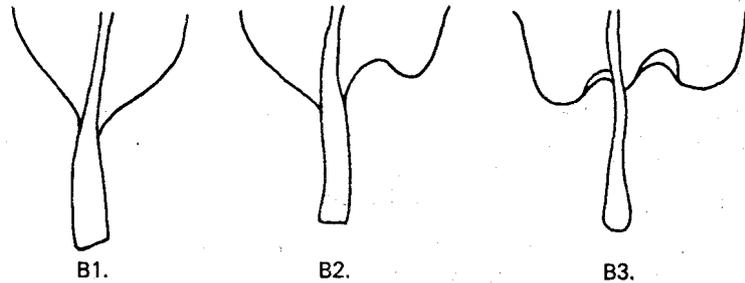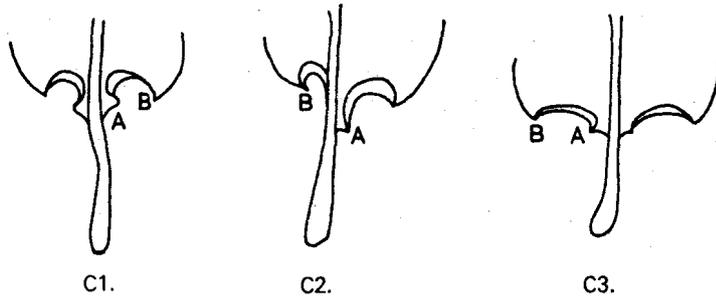
FIGURE 6. Variations in the leaf base of *Quercus* (after Cousens 1962)
          A aff. *robur*: A1 composite diagram to show auricle structure, A2 abaxial
          view, A3 adaxial view.
          B aff. *petraea*: B1 cuneate base, B2 partially cordate base, B3 cordate base
          with lamina reflexion.
          C Intermediate forms: C1 'medium auricles', C2 medium auricles only
          partly developed, C3 weak lamina reflexion but points produced.

vary from one to four cells in length and may be up to 90 μm in length, some
appressed, some more or less erect, straight or flexuous, clearly arising from
epidermal cells. I first observed these hairs when examining very young leaves
for the developing mycelium of the fungus *Microsphaera alphitioides* Griff.
& Maubl. The terminal cells of the hairs tend to be bulbous. They are difficult
to observe with a hand lens, but can be seen with a binocular microscope and
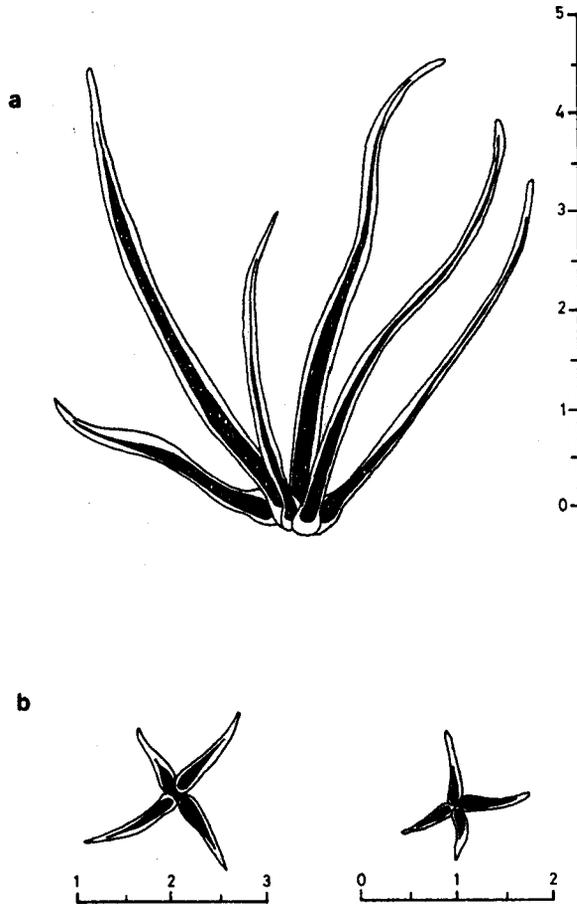
FIGURE 7. The abaxial pubescence of *Quercus* aff. *petraea*. (Scale 0·01 mm). (a) Large stellate hairs on the midrib and in the axils of the main veins with ascending rays ('side' view), (b) Small stellate hairs on the lamina with appressed rays ('surface' view).

are clearly seen in leaf-surface prepations under × 100 magnification. As they occur on both *Q. robur* and *Q. petraea* they are of no discriminatory value.

Type (b) hairs are normally regarded as diagnostic for *Q. petraea*. The hairs may be seen with a hand lens, but are best viewed with a binocular microscope. Type (a) hairs are not cited by most authorities although Cousens (1962) regarded them as also diagnostic for *Q. petraea*. Most authorities cite the occurrence of tufts of simple hairs along the midrib and the axils of the main veins, which are visible to the naked eye and clearly seen with a hand lens, as being characteristic of *Q. petraea*, but these are not mentioned by Cousens (1962, 1963, 1965).

Microscopic examination of what appeared under a hand lens to be clusters of simple hairs from the midrib and vein axils of *Q. petraea* leaves proved to be the ascending rays of stellate hairs, the rays ascending from a common base (Fig. 7). It seems likely that the mention of tufts of simple hairs, commonly

C

occurring in descriptions of *Q. petraea*, refers to the large stellate hairs described by Cousens (1962); these are only discernible as such under the microscope.

Type (c) hairs are uncommon but characteristic of *Q. robur* (Cousens 1962) and correspond to the 'occasional simple hairs' described in Table 1. Because of their rarity the presence of such hairs cannot be used as a diagnostic character. Under a hand lens they may be confused with type (a) hairs, but they do not occur in the axils of the veins. If apparently simple hairs are found both on the midrib and in the axils of the main veins, presence of type (a) hairs may be assumed. If simple hairs occurred on the midrib only, their presence was not recorded. Type (d) hairs are found on both oak species (Cousens 1962) but they are difficult to see with a hand lens and their presence was not recorded. They may be distinguished from the hairs described by Jones (1974) by their swollen basal cell; in the latter hairs the terminal cell is swollen.

Initially, type (a) and type (b) hairs were scored as 1: present and abundant (*Q. petraea*), 2: present but sparse (intermediate), 3: absent (*Q. robur*). Presence and absence were easily noted, but considerable difficulties were encountered between scoring abundant and sparse. Also, of all the characters used, pubescence is most likely to be affected by damage and partial decay. Using leaf litter for taxonomic assessment some pubescence would be observed on a reasonably well-preserved leaf, but the amount may not reflect that originally present. For these reasons, stellate vein/axillary pubescence and stellate lamina pubescence were recorded separately as present, scoring 1, or absent, scoring 3.

The leaf-litter of both species often possesses what appear under a hand lens to be stiff black hairs on the abaxial midrib. These are clearly distinguished from type (a) hairs by their large size and colour, and appear to be part of the fruiting body of an ascomycete which presumably invades the leaf after leaf-fall.

SCORING OF LEAF-LITTER SAMPLES

Having defined suitable leaf characters for assessing the taxonomic status of oak populations, it is necessary to examine whether such an analysis is applicable to leaf-litter as well as fresh material. The problems of using leaf-litter involve the possibility of changes of characters after leaf-fall, and the absence of any regular, comparative sampling procedure. Even if the characters do not appreciably change after leaf-fall, the litter will contain both lammas and spring growth from trees of varying age and subject to varying exposure. Lammas growth appears to be distinguishable from spring growth (Jones 1959) and is usually excluded from taxonomic analysis, while juvenile leaves from young trees of both species are very similar and differ markedly from the adult leaves (Jones 1959).

To assess the possible effects of leaf-fall and drying on the chosen leaf characters, a number of samples of fresh leaves from both reference populations were taken and the characters for each leaf scored and recorded. The leaves were then allowed to dry for several weeks. This process is not strictly comparable to changes after leaf-fall as the leaves are protected from decomposers and detritivores. However, incomplete leaves from a litter sample would be excluded from analysis, and it is assumed that changes in intact leaves would largely be due to periodic desiccation and re-wetting. The dried leaves were eventually soaked in water and at intervals the leaves were removed and quickly but carefully blotted between sheets of absorbent paper. The initial weights and

interval weights of the samples were noted. After each weighing the leaves were replaced in the water. Uptake of water was found to be largely complete within half an hour. The leaves were then removed and, whilst still damp, the characters re-scored. It was found that there were no changes in the states of secondary characters within the limits of variability of scoring established from fresh material. The primary quantitative characters exhibited some variation and were subjected to a *t*-test to ascertain whether any differences between initial and final scoring were statistically significant at the 0·1 % level ($p = 0.001$). The values of *t* for each sample were not significant.

COMPARISON OF SPRING, LAMMAS AND LEAF-LITTER ANALYSIS

Fig. 8 (legend in Table 2) shows PSD analysis of spring, lammas and leaf-litter samples from the reference populations. Each coded point represents an individual leaf. The diagrams suggest that *Q. robur* and *Q. petraea* can be distinguished on the basis of each type of growth and mixed as leaf-litter. However, there appears to be separation in the scatter of points of spring and lammas growth, particularly for *Q. robur*. Table 3 shows the results of discriminatory analysis (Fisher 1963; Wigston 1971, 1974) on the character values from spring, lammas and leaf-litter samples between the populations, and on spring and lammas growth within the populations. The frequency distributions of discriminant functions of individual leaves for each analysis are shown in Fig. 9.

Within the Steps Bridge (*Q. petraea*) population the results of discriminatory analysis suggest that there is no significant difference in taxonomic assessment judged on either growth form. The results from the Wistmans Wood (*Q. robur*) population indicate a significant difference between spring and lammas growth, mainly due to a change in leaf-shape index. However, it must be noted that characters 5 & 6 (stellate and vein/axillary pubescence) had to be eliminated from the analysis. All spring and lammas leaves from Wistmans Wood were glabrous, i.e. aff. *robur* for both characters. The computer programme used for the solution of discriminatory analysis cannot accept identical character distributions in the two groups being compared, and therefore the two characters giving absolute similarity between *Q. robur* spring and lammas growth had to be excluded.

The important conclusion for the assessment of taxonomic status of oak populations from leaf characters is that on the results of discriminatory analysis the aff. *robur* and aff. *petraea* populations are significantly different for both growth forms and for leaf-litter on the basis of the associated *F*-test at the 0·1 % level.

APPLICATION OF LEAF-LITTER ANALYSIS TO NON-REFERENCE POPULATIONS

It has been shown that two reference populations, preliminarily ascribed to *Q. robur* (Tansley 1949) and *Q. petraea* (Harvey & St Leger-Gordon 1953), were clearly distinguished into separate taxa on the basis of PSD and discriminatory analysis of characters scored from leaf-litter. The use of leaf-litter simplifies sampling and allows assessment of the taxonomic status of an oak *population* at any time of the year. It has also been shown that fresh spring or lammas
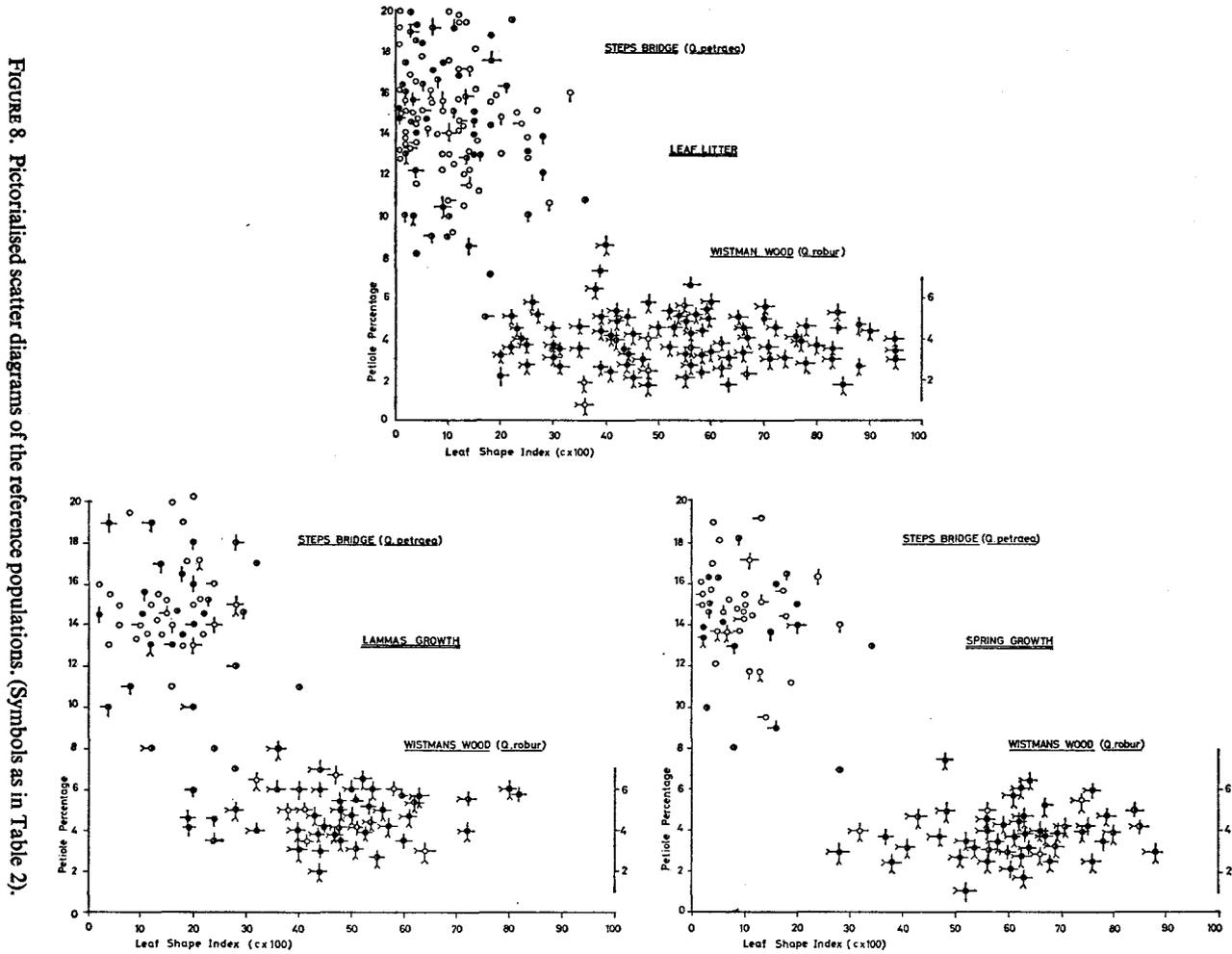
FIGURE 8. Pictorialised scatter diagrams of the reference populations. (Symbols as in Table 2).

TABLE 2. THE DIAGNOSTIC RANGES FOR SECONDARY CHARACTERS AND THEIR PSD SYMBOLS

Character	Character state	Status	PSD Symbol
Nature of lobing	Deep, irregular	Aff. *robur*	
	Shallow, irregular/deep, regular	Intermediate	
	Shallow, regular	Aff. *petraea*	
Lobe pair number	≤4	Aff. *robur*	
	5	Intermediate	
	≥6	Aff. *petraea*	
Base of leaf (Based on the development of the basal lobes and reflexion of the lamina where it joins the petiole)	'Strong' auricles	Aff. *robur*	
	'Medium' auricles	Intermediate	
	'Weak' auricles, or none	Aff. *petraea*	
Abaxial pubescence a) Large stellate hairs with ascending rays on midrib and in axils of main veins	Present	Aff. *petraea*	
	Absent	Aff. *robur*	
b) Small stellate hairs with appressed rays on lamina	Present	Aff. *petraea*	
	Absent	Aff. *robur*	

TABLE 3. DISCRIMINATORY ANALYSIS OF REFERENCE POPULATIONS

1–7: Leaf-shape index, petiole %, auricle status, lobing, axillary pubescence, stellate pubescence, and lobe-pair number, respectively.
(a) and (b) means of characters sums.   (c) weighting coefficients for each character.
8: group discriminant function. Significant values of F are underlined.
Characters 5 and 6 were not included in the final analysis (p. 360).

|		1	2	3	4	5	6	7	8				
Leaf-litter													
Steps Bridge	a)	0·11	14·5	1·16	1·34	1·24	1·27	1·62	−3·45	T^2	2481·8	F	344·65
Wistmans Wood	b)	0·55	4·0	2·71	2·88	3·00	3·00	2·75	−49·48	n_1	7	$F_{0·001}$	3·47
	c)	−19·18	1·23	−5·12	−2·71	−5·02	−1·41	−1·03		n_2	209		
Spring growth													
Steps Bridge	a)	0·11	14·47	1·33	1·40	1·21	1·21	1·54	9·38	T^2	2009·6	F	269·15
Wistmans Wood	b)	0·62	3·86	2·84	2·74	3·00	3·00	2·58	−72·68	n_1	7	$F_{0·001}$	3·95
	c)	−41·60	2·70	−4·69	−1·31	−2·62	−9·38	−1·77		n_2	90		
Lammas growth													
Steps Bridge	a)	0·17	14·14	1·34	1·42	1·17	1·30	1·64	3·45	T^2	1217·26	F	164·23
Wistmans Wood	b)	0·49	4·78	2·63	2·53	3·00	3·00	2·37	−41·04	n_1	7	$F_{0·001}$	3·85
	c)	−22·43	1·59	−0·86	−0·23	−10·18	−1·44	−0·02		n_2	102		
Steps bridge													
Spring growth	a)	0·11	14·47	1·33	1·40	1·21	1·21	1·54	1·01	T^2	18·21	F	2·45
Lammas growth	b)	0·17	14·15	1·34	1·42	1·17	1·30	1·63	1·70	n_1	7	$F_{0·001}$	3·85
	c)	10·16	0·00	0·14	0·08	−0·67	0·48	−0·06		n_2	99		
Wistmans Wood													
Spring growth	a)	0·61	3·86	2·84	2·74	—	—	2·58	−6·07	T^2	48·1	F	9·23
Lammas growth	b)	0·48	4·78	2·63	2·53	—	—	2·39	−4·16	n_1	5	$F_{0·001}$	4·60
	c)	−8·19	0·63	−0·57	−0·50	—	—	−0·19		n_2	95		
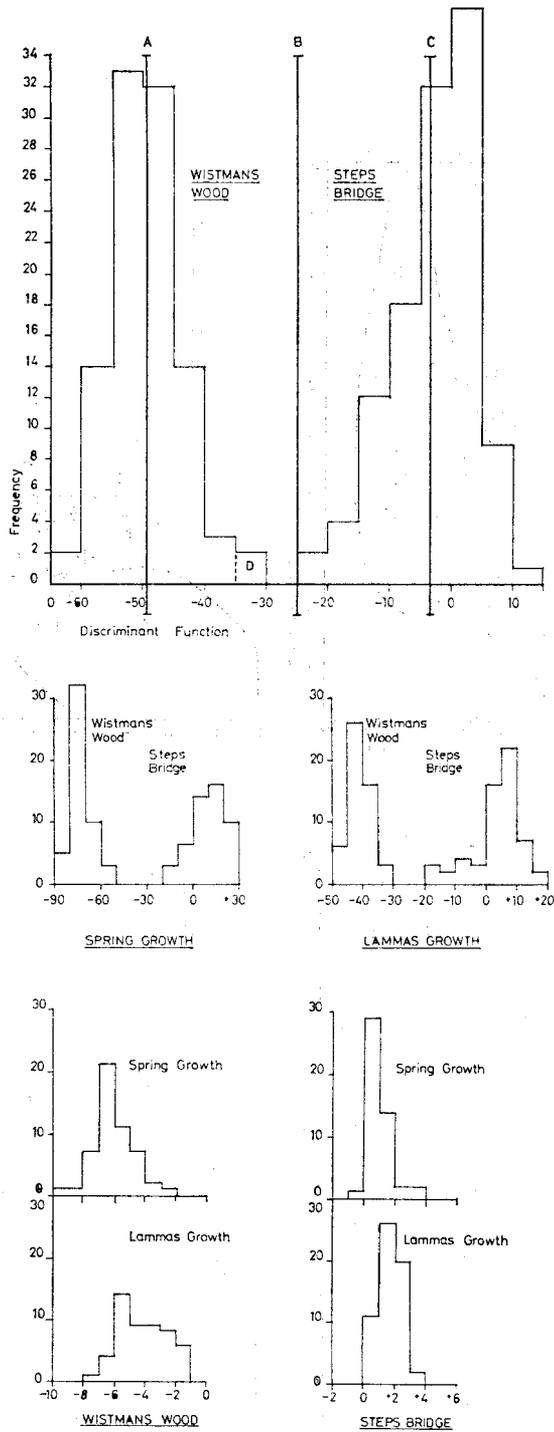
FIGURE 9. Histograms of reference populations individual discriminant functions. A. Wistmans Wood group function. B. Between group average function. C. Steps Bridge group function. D. Overlap between groups.

FIGURE 10. Pictorialised scatter diagrams of selected populations. (Symbols as in Table 2).
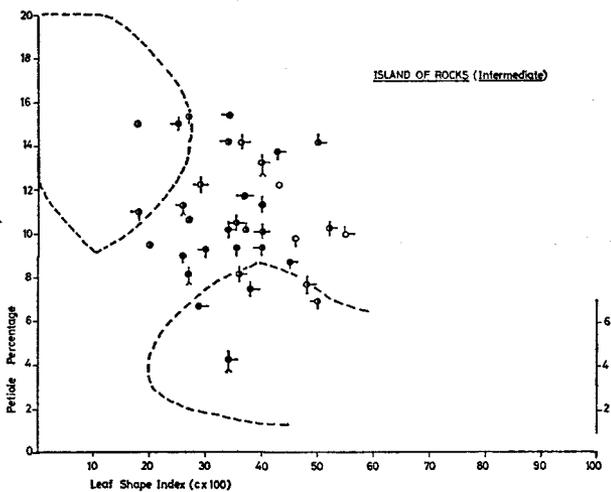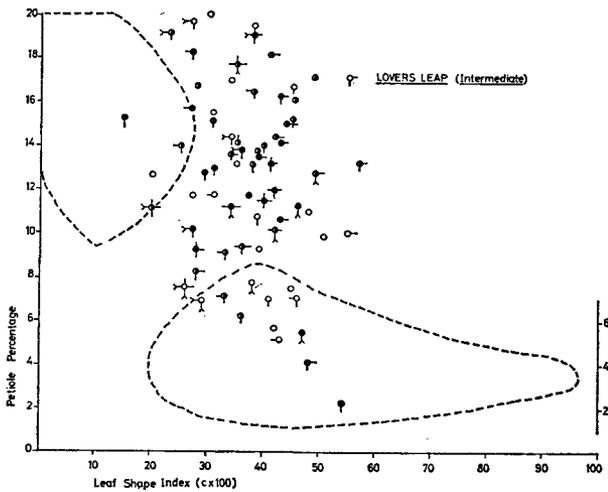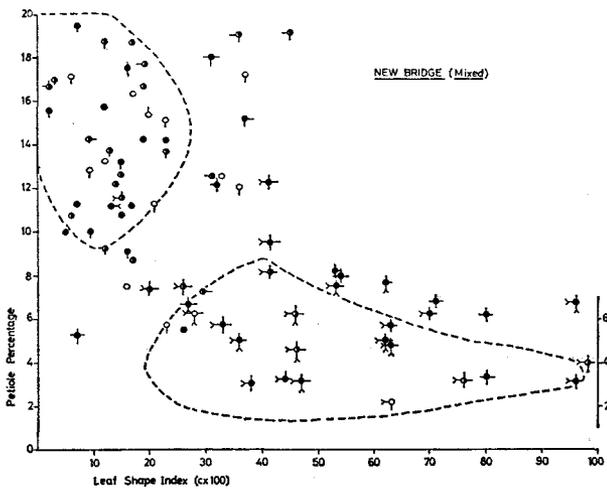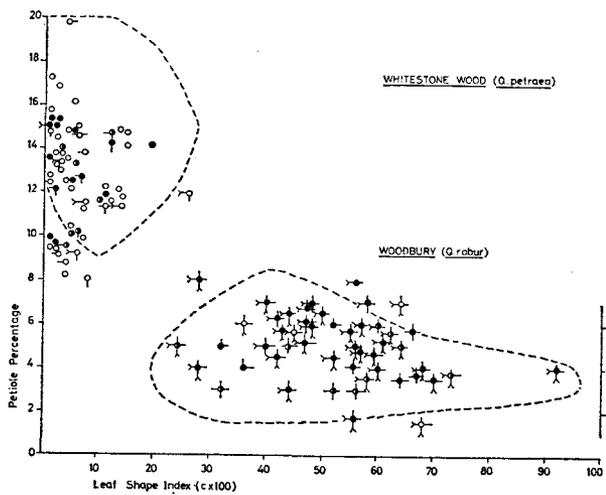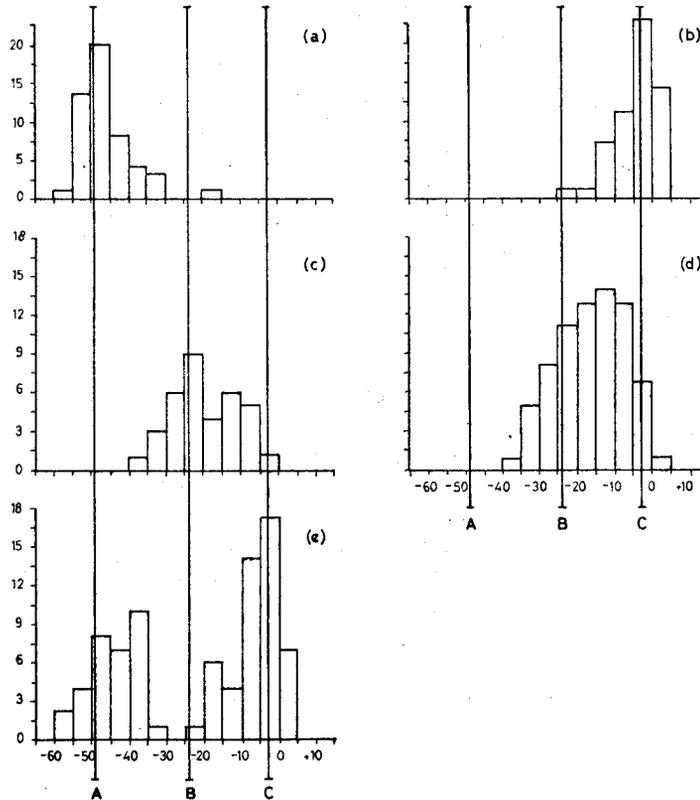
FIGURE 11. Distribution of discriminant functions for selected populations.

A. Wistmans Wood group function.
B. Between group average function.
C. Steps Bridge group function.

(a) Woodbury
(b) Whitestone Wood
(c) Island of Rocks
(d) Lover's Leap
(e) New Bridge

growth give similar results; this therefore allows identification of *individual trees*. It might be expected that variation of leaf characters for a single tree would be less than that for the whole population. However, the polygenic nature of the characters used results in almost as much variation on single trees as within a population (Wigston 1974).

It is necessary to examine whether the technique of leaf-litter analysis can be used for the taxonomic assessment of further populations, including those of possibly mixed or intermediate taxonomic status. The method was applied to leaf-litter samples from over one hundred populations from south-western England and two from the English Lake District. Figs. 10 & 11 show pictorialised scatter diagrams and the frequency distributions of leaf discriminant functions from five of these populations:

a) Woodbury Common, v.c. 3, GR 30/032.875, overlying the Budleigh Salterton pebble beds. The scatter of points of the PSD mainly lies within the Wistmans Wood scatter boundary and the secondary character

codings are largely those of pedunculate oak. Similarly, the distribution of leaf discriminant functions is comparable to that for Wistmans Wood, the modal value being near to the Wistmans Wood group function. A *Q. robur* diagnosis is indicated for this population.

b) Whitestone Wood, v.c. 3, GR 20/860.955, an oakwood now much replaced by conifers, overlying predominantly Carboniferous rocks on the north-east-facing catchment of the Shuttern Brook near Exeter. The PSD scatter and secondary coding is within the Steps Bridge *Q. petraea* theoretical species type (Wigston 1974) and the distribution of leaf discriminant functions is similar to that for Steps Bridge.

c) The Island of Rocks, v.c. 3, GR 20/560.899, an oakwood on the west bank of the West Okement River overlying the metamorphic aureole of the Dartmoor granite. The scatter of PSD points and secondary coding is intermediate between the two reference populations and the modal value of the leaf discriminant functions corresponds to the between group average function. An intermediate taxonomic diagnosis is indicated.

d) Lover's Leap, v.c. 3, GR 20/726.723 on the north-eastern bank of the River Dart where it flows down off the margins of the Dartmoor granite. A similar intermediate taxonomic diagnosis to that of the Island of Rocks is indicated, although it should be noted that both the PSD and discriminatory analysis diagrams show a 'drift' towards *Q. petraea* values.

e) New Bridge, v.c. 3, GR 20/712.704, a National Trust wood on the east bank of the River Dart overlying granite and the metamorphic aureole. The PSD has two components of scatter and secondary coding, one within the *Q. robur* boundary and one within that for *Q. petraea*, with some intermediate points. The frequency distribution of leaf discriminant functions is bimodal, with maxima similar to those for the *Q. robur* and *Q. petraea* populations.

The causes of mixed and intermediate populations requires further consideration, and will be examined in the second paper.

DISCUSSION

The analysis of oak populations described above suggests that *Q. robur*, *Q. petraea*, mixed and intermediate oak populations can be recognised. In the absence of any truly diagnostic characters, highly variable and closely related species, such as *Q. robur* and *Q. petraea*, present problems when a population or sample is to be ascribed to either taxon or some compound category. The range of variation 'overlaps' and to assess taxonomic status it is necessary to consider a combination of a number of reasonably independent observations from large samples of each taxon under consideration, making no *a priori* assumptions concerning the relative importance of variables (Heslop-Harrison 1962). A number of investigations of *Q. robur* and *Q. petraea* have utilised this multi-character approach, including reproductive features (Cousens 1962, 1963, 1965; Carlisle & Brown 1965), which restricts the sampling period to mid-July/ October in flowering and fruiting populations. In order to assess the taxonomic status of oak populations at any time it is necessary to examine characters available at all times of the year, such as features of the trunk and crown (Carlisle & Brown 1965) or characters derived from leaf-litter. A number of leaf

characters are usually included in taxonomic investigations of oaks, and it has been shown above that quantitative and qualitative characters from whole, soaked leaves derived from leaf-litter reliably reflect the properties of fresh material, i.e. mixed spring and lammas growth. On the basis of leaf characters alone it is possible to assign an oak population to aff. *robur*, aff. *petraea*, mixed or intermediate status, or an individual tree to either species or hybrid category.

The necessity for computer analysis of the elliptical/obovateness leaf-shape index limits the general application of the methods described; however, substitution of the ovate/elliptical/obovate formula for leaf-shape, although less sensitive, allows reasonably rapid field assessment (Wigston 1974) and establishes that *Q. petraea* leaves are usually elliptical and only occasionally ovate.

The exclusion of important fruiting characters and the absence of any standardised collecting procedure might elicit the criticism that variability of material is emphasised, whereas usual taxonomic practice is to minimise sources of variation. However, the approach in this investigation is comparative and has the finite objective of delimiting the range of variation within and between *Q. robur* and *Q. petraea* on the basis of selected characters.

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APPENDIX 1

LEAF-SHAPE ANALYSIS: METHOD 1

Computational Steps

1. Input: a, the principal semi-axis of the lamina,
   b, the secondary semi-axis of the lamina,[1]
   h, the number of lobes whose co-ordinates are measured,[2]
   $x_1, y_1 \ldots x_i, y_i \ldots x_h, y_h$, the co-ordinates of the apex of each lobe.
2. The expected x and y co-ordinates for a perfect ellipse with semi-axes a and b are calculated from the formula $(x^2/a^2)+(y^2/b^2) = 1$, with the actual x values substituted, and the y values calculated.
3. The point representing the mean of the x values and the mean of the y values (the $\bar{x}, \bar{y}$ point) of the leaf (L) and the ellipse (E) are respectively calculated.
4. The co-ordinate diagram of the leaf is held fixed and that of the ellipse is 'rotated' through θ degrees about the $\bar{x}, \bar{y}$ point to the position of 'best-fit'. This fit is measured by the sum of squares of the distances between corresponding co-ordinate points on L and E. This quantity is minimised and divided by the number of lobes, h, to give $d_h{}^2$, the mean square distance between corresponding points:

$$d_h{}^2 = \frac{1}{h}\left[\sum_{i=1}^{i=h}(x_{Li} - x_{Ei})^2 + \sum_{i=1}^{i=h}(y_{Li} - y_{Ei})^2\right]$$

5. The square root of $d_h{}^2$ is the overall difference in shape of the leaf from the corresponding ellipse, and is taken as the leaf-shape index.

Notes:

1. On some leaves, particularly those of *Q. robur*, there may be more lobes on one side of the leaf than the other. This does not affect the calculations and the co-ordinates of all lobe apices are considered.
2. If the secondary semi-axis does not correspond to a lobe apex, the boundary of the leaf must be estimated.

APPENDIX 2

LEAF-SHAPE ANALYSIS: METHOD 2

Computational Steps

1. Input: as for method 1.
2. Calculate the perfect ellipse as in method 1.
3. Calculate chi-squared between observed and calculated co-ordinate values.
4. If chi-squared is $\neq$ zero, co-ordinate values are calculated from the formula $(x^2/(a-c.x)^2)+(y^2/b^2) = 1$, substituting values of c from zero to unity.[1,2]
5. The value of c which gives a minimum value of chi-squared is taken as the degree of obovateness and used as the leaf-shape index.[3]

Notes:

1. The roots of the equation are:

$$x = \frac{-(2.ac-(y^2/b^2).2.ac) \pm \sqrt{(2.ac-(y^2/b^2).2.ac)^2 - 4.(1-c^2+(y^2/b^2).c^2).(a^2-(y^2/b^2).a^2)}}{2 \cdot (1-c^2+(y^2/b^2).c^2)}$$

and y may be calculated as: $y = \sqrt{b^2-(b^2x^2/a^2-2.acx+c^2x^2)}$

As these functions are time-consuming to calculate, it is computationally simpler to standardise the x and y values by dividing each by the corresponding a and b value; the equation is then modified around a distorted circle and all a and b^2 values in the above are eliminated.

2. The iterative procedure is to calculate the formula substituting stepwise 0·1 values of c; 0·01 values are then calculated between the 0·1 values giving minimum chi-squared. The 0·01 value giving final minimum chi-squared is output as leaf-shape index.

3. The final values of c should exhibit less variation from expected (calculated as chi-squared) than the acceptable inherent population variation. A probability of $p = 0.001$ is desirable, but owing to rounding errors in the iterations, $p = 0.01$ is taken. All values of c calculated were non-significant at this level.