An analysis of variation of leaf characters in *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl. population samples from Northern Ireland

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SUMMARY

The levels of hybridity in 35 population samples of oak (*Quercus* spp.) from Northern Ireland were assessed using leaf characters analysed by Principal Components Analysis and Cluster Analysis. Eight population types were recognised:

1. Populations of pure *Q. robur* (two populations);
2. Mixed populations with no hybrids and a predominance of *Q. robur* trees (two populations);
3. Predominantly pure *Q. robur* with a small number of hybrids (four populations);
4. Predominantly pure *Q. robur* with a small number of *Q. petraea* and hybrid trees (five populations);
5. Approximately equal proportions of *Q. robur* and *Q. petraea* with a small number of hybrids (nine populations);
6. Mixed populations with a high proportion of hybrids (three populations);
7. Predominantly *Q. petraea* with a small number of hybrid and *Q. robur* trees (four populations);
8. Predominantly *Q. petraea* with a small number of hybrid trees (six populations).

It is argued that the level of hybridity (13.3%) observed is not substantially different from earlier surveys of the two species in England and Wales. The pattern of hybridisation suggests relatively ancient hybridisation although some populations showed evidence of more recent crossing. There was also evidence that some hybrids had been planted along with the parental species.

Mixed populations predominated in the survey possibly owing to the inclusion of obviously planted stands. In some mixed populations, there was evidence of a mosaic pattern with *Q. petraea* on the drier areas.

INTRODUCTION

In the British Isles, there are two oak species that have been considered native: *Quercus robur* L., the pedunculate oak, and *Q.*

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petraea (Matt.) Liebl., the sessile oak (Jones 1959). *Q. robur* is considered to be a species of basic clay soils, tolerant of waterlogging and poorly aerated conditions, whilst *Q. petraea* is a species of more acid sandy soils, intolerant of waterlogging and preferring well-aerated soil conditions. These ecological differences between the species are not, however, very clearly defined and the effect of man, through planting and land drainage, has blurred the distinctions even further. Consequently, in several areas, the species grow together (c.f. Carlisle and Brown 1965). In areas where the species are sympatric, they may interbreed to produce initially F_1 hybrids and then, by subsequent backcrossing to one or other of the parental types, a series of backcrossed hybrids or introgressants (Cousens 1963).

Whilst the results of all large scale population surveys in Scotland (Cousens 1963, 1965), Wales (Rushton 1974, 1979), and England (Cousens 1965, Rushton 1974, 1979, Wigston 1974, 1975) have shown that hybrids do occur between *Q. robur* and *Q. petraea*, the estimated level of hybridisation has varied between 7-12% (Rushton 1974, 1978) and 50% (Cousens 1963) although this latter estimate was later revised (Cousens 1965).

Extensive surveys of oak populations for hybrids in Ireland have been few. Cousens (1965) included populations from Ireland in his survey of oaks in Britain but, since the Irish populations were chosen to represent "good" *Q. petraea* the results do not accurately reflect the taxonomic status of oaks in Ireland. Kelly and Moore (1975) record some results for similar quantitative investigations of a small number of woods. Generally, these have utilised the hybrid index method of analysis (Cousens 1963) rather than the multivariate approaches of Rushton (1978) or Wigston (1975).

The work reported in this paper was designed to investigate the taxonomic status of oak trees and levels of hybridity in population samples from Northern Ireland utilising the methodology previously developed (Rushton 1978).

Materials and Methods

1. Detection of hybrids

Hybrids may be detected by a variety of means (Gottlieb 1972) but, in the case of *Q. robur* and *Q. petraea*, only two methods have been employed to date — morphology of leaves and fruits (Carlisle and Brown 1965, Cousens 1963, Rushton 1974, 1978, Wigston 1974, 1975) and pollen viabilities (Minihan and Rushton In Press, Olsson 1975, Rushton 1974, 1978).

Analysis of leaf and fruit samples has proceeded broadly along two lines. Cousens (1963, 1965) utilised a hybrid index, pictorialised scatter diagrams, and the "introgression path" approach pioneered by Anderson (1949), and this was also adopted by Carlisle and Brown (1965). However, this procedure has been criticised (Rushton 1978) and several authors have since developed a multivariate approach to such problems (e.g. Jensen 1977, Rushton 1974, 1978, Wigston 1974, 1975). The analyses used in this present study are of the latter type and generally follow the methodology established for the study of oak hybridisation in England and Wales (Rushton 1974, 1978, 1979). A range of characters was examined. The data for each population were organised in the form of a Tree x Character matrix (character means being calculated for each tree) and these data subjected to both a Cluster Analysis (CA) and a Principal Components Analysis (PCA). In order to interpret the results, reference populations, both *Q. robur* and *Q. petraea*, were included in each data set. Initially, only two reference populations were used but the results were then substantiated with a range of other reference populations. Rushton (1978) provides a full discussion of this technique of multivariate data analysis with reference to hybrid problems.

2. Characters utilised

The characters utilised were more or less the same as reported in earlier work (Rushton 1974, 1978).

Sixteen leaf characters were used:

a. Lamina regularity (LR)

This was scored an an index ranging from 0 to 4. A perfectly regular lamina scored 4 and one index unit was deducted for each of the following irregularities:

i. Presence of subsidiary lobes on the sides of the main lobes;

ii. Lobe depths of opposite sides of the lamina markedly different;

iii. Different number of lobes on opposite sides of the lamina;

iv. Leaf outline on opposite sides markedly different.

A leaf showing all the above traits was therefore scored as zero.

b. Number of lobe pairs (LN)

This count did not include the terminal lobe. Cases where the number of lobes on each side of the lamina varied were usually resolved by reference to lamina venation.

c. Number of intercalary veins (SN)

Decisions as to what constituted an intercalary vein proved difficult and, in consequence, the following definition was used: An intercalary vein was deemed to be present if a vein ran more than half-way to the sinus, and was a vein of equal or nearly equal size to those running to the tips of the lobes. This in practice proved a useful definition, but it should be noted that Wigston (1975) found difficulty in scoring this character and later abandoned it. The character was scored as a simple count of the number of intercalary veins per leaf (see Fig 1.1). In Fig 1.1, an intercalary vein is identified (I) whilst another more minor vein (arrowed) would not be counted.

d. Percentage venation (VN)

A ratio expressed as:

$$\frac{\text{Number of intercalary veins x 100}}{\text{Total number of lamina sinuses}}$$

e. Abaxial pubescence (HR)

In the previous surveys, pubescence was considered as two separate characters — stellate hairs and simple hairs. In this study, the two were combined and scored on a scale of abundance (a glabrous leaf scoring 0, a very hairy leaf scoring 4) using a series of type leaves for comparison. Previous surveys (Rushton 1974, 1978) had shown that there was a highly significant correlation between the abundance of stellate and simple hairs.

f. Length of petiole (PL), see Fig 1.1.

g. Lamina length (LL), see Fig 1.1.

h. Total leaf length (LL+PL)

The total leaf length including both lamina and petiole.

i. Petiole ratio (PR)

A ratio defined as:

$$\frac{\text{Total leaf length}}{\text{Length of petiole}} \qquad \frac{(LL+PL)}{PL}$$

j. Length of lamina from the lamina base to the widest part (WP)

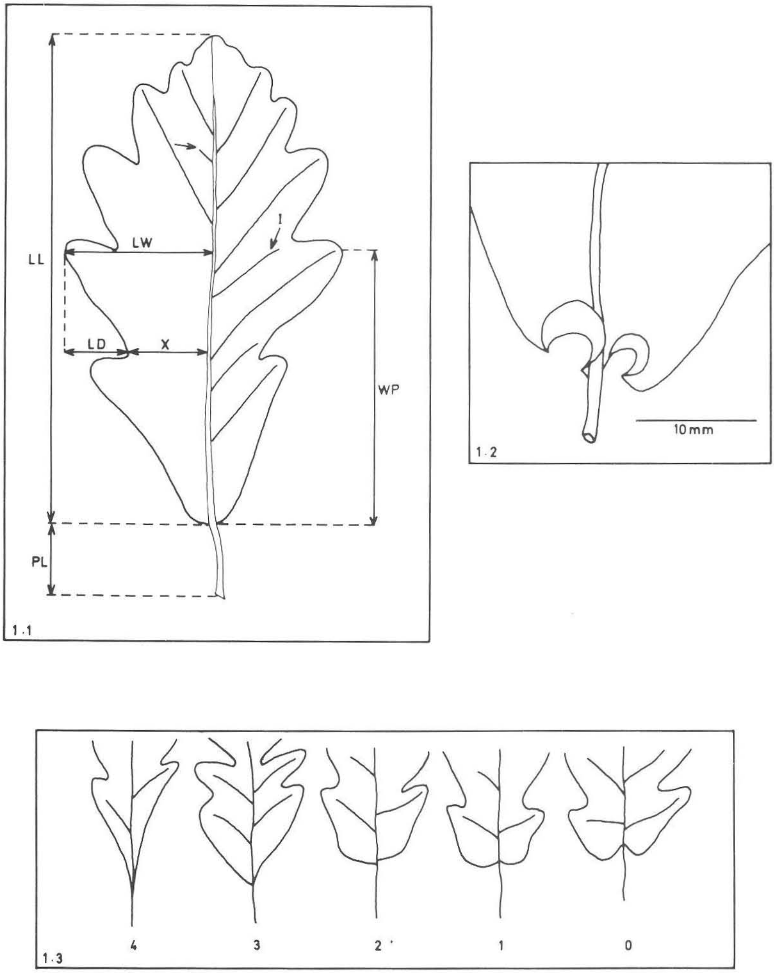

Fig. 1 The estimation and measurement of certain leaf characters in *Quercus* L.

1.1 Quantitative characters (LL=lamina length; PL=length of petiole; LW=lobe width; LD=depth of sinus; X=lamina width; I= an intercalary vein; WP=length of lamina from the lamina base to the widest part).

1.2 The abaxial leaf surface showing a well developed auricle.

1.3 Variation and scoring of the basal shape of the lamina. The numbers refer to the index score.

k. Lamina shape or obversity (OB)

Obversity was determined by use of the following ratio (see Fig 1.1):

$$\frac{\text{Lamina length}}{\text{Length of lamina from the lamina base to the widest part}}$$

l. Lobe width (LW)

This was measured from the midrib to the tip of the lobe at, or immediately below, the widest part of the lamina (see Fig 1.1).

m. Depth of sinus (LD)

Depth of sinus was computed as follows: Lamina width measured from midrib to the base of the sinus at, or immediately below, the widest part of the lamina=X. Then LD=LW–X (see Fig 1.1).

n. Lobe depth ratio (LDR)

Lobe depth ratio has been calculated as the ratio of the width of the lobe to the depth of the sinus immediately below e.g. Maze (1968), Silliman and Leisner (1958), Tucker (1963) i.e. LW/LD. This method of assessment was retained specifically for that lobe at, or immediately below, the widest part of the lamina.

o. Auricle development (AU)

This was scored as an index 0 to 4; a strong auricle scored 0, no auricle 4. A series of type leaves was used for comparison (see Fig 1.2).

p. Basal shape of lamina (BS)

This was scored as an index 0 to 4; a cordate base scored 0, a cuneate base 4. A series of type leaves was used for comparison (see Fig 1.3).

3. Sample collection, measurement and analysis procedure

Members of the Forest Service supplied oak leaf samples. The geographical distribution of the material collected is shown in Fig 2. Generally, these were collected during September/October from oak populations, and consisted of a sample of five leaves/tree from a standard canopy position (Rushton 1978). Selection of trees within populations was random. Collecting instructions issued to the Forest Service indicated that up to 50 trees could be collected per site. At the same time, acorns and peduncles were collected. The

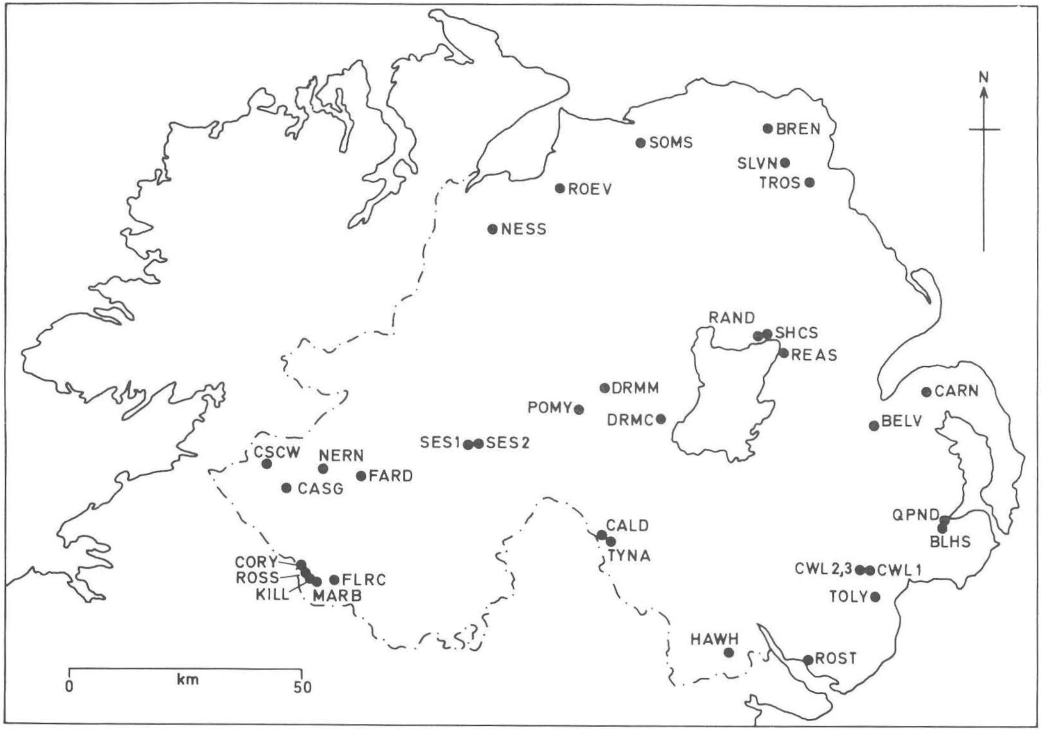

Fig. 2. Distribution of the 35 population samples of oak (32 sites).

sites, together with sample sizes, are listed in Table 1. The author relied on the goodwill of the Forest Service to supply material and no control was exercised over which populations were sampled, nor over sample sizes. Consequently, in some instances, sample sizes were very small but have been included for completeness.

Correlations established between leaf, acorn and peduncle characters have shown that hybrids between *Q. robur* and *Q. petraea* can be efficiently and accurately assessed using leaf characters alone (Rushton 1974, 1978). Since only a small proportion of the samples had well developed fruiting structures, they have not been included in this survey.

Each leaf was assessed for the 16 leaf characters described above and a mean value calculated for each character for each tree. Some leaves, and in some instances all the leaves from a single tree, were not recorded as poor preservation had caused extensive fungal growth which masked such characters as hair development, auricle development and veining patterns. A total of 1087 usable tree samples were supplied from 35 "populations" from 32 sites. For each population in turn, the data matrix consisting of 16 Characters x N Trees was combined with two other data matrices, one of 16 Characters x 25 reference *Q. robur* trees and the second of 16 Characters x 22 reference *Q. petraea* trees. These two reference populations were the same as used in previous work (Rushton 1974, 1978). They were a sample from the Wyre Forest (SO 748 763, *Q. petraea)* and one from Austy Wood (SP 173 633, *Q. robur*). The combined data matrix was then subjected to a PCA using a PASCAL program developed for the VAX 11/780 computer and a CA from the CLUSTAN 2.1 suite of FORTRAN IV programs (Wishart 1982). The cluster analysis used was Ward's Error Sums of Squares Method, a polythetic, agglomerative clustering strategy, using squared Euclidean distance as the similarity coefficient (Ward 1963, Wishart 1969).

The results of each PCA of the combined data matrix were then examined for the presence of trees intermediate between the two reference populations. Earlier work (Rushton 1974, 1978) had indicated that, on grounds of pollen viability, these could be regarded as having hybrid ancestry. The assessment of individual trees was confirmed using the CA results and a series of PCA results using alternative reference populations.

By way of example of the method of PCA interpretation, the PCA results for four populations are given in Fig 3. These illustrate a population which is predominantly *Q. robur* with a single hybrid tree (Fig 3.1), a mixed population with a small number of hybrids (Fig 3.2), a population which is composed predominantly of hybrids

Table 1 Site details including grid references and sample size for the 35 populations.

Name of Forest	Code	Grid Ref.	Sample Size	
Ballyhassen Wood	BLHS	J4947	50	Adjacent Strangford Lough. An old mixed wood with evidence of extraction and regrowth from stools. 0-15m. Acid brown earth.
Belvoir Park, FNR	BELV	J3469	50	Mixed woodland. 15-30m. Acid brown earth.
Breen Wood, NNR	BREN	D1233	40	Old oakwood clothing the sides of a series of glacial overflow channels. 90-150m. Brown earth.
Cairn Wood, FNR	CARN	J4577	38	An old woodland on slopes of Cairngaver. 150-210m. Acid brown earth.
Caledon Estate	CALD	H7443	4	Estate planting. 50m. Grey-brown podsol overlying sandstone.
Cassol Glen, (Lough Navar Forest)	CASG	H0754	20	Alongside small river. 90-120m.
Castle Caldwell, FNR	CSCW	H0206	40	Small woodland on promontory on Lower Lough Erne. 30m.
Castlewellan FP, Sample 1	CWL1	J3337	25	Estate planting of Oak and Sycamore. 120-150m. Acid brown earth.
Castlewellan FP, Sample 2	CWL2	J3237	15	Estate planting of hardwoods. 150m. Acid brown earth.
Castlewellan FP, Sample 3	CWL3	J3237	32	Estate planting of Oak and other hardwoods. 150-180m. Acid brown earth.
Corry Point Wood, (Florence Court Forest), FNR	CORY	H0937	33	A mixed hardwood stand on promontory on Lower Lough Macnean. 30m. Gleyed soil and peat.
Drumcairne Forest	DRMC	H8870	40	Sample included part of the "Old Wood". 60-90m. Acid Brown earth.
Drum Manor, FP	DRMM	H7677	34	Estate planting around small lakes. 60-90m. Acid brown earth.

Florence Court Forest	FLRC	H1734	35	Oak and other hardwood plantation and estate plantings. 30m. Gleyed soil and peat.
Glenariff Forest, (Trostan Forest), NNR	TROS	D2021	10	Alongside Glenariff River, total population about 65 trees. 200m.
Hawthorn Hill, FNR	HAWH	J0319	47	Mixed woodland including Oak on slopes of Slieve Gullion. 150-210m. Acid brown earth.
Inishmakill Island, (North Erne Forest), NNR	NERN	H1558	50	Island in middle of Lower Lough Erne formed as a result of lowering of the lough in the 1890s. Some mature oaks. 30m.
Killesher, FNR	KILL	H1235	11	Mixed woodland developed on limestone on the lower slopes of the Cuileagh Mountains. 90-120m.
Marble Arch, (Marlbank Forest), NNR	MARB	H1234	20	Wooded (predominantly Ash) limestone gorge of the Cladagh River. 60-150m.
Mullock Moss Wood and Derue Wood	FARD	H2356	50	No site details available. 60-90m.
Ness Wood	NESS	C5211	40	Alongside deep-sided gorge of the Burntollet River; Oak removed in the 1840s but now substantially regenerated. 60-120m. Acid brown earth.
Pomeroy Forest, FNR	POMY	H7072	40	Old estate planting. 150-180m. Acid brown earth.
Quoile Pondage, NR	QPND	J5048	40	Adjacent to Strangford Lough; Oak spreading after a barrage was built across the River Quoile 20 years ago. Trees now up to 6m tall and bearing acorns. 0-15m. Nutrient rich.
Randalstown Forest, NNR	RAND	J0988	50	1936 plantation of Oak in mixture with Norway Spruce. 15-60m.
Rea's Wood, NNR	REAS	J1485	9	A colonising woodland on the shore of Lough Neagh. Alder, Ash and Sycamore with Oaks in the drier areas. 15-30m.
Roe Valley Country Park	ROEV	C6720	40	Deep sided gorge of the River Roe. 15-30m. Acid brown earth.
Rossaa, NNR	ROSS	H1036	13	Part of the ribbon of woodland around the Cuileagh Mountains. 90-120m.

Name of Forest	Code	Grid Ref.	Sample Size	
Rostrevor Oak Wood, NNR	ROST	J1718	40	On steep slopes; evidence of clearing in the 1740s followed by regrowth. 60-150m. Acid brown earth.
Seskinore Forest, Sample 1	SES1	H4864	14	Estate planting from the 19th century. 90-120m. Gleyed peat.
Seskinore Forest, Sample 2	SES2	H4764	20	Possibly a more recent planting than SES1. 90-120m. Gleyed peat.
Shanes Castle	SHCS	J1188	40	Original estate planting (150 years ago) with Lime, Elm and Beech. 15-30m. Gleyed brown earth.
Slieveanorra Forest	SLVN	D1526	40	No site details available.
Somerset Forest	SOMS	C8430	2	Recent (1950s) planting. 15-30m. Gleyed brown earth.
Tollymore FP	TOLY	J3431	48	Large scale planting dating back to 1756. 15-250m. Acid brown earth and coarse drift.
Tynan Abbey Estate	TYNA	H7542	7	Estate planting. 50m. Grey-brown podsol.

(FNR=Forest Nature Reserve; FP=Forest Park; NNR=National Nature Reserve; NR=Nature Reserve)

N.B. Many of the sites possess a varied soil and geological make-up and therefore the details above should be taken only as a general indication of site conditions. The height above sea level is given for each population.

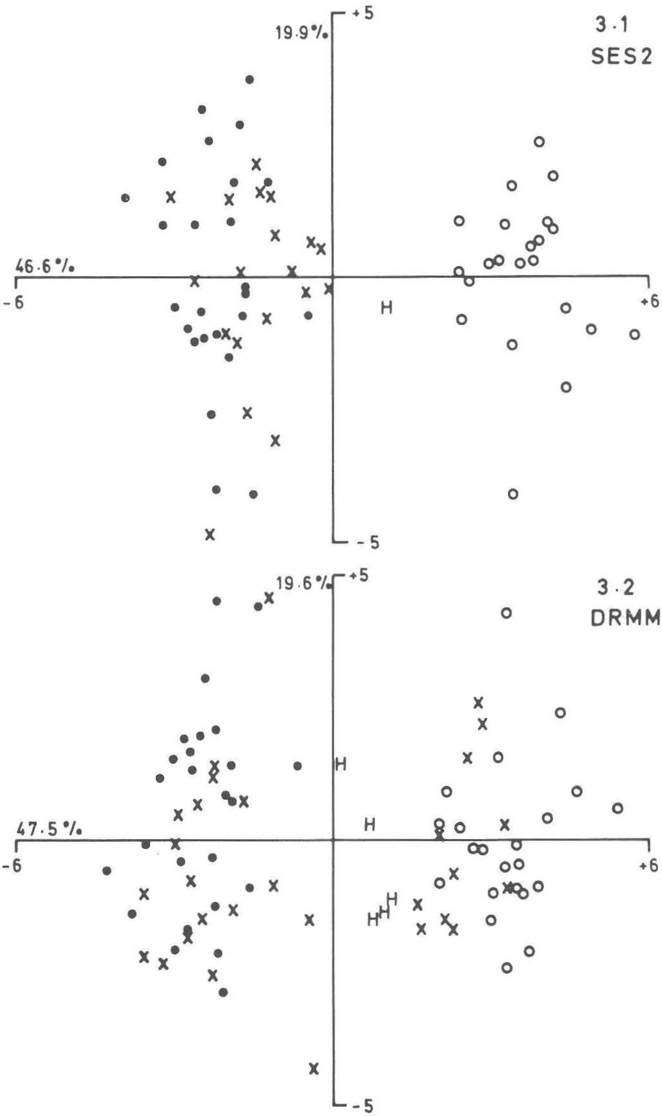

Fig 3. Illustrative PCA results showing a reference pure *Q. robur* population (●), a reference pure *Q. petraea* population (O) and a sample oak population from Northern Ireland. In the sample population, hybrids are identified by H and non-hybrids by X. The percentage of variance accounted for by each component is also shown.

3.2 Seskinore Forest Sample 2 (SES2): predominantly *Q. robur* with only one hybrid tree.

3.2 Drum Manor Forest Park (DRMM): a mixed population with a small number of hybrids.

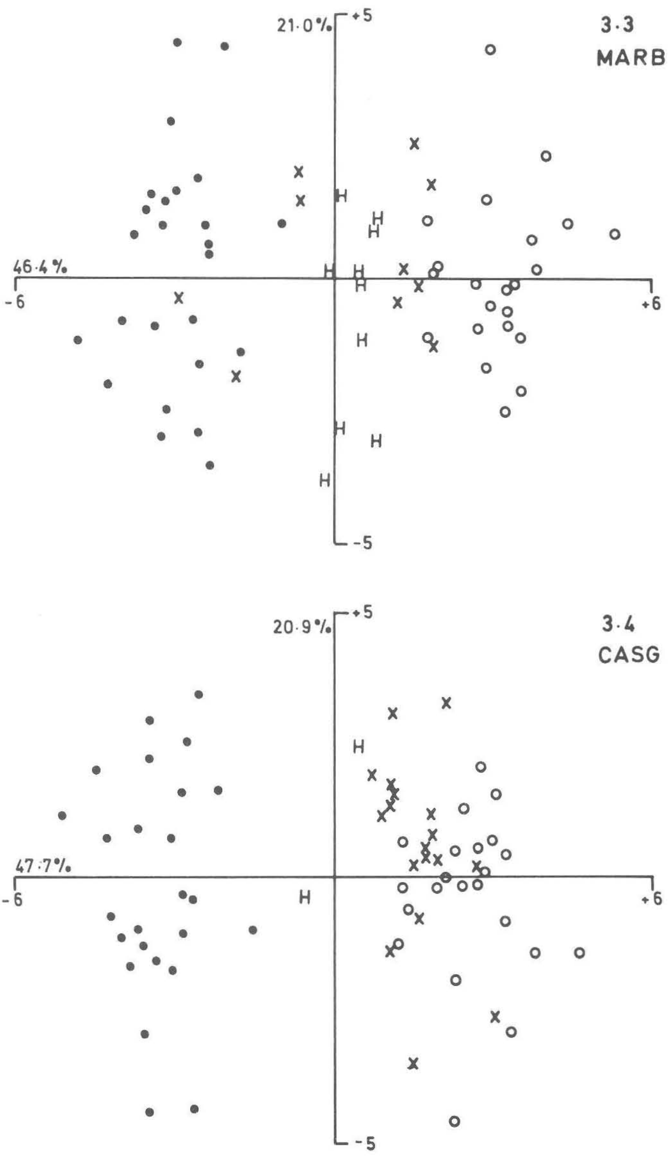

Fig 3 continued
3.3 Marble Arch (MARB): predominantly hybrids.
3.4 Cassol Glen (CASG): predominantly *Q. petraea* with a small number of hybrids.

(Fig 3.3), and a population which is primarily *Q. petraea* with a small number of hybrids (Fig 3.4). Rushton (1978) includes details of the use of CA along with PCA.

RESULTS

The results may be examined in three ways:

A. The general pattern of results within Northern Ireland;

B. A comparison of results with those of earlier surveys particularly those of Rushton (1978, 1979), who used equivalent survey and sampling methods;

C. Individual population results.

A. The general pattern of results

The main results of this study are included in Fig 4. The trees for each population were designated, on the basis of the PCA and CA, as either *Q. robur, Q. petraea* or hybrid. The proportions of each, in each population, were calculated and the results expressed as a histogram for each population. The populations fell, more or less, into five different categories:

1. Populations with only *Q. robur* trees. Two populations were of this type (Fig 4.1, 4.2) although both were represented by very small sample sizes.

2. Mixed populations with both *Q. robur* and *Q. petraea* trees but no hybrids (Fig 4.3, 4.4). In both populations comprising this type, the predominant tree was *Q. robur* accounting for 96% and 89% of the trees in the two populations.

3. Predominantly *Q. robur* trees with hybrids, but with no evidence of *Q. petraea* trees (Fig 4.5-4.8). Four populations comprised this category, and the percentage of hybrids in these populations was generally small — 5%, 5%, 5% and 25%.

4. Mixed populations with *Q. robur, Q. petraea* and hybrids. The majority of population samples (21 out of 35) fell into this category, but four subcategories were observed:

a. Populations with a predominance of *Q. robur* and generally with fewer *Q. petraea* and hybrid trees (Fig 4.9-4.13).

b. Populations with more or less equal proportions of *Q. robur* and *Q. petraea* and with a generally much lower percentage of hybrids (Fig 4.14-4.22). This was the largest category with nine populations.

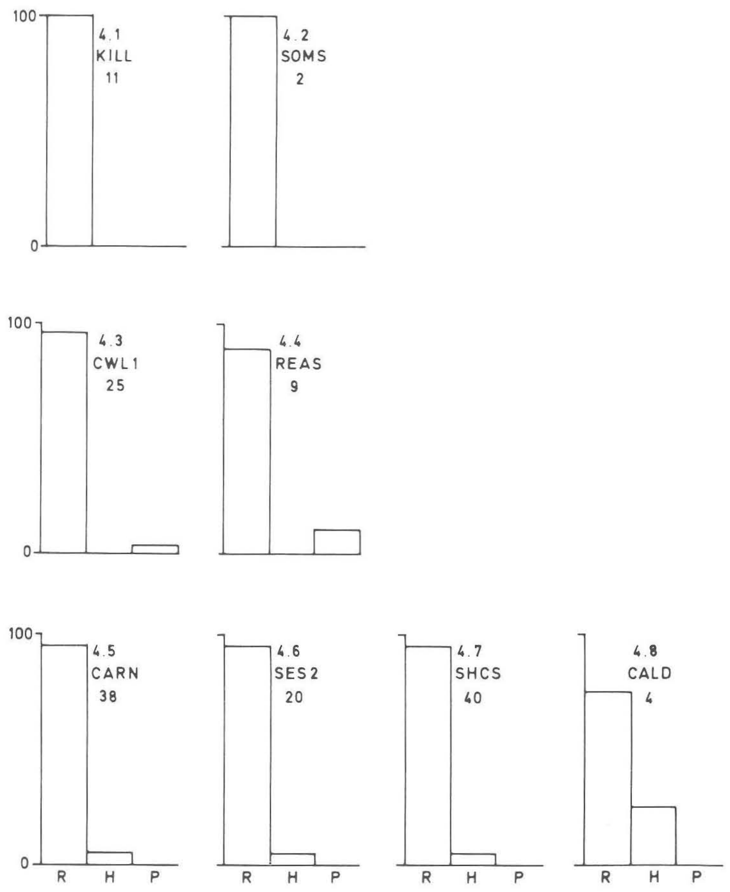

Fig 4 Percentage occurrence of *Q. robur* (R), *Q. petraea* (P), and hybrids (H) in oak population samples. Population code letters are listed in Table 1. The population sample size is also given.

4.1-4.2 Category 1: pure *Q. robur*.

4.3-4.4 Category 2: mixed populations with no hybrids and a predominance of *Q. robur* trees.

4.5-4.8 Category 3: predominantly pure *Q. robur* with a small number of hybrids.

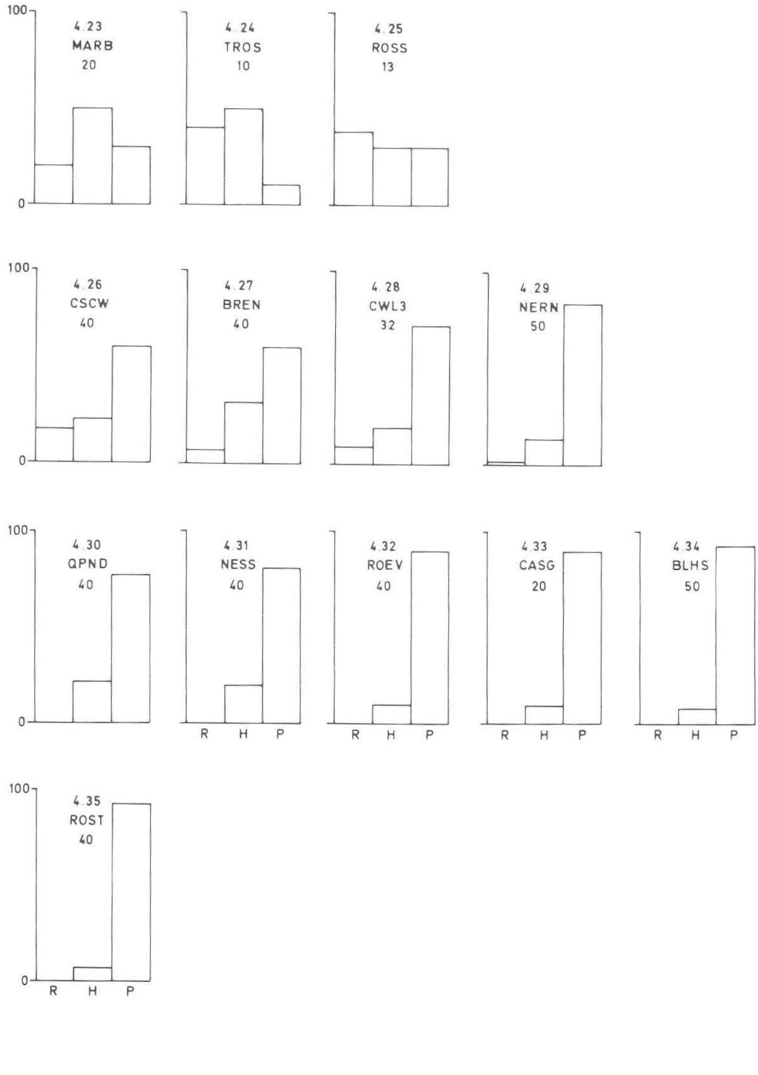

Fig 4 continued

4.9-4.13 Category 4a: predominantly *Q. robur* with a small number of *Q. petraea* and hybrid trees.

4.14-4.22 Category 4b: approximately equal proportions of *Q. robur* and *Q. petraea* with a smaller number of hybrids.

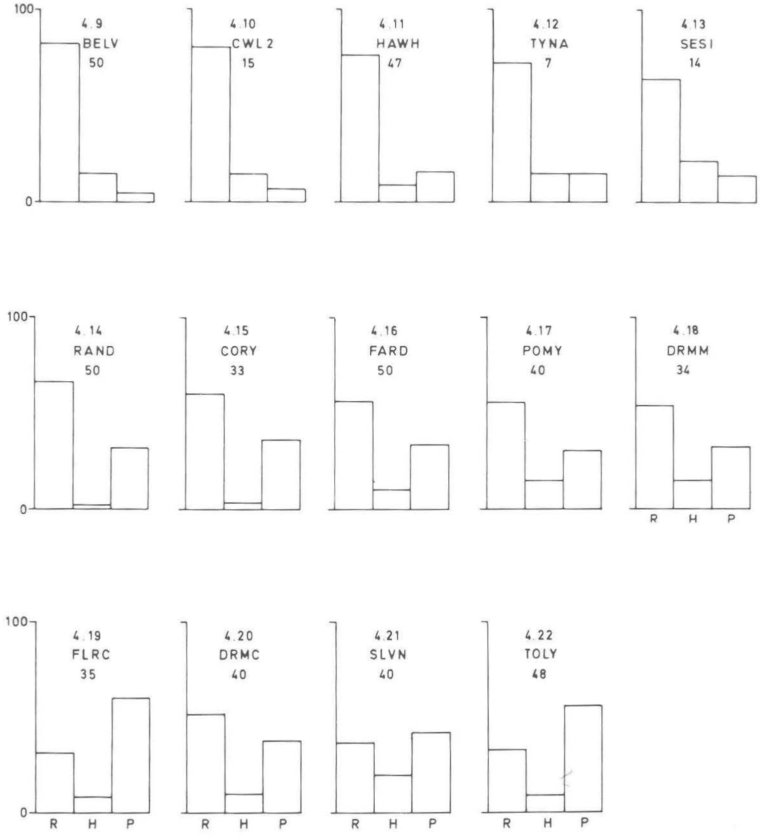

Fig 4 continued

4.23-4.25 Category 4c: mixed populations with a high proportion of hybrids.

4.26-4.29 Category 4d: predominantly *Q. petraea* with a small number of hybrid and *Q. robur* trees.

4.30-4.35 Category 5: predominantly *Q. petraea* with a small number of hybrid trees.

c. Populations in which the proportion of hybrids was generally high, usually exceeding the proportions of the two parental types. Three samples fell into this category (Fig 4.23-4.25), the percentage of hybrids being 50% (MARB), 50% (TROS) and 31% (ROSS). These population samples were generally small.

d. Populations with a preponderance of *Q. petraea* and generally with fewer *Q. robur* and hybrid trees (Fig 4.26-4.29). These populations were the reverse of Category 4a above.

5. Population samples with a high percentage of *Q. petraea* trees and a generally low percentage of hybrid trees, but with no *Q. robur* (Fig 4.30-4.35). This was the second largest category with six populations and is the reverse of Category 3 above. The percentage of hybrids ranged from 7.5% (ROST) to 22.5% (QPND).

Overall, of the 1087 trees recorded, 455 were *Q. robur*, 487 were *Q. petraea* and 145 were thought to have some hybrid ancestry.

B. A comparison with earlier surveys

The results from this survey have been compared to those of the earlier survey in England and Wales (Rushton 1978, 1979) in Table 2. In England and Wales, the populations with *Q. robur* affinities (Categories 1, 2, 3, and 4a above) accounted for about 58% of all sampled populations. In Northern Ireland, these populations were only 37% of the total. However, further differences were evident between these *Q. robur* populations — the hybrid populations (Categories 3 and 4a) accounted for only 14.8% of the England/Wales populations whilst in Northern Ireland they accounted for 25.7%; in England and Wales the pure *Q. robur* populations accounted for 43.7% whilst in Northern Ireland it was only 11.4%. Indeed, the general absence of pure populations, both *Q. robur* and *Q. petraea,* from the results represents a major difference between this and the England/Wales survey.

The *Q. petraea* populations (Categories 4d and 5) were very similar between the two surveys except that no pure *Q. petraea* populations nor populations of pure *Q. petraea* with a small number of *Q. robur* trees were found in Northern Ireland.

A very large difference was evident between the mixed populations which accounted for 25.7% of populations in Northern Ireland but only 5.2% in England/Wales.

The level of populations with hybrids was similar in both areas. In the earlier survey, the level of hybridisation was estimated to be between 7.7% and 12.6% depending on the limits set for hybrid definition. In this survey, the level of hybridisation was 13.3%

Table 2 A comparison of the results of the present survey with those of an earlier survey in England and Wales (Rushton 1978)

Category of Population	England/Wales (Rushton 1978) No. Pops.	%	Northern Ireland (Present Survey) No. Pops.	%
1. Pure *Q. robur*.	50	37.0	2	5.7
2. Pure *Q. robur* with a small number of *Q. petraea* trees.	9	6.7	2	5.7
3. Pure *Q. robur* with a small number of hybrid trees.	5	3.7	4	11.4
4a. Pure *Q. robur* with a small number of *Q. petraea* and hybrid trees.	15	11.1	5	14.3
4b. Mixed populations with more or less equal numbers of *Q. robur* and *Q. petraea* trees, usually with a small number of hybrids.	7	5.2	9	25.7
4c. Populations dominated by hybrids often with a small number of *Q. robur* and *Q. petraea* trees.	8	5.9	3	8.6
4d. Pure *Q. petraea* with a small number of *Q. robur* and hybrid trees.	15	11.1	4	11.4
5. Pure *Q. petraea* with a small number of hybrid trees.	9	6.7	6	17.1
6. Pure *Q. petraea* with a small number of *Q. robur* trees.	7	5.2	0	0.0
7. Pure *Q. petraea*.	10	7.4	0	0.0
TOTAL	135	100.0	35	100.00

(i.e. 145 trees out of 1087). This level of hybridisation is comparable with the England/Wales survey. Unlike the earlier work, there did not appear to be any discernable pattern to the distribution of population types.

Cousens (1965) concluded that in populations of *Q. petraea* in Ireland, there was evidence of past hybridisation but truly intermediate trees accounted for less than 2.0% of the total. It should be pointed out however that this was not a random sample of populations and that populations had been chosen to represent "good" *Q. petraea.*Direct comparisons are not therefore possible. Kelly and Moore (1975) have noted that where *Q. petraea* occurs on limestone near to geological boundaries, hybridisation between the two species is quite frequent.

C. Individual population results

Rea's Wood — REAS

Rea's Wood consisted of a sample of only nine trees, which were identified as eight *Q. robur* and one *Q. petraea* tree. The population is actively colonising part of the Lough Neagh shore-line recently exposed as a result of lowering of the lough. The site is relatively water-logged. The colonising trees appear to be *Q. robur* which is recorded as being more tolerant of water-logging conditions (Jones 1959).

Quoile Pondage — QPND

Quoile Pondage also represents a site where oak is spreading — in this case after the construction of a barrage across a river. Of the 40 trees in the sample, 25 were collected from areas closely adjacent to the BLHS population from which the QPND trees are probably spreading. The profiles of the two populations were very similar — neither population has *Q. robur* trees; the percentage of *Q. petraea* is 77.5% in QPND and 92% in BLHS.

Rossaa, Killesher, and Marble Arch — ROSS, KILL, and MARB

The ROSS and KILL samples are part of a long ribbon of woodland which follows the 90-120m contour around the northern base of the Cuileagh Mountains. MARB, within one km of the KILL sample follows the course of the Cladagh River. The composition of the MARB and ROSS samples is remarkably similar (Fig 4.23 and 4.25); both contain more or less equal proportions of *Q. robur, Q. petraea* and hybrids (Category 4c). However, the KILL sample is very different, being composed of only pure *Q. robur* trees (Fig 4.1, Category 1). Such a mosaic is not unique and similar instances have been recorded, e.g. Wyre Forest (Hickin

1971), and usually the mosaic can be interpreted by reference to underlying soil type, parent rock or drainage pattern. In the case of ROSS, KILL, and MARB the actual reasons remain unknown and warrant further investigation. At MARB, there is a very high number of hybrids. Ash (*Fraxinus excelsior* L.) dominates this wood and this is particularly true of the wetter areas adjacent to the Cladagh River. The oak is confined to the higher slopes in mixture with both ash and beech (*Fagus sylvatica* L.) (Tomlinson 1982). Because of their even size and spacing the oaks are thought to have been planted (Tomlinson 1982). If they are of planted origin, then the large number of hybrids is probably derived not from *in situ* hybridisation but from hybridisation in the original parental population from which the seed was derived. Planting might also account for the very different profiles of the ROSS and KILL populations.

Castle Caldwell — CSCW

This population was collected from the long promontory stretching into Lower Lough Erne between Bleanalung Bay and Castle Bay. The sample was predominantly *Q. petraea*, but with a small number of both hybrids and *Q. robur* trees (Fig 4.26, Category 4d). In this case, careful records were kept of the positions of individual trees. All seven *Q. robur* trees came from the wetter areas, the *Q. petraea* trees from the drier parts and the nine hybrid trees were scattered throughout the wood.

Inishmakill Island — NERN

Tomlinson (1982) records this site as consisting of several kinds of intermixed woods some of which have developed since the lowering of Lower Lough Erne in the 1890s. The vegetation shows a marginal fringe of mixed scrub and alder/ash scrub with both wet and dry oakwoods occurring inland of these. Tomlinson notes that *Q. petraea* occurs to the west of the island in the drier parts. The sample examined in this survey indicated a predominantly *Q. petraea* wood land but with a small number of hybrids and one *Q. robur* tree (Fig 4.29, Category 4d).

Discussion

Although it is not possible to draw firm conclusions concerning the natural distributions of the two oak species and their hybrids in Northern Ireland owing to the extensive removal of natural woodland and its replacement by plantations (McCracken 1971, Tomlinson 1982), it is possible to make some general points.

The supply of samples by the Forest Service, Northern Ireland has undoubtedly influenced the pattern of the results in that many of the populations were from estate plantings or non-natural woodland stands. Many of the populations dominated by *Q. robur* appear to be either estate plantings (e.g. SHCS) or more recent commercial plantings (e.g. SOMS). Conversely, many of the populations of natural or semi-natural status showed *Q. petraea* affinities. Mixed populations predominated in the samples, in contrast to the earlier survey in England and Wales (Rushton 1978), and many of these were also of planted status e.g. POMY and RAND which was planted in 1936 in mixture with Norway Spruce (*Picea abies* (L.) Karst.).

Several factors are important in interpreting these results but two will be examined here — firstly, the history of planting and species preference and secondly the status of *Q. robur* as a native tree in Ireland and the spread of oaks to Ireland from Britain after the last Ice Age. Cousens (1965) provides background information on both these points.

Tree planting in Ireland was not recorded until the 16th century and by the 18th century planting included many exotic species. By the 1820s charcoal smelting had become unprofitable and consequently oak felling was largely suspended. Cousens (1965) argued that the majority of the oak in Ireland today is derived from woodland that was last felled in the early 1800s. Jones (1959) and Gardiner (1974) have noted that, towards 1800, gardeners and foresters were advocating the planting of *Q. robur* in preference to *Q. petraea* as the wood of the former was thought to be superior. Furthermore, the two species differ in their response to acorn storage and shipment. Acorns of *Q. robur* are said to withstand transport and storage much better than those of *Q. petraea* (Jones 1959). The *Q. robur* acorns were also larger, produced in larger numbers and probably produced larger seedlings (Jones 1959) and this led to *Q. robur* being planted in preference to *Q. petraea* in England and other parts of Europe. Cousens (1965) has argued that *Q. petraea* was seldom used for planting. In Ireland, McCracken (1971) notes that various species of oak were available for sowing from the early 1700s. For example, the Royal Dublin Society sponsored plantings and by the 1780s had a species list which included several oak varieties and species including scarlet, turkey, prickly, Turner, Luccombe, American swamp, champagne, black and white oaks. However, McCracken does not mention whether *Q. robur* and *Q. petraea* were separately listed. At about this time, McCracken records nurserymen's lists in Dublin offering various species of oak for sale. Thus, estate planters of the time presumably would have had the choice of *Q. robur* or *Q. petraea* but may have chosen to plant *Q. robur* because of the adverse publicity.

It is almost certain that the purity of the seed available from nurserymen would have been questionable. The reasons for this are related to the taxonomy of the species and also to the remarkable range of variation present within the species. The taxonomy of the two species was also in a state of flux and, although the two species descriptions were well documented, there were still misleading accounts published and mistakes made. Indeed, quite recent accounts of the species have been erroneous e.g. Harris (1927). The range of species variation also would have led to trees being misidentified and even to hybrids being confused with the pure types.

Proof that *Q. robur* was actually planted in preference to *Q. petraea* or, indeed, that planters knew which species they were planting is difficult to establish with certainty. There are instances of *Q. petraea* plantation. For example, Kelly and Moore (1975) have recorded the planting of (presumably) *Q. petraea* in Killarney during the 1800s. One confusing aspect is the practice of "dibbing" or "dibbling" — planting acorns freshly fallen from the trees into their final position (Fitzpatrick 1966, Forbes 1933) which would have led to local consolidation of variation patterns.

Many of the estate plantings sampled here have yielded samples dominated by *Q. robur* e.g. SHCS. However, these usually have a proportion of *Q. petraea* and hybrids as well and, in many instances, the proportion of *Q. petraea* is equal to that of the *Q. robur* trees. Whether these represent contaminants of the original seed source or whether they represent regeneration from existing woodland at the time of planting cannot be ascertained. The hybrids themselves could also represent part of the original plantings or they could reflect hybridisation that has occurred since the plantings were established. The presence of hybrids in more recent plantings e.g. RAND which was planted in 1936, is almost certainly due to contamination of the original seed supply. The RAND plantation also contains 66% *Q. robur* and 32% *Q. petraea* — the conclusion must be that "oak" was planted with little attempt to differentiate the species. Of course, it could be argued that such indiscriminant planting also occurred in the past. The MARB population may represent an example of a substantially hybrid planted population.

No populations have been detected which were composed of only pure *Q. petraea*. All populations with a substantial percentage of *Q. petraea* (i.e. Fig 4.26-4.35) had a small proportion of hybrid trees and, in many instances, a small proportion of *Q. robur* trees as well (Fig 4.26-4.29). Many of the sites on which these woodlands are developed are comparatively wet. In some *Q. petraea* populations in England, *Q. robur* and hybrids have been observed in the wetter areas (Rushton 1979) and it is likely that the *Q. petraea* populations in Northern Ireland with either a small proportion of hybrids or a small proportion of hybrids and *Q. robur* trees may represent similar examples (e.g. Castle Caldwell, CSCW).

The native status of *Q. robur* has recently been argued by Kelly and Kirby (1982). McEvoy (1943) has also concluded that *Q. robur* is native to Ireland and was naturally the main species of the central plain. Other woodland remnants on the siliceous rocks of the periphery of this central area were of *Q. petraea* affinity (Cousens 1965). The majority of the supposed natural or semi-natural woodlands in this survey also showed *Q. petraea* affinities. One of these, the Rostrevor Nature Reserve (ROST) has been described (Tomlinson 1982) as being the successor of the oakwoods that were once extensive over much of Ireland. Tomlinson has argued that, in the case of ROST, the woodland escaped clearance owing to its inaccessible position. Similar examples occur — the Roe Valley (ROEV), Ness Wood (NESS) etc.

The intermediate trees identified in this survey have been interpreted as having a hybrid origin. In the earlier survey of England and Wales (Rushton 1978, 1979) supporting evidence for the hybrid status of these intermediate trees was supplied from pollen viability studies. For the present survey, one population (BREN) has been checked for pollen viability and, although a relatively complex situation was found (Minihan and Rushton, in press), generally the analysis of pollen viability supported the view that the trees with intermediate morphology were of hybrid status. Further, there is strong evidence from the PCA results that many of the samples with hybrids show a distribution of intermediates compatible with that expected from introgressed populations.

Cousens (1965) has argued that there are four recognisable stages in introgression:

1. Establishment of F_1 hybrids and the start of backcrossing;
2. Continued hybridisation and well-advanced introgression;
3. Cessation of hybridisation and continued backcrossing resulting in a gradual assimilation of the "alien" genes;
4. The process of assimilation is complete and only comparison with non-introgressed populations would indicate any evidence of past introgression.

From his observations in Ireland of 12 populations (13 samples, 329 trees) Cousens (1965) concluded that generally the Irish material was in a late phase of Stage 3. Observations of the results for the large majority of the populations with hybrids in the present survey indicate that the hybrids are probably of backcross status and the populations also in Stage 3 above. There are, however, some exceptions. For example, of the nine intermediate trees in Quoile Pondage Nature Reserve (QPND), six were morphologically completely intermediate between *Q. robur* and *Q. petraea* and were probably F_1 hybrids.

In this survey no completely intermediate populations were detected unlike the survey of England and Wales (Rushton 1978, 1979) although Mercer (1967) has described one such population from Co. Wicklow. Kelly and Moore (1975) have noted mixed populations with varying amounts of hybrids where soil enrichment caused by nutrient flushing allows *Q. robur* to become established on siliceous rock. It is felt that in Northern Ireland, mixed populations are more likely to have arisen through plantation rather than spread.

It would appear, therefore, that within the samples there is evidence of both ancient and relatively modern hybridisation between *Q. robur* and *Q. petraea* in Northern Ireland. Furthermore, the extensive presence of *Q. robur* and backcrossed hybrids in natural and semi-natural woodlands is evidence of the native status of *Q. robur* in Ireland. There is also evidence that several woodlands show a mosaic arrangement with *Q. robur* in the wetter and *Q. petraea* in the drier parts.

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