VARIATION OF SOME DIAGNOSTIC CHARACTERS OF THE SESSILE AND PEDUNCULATE OAKS AND THEIR HYBRIDS IN SCOTLAND

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Abstract

A collection of Scottish oaks including nearly 1,000 fertile specimens has been analysed in respect of selected diagnostic characters. Pictorialized scatter-diagrams confirm that only two taxa are involved and that considerably more than half the fertile material cannot be diagnosed with confidence as belonging to either. The variation patterns within population samples are so exactly what would be expected from widespread and massive introgression that the objections to this interpretation are called into question. All the *robur*-dominated woods appear to be quite strongly introgressed but there are a few *petraea* woods which are relatively homogeneous and show no evidence of introgression. The latter are used to demonstrate the variation that may be expected from reasonably good *petraea* in Scotland.

Introduction

Q. robur L. and *Q. petraea* (Matt.) Liebl. have been described in varying detail many times since they were first distinguished. Jones (1959) has recently summarised the more important British and Continental contributions to our knowledge of the two species. The list below of some of the more reliable diagnostic characters is extracted from his account.

Character		*robur*	*petraea*
Leaves of spring shoots of the crown	Shape	obovate	ovate
	Lobing	deep, irregular, 3–5(–6) pairs	shallow, regular, 5–6(–8) pairs
	Petiole	short 2–3–7 mm	long 13–25 mm
	Leaf base	cordate with strong auricles	cordate to cuneate, weak auricles
	Abaxial surface	glabrous, occasional simple hairs	always some stellate hairs
Acorns	Colour	pale fawn	uniform dark brown
	Longitudinal stripes	olive green on fresh mature acorns	absent
Fruiting peduncle	Total length	2–9 cm	0–3(–4) cm
	Thickness	slender	stout
	Pubescence	glabrous	some pubescence
Buds	Size	small	large
	Apex	obtuse	acute

Two of these characters are reputedly qualitative : the striations on the maturing acorn of *robur* and the abaxial stellate pubescence on the leaf of *petraea*. The first is of little practical use in the field unless collecting is confined to the critical periods of good fruiting years. The second is disputed : Jones follows Moss (1914) in accepting abaxial stellate hairs as a *petraea* character, but several Continental workers have described aff. *robur* forms as having them (*e.g.* Weimarck 1947). Of the remaining quantitative characters only petiole length has ranges for *robur* and *petraea* which do not overlap. Scottish collections however, do not conform to the specifications above; they show overlap in this as well.

Confident identifications of oaks in Scotland can therefore be made only when the individual exhibits most of the diagnostic characters in the extreme forms associated with one of the two species. A majority of individuals have to be classified as intermediate either because intermediate values for diagnostic characters predominate or because extreme *robur* and *petraea* characters occur on the same tree. Many Scottish woods have a very high proportion of such intermediate forms and for many years it was commonly assumed that they were of hybrid origin (*e.g.* Burtt Davy 1933, Tansley 1940). Opinion changed as the results of work by Pyatnitski and Dengler (refs. in Jones 1959) became known; they had demonstrated experimentally that the two species when crossed set on the average only 2% fertile seed. Jones expresses the new views when he defines the species more broadly than before and claims that hybrid forms, even in woods where both species are present, are unlikely to exceed 5%. While I agree that Jones' descriptions of the two species are a great improvement on former ones, they do not seem to clarify the position in Scotland (*cf.* attempts to apply earlier descriptions in Scotland by Greville (1841)).

The field botanist has neglected the oaks. The reasons are probably the obvious ones, the difficulty of collecting comparable material from mature trees and the long history of planting of these economically important species. If the field botanist has to accept the possibility of planting he can no longer place much ecological significance on the presence or absence of one or other species in a particular site.

Anderson (unpublished) has studied the history of oak planting in Scotland in great detail. There appear to be old planting records in all the areas where oak woodland occurs today and there are many records in what now seem the most unlikely places by reason of their remoteness or the roughness of the terrain. Tansley (1939) evades the problems of planting by classifying the older oak woodlands as semi-natural and saying that a plantation on an oak site would eventually become indistinguishable from a natural wood; but he makes no stipulations about the provenance of the planting stock used to form the plantation. There is considerable evidence, discussed by Jones (*ibid.* pp. 175 and 215), to show that *robur* was consistently preferred for planting irrespective of the species originally occupying the site.

A majority of the older oakwoods remaining in Scotland include many stems which have patently developed from coppice stools. Some areas, as in the Trossachs, are known to have been under intensive coppice management (or coppice with standards) for long periods. Between 1600 A.D. and 1900 A.D. coppice management spread throughout Scotland, at first for rural produce and later for tan-bark production and charcoal for smelting. The woodlands least intensively managed are likely to have been those least accessible from the sea and the main land-routes; the north-shore oakwoods of some of the inland lochs of the north-west may come in this category. The youngest coppice woods date from the First World War but many still obviously coppice woods are more than twice that age. Generally few standards remain though large stumps often show that they were present. On the better sites stools have usually been singled but very few stems show conspicuously good form. Woods derived from coppice have an unnaturally high stocking of oak; other woody species (except hazel) have presumably been eliminated deliberately. High oak stocking could conceivably have been attained with natural regeneration alone, but it seems more likely that planting was frequently necessary.

Objects

The original objective, which led to the work described in this paper, was the location of oakwoods of indigenous Scottish stock. The immediate objective was a practical definition of *robur* and *petraea* in terms of suitable diagnostic characters. As will be seen, the work carried out to this end has gone a long way towards the next objective – to discover whether there were distinctive variation patterns within oak populations which could be used to assess their status.

Collecting methods and choice of diagnostic characters

Variation on the tree is considerable and if comparisons between trees are to be meaningful an attempt must be made to minimise variation from this source. A preliminary study was therefore made of variation patterns on the tree and through the growing season with the aim of determining the most reliable diagnostic characters and the best general collecting procedure.

While the results of this study suggest that there may be significant differences in the variation patterns of *robur* and *petraea* it is the resemblances that are more important at this stage before the species have been defined. The pattern of leaf variation on the sun-shoot, for example, is remarkably consistent. There is a gradation from small basal leaves which are rather irregular, comparatively broad with deeper lobes, more ovate and have a more cordate base, through larger mid-shoot leaves to the apical leaves which are also smaller than average but are more regular, narrower with shallower lobes, more obovate and have a less cordate (or even cuneate) base. Mid-shoot leaves are most representative and also show the best auricle development. On horizontal shoots leaves arising from the under side are larger. A trial was made using two mid-shoot leaves for biometric measurements. A comparison of average figures for all leaves with those obtained from pairs of mid-shoot leaves can be made in Columns A and B of Table 1 below.

Table 1
Variation of leaf-length and petiole-length with position on the tree

Tree No.	*Part sampled*	*Leaf-length* (mm) A*	B	*Petiole-length* (mm) A	B	*Petiole %* A	B
1. *petraea*	Lower crown—W	80·2	92·0	9·4	10·3	11·7	11·2
(isolated)	Lower crown—N	82·1	91·9	9·2	10·2	11·2	11·1
	Lower crown—E	76·3	88·4	9·9	12·2	13·0	13·8
	Lower crown—S	74·7	86·7	12·3	14·4	16·5	16·6
2. Hybrid	Lower crown—W	90·4	107·1	6·3	7·5	7·0	7·0
(*robur* affinity)	Lower crown—N	89·4	100·0	6·7	7·1	7·5	7·1
	Lower crown—E	97·0	106·3	8·0	8·5	8·2	8·0
	Lower crown—S	96·3	104·4	6·9	7·1	7·2	6·8
3. *robur*	Lower crown—N	72·8	86·2	3·9	4·9	5·4	5·7
(isolated)	Lower crown—S	86·3	102·9	4·6	6·2	5·3	6·0
4. *robur*	Top of crown		76·8		2·6		3·3
(NW of a	Upper crown—SSE		77·3		2·6		3·6
large gap)	Lower crown—SSE		85·0		2·4		2·8
	Inside crown (shade shoots)		101·8		3·5		3·4
	Epicormic shoots		99·8		3·0		3·0

*A – Averages for all leaves on 5 representative terminal shoots (sun-shoots except as indicated).
B – Averages for two mid-shoot leaves from each of the shoots (ten leaves).

These data show that there is marked variation with position on the tree; the collecting position should thus be standardised. The south-east aspect was eventually chosen because it appeared that the difference in petiole-length for *robur* and *petraea* would then be greatest. The figures also suggest a relationship between leaf dimensions and insolation or exposure.

For a study of variation through the growing season 12 trees were selected in Dalkeith Old Wood. This wood includes both *robur* and *petraea* with many intermediate types (see Table 3 below). Collections were made at the same point (SE of the accessible part of the crown) at increasing intervals from the time the buds began to swell. The pertinent observations from these data were :

(a) abaxial stellate pubescence remained substantially the same from the time the leaf was fully expanded till it fell in autumn even though scored from different leaves at each collection,

(b) buds of all specimens were small and obtuse at first – only towards autumn were *robur* and *petraea* types readily distinguishable,

(c) flowering peduncles reached their maximum length about mid-June but continued to increase in diameter for several weeks,

(d) after July the peduncle beyond the most distal developing acorn shrivelled and sometimes fell off; it follows that total length of fruiting peduncle must be an unreliable character for comparative purposes,

(e) during the same period the peduncle became more woody at the base and decreased in diameter roughly to the same extent as peduncles collected in July (after drying),

(f) peduncles of all specimens were densely pubescent at first; aff. *robur* forms were practically glabrous by mid-June; on aff. *petraea* forms the pubescence persisted at least on those parts protected from rubbing,

(g) peduncle length, particularly on aff. *robur* forms, could show considerable variation on the tree and sometimes on the shoot.

The period available each year for collecting ran from mid-June till early October. It was desirable therefore to select characters which would be comparable throughout this period. Leaf characters were suitable but buds and the acorn with its fruiting peduncle were not. In view of the importance attached to peduncle characters in diagnosis alternative biometric measurements were investigated. Length to the first flower locus proved very satisfactory; it does not change as the acorns develop and the flower bract persists even if the fruit does not develop; using this character the proportion of nominally fertile specimens is increased and better separation of typical *robur* and *petraea* is obtained. As both peduncle pubescence and peduncle diameter seemed promising diagnostic characters, collecting was planned to start not earlier than mid-July.

The following characters were eventually selected for recording : leaf length, petiole length, auricle type, abaxial stellate pubescence, lobe number, lobe depth, length of peduncle (total and to the first bract), peduncle diameter and peduncle pubescence.

Field collections were made with a pole-cutter reaching to twenty feet. A small branch was cut and a fertile (if present) terminal sun-shoot selected as typical of such shoots on it. Two representative mid-shoot leaves were detached and pressed and dried separately. After measurement shoots and leaves were mounted and retained for reference. Collection presented no problems in the open or scrub woods which predominate in Scotland. In woods with a closed high canopy samples had to be taken from the nearest gap at paced intervals or along roads and rides running roughly east-west. In a few woods sampling had to be done along the southern margin after checking that these marginal trees were similar to those inside the wood.

In practice it was some time before the importance of taking a satisfactory population sample was appreciated. Many of the earlier collections were rather small and some were selective. Collections have now been made in 127 different woods well distributed throughout Scotland (details appear in the *Forestry Commission Research Reports* for 1961 and

1962) and 55 of them include sufficient fertile specimens, systematically collected, for complete analysis as population samples on the lines described below.

ANALYSIS

Of the characters recorded as continuous variables only petiole (as petiole % of leaf length) and peduncle length (to first bract) provided reasonable separation of typical examples of *robur* and *petraea;* leaf length, lobe number and lobe depth all provided minimal separation. Six characters were thus used, the two above (the primary characters) and four secondary characters – auricle type, stellate pubescence (abaxial), peduncle pubescence and peduncle diameter. The latter were first studied in some detail to determine which parts of their ranges were diagnostic of one or other species. Arbitrary limits were set and then each character was considered in turn, but only for those specimens for which all the other characters were positively diagnostic of *robur* or *petraea.* Each reappraisal was followed if necessary by reclassification and the process repeated until no further adjustment of limits was required. The definitions arrived at may be seen in Table 4. A specimen showing all four secondary characters within the diagnostic range for one species belongs to what is hereafter called the Theoretical Species Type (or TST). A specimen showing one character in the indeterminate range lies within the apparent normal range of the species but may not belong to it if the difference is actually due to hybridisation. The four characters each with a *robur*, indeterminate and *petraea* range provide 81 (3^4) possible combinations which can be classified according to their differences from either TST.

TABLE 2
Classification of Secondary Character Combinations

Character Combinations	*Secondary character combination classes*								
	I	II	III	IV	V	VI	VII	VIII	IX
	Theoretical *petraea* combination	Degrees of difference							Theoretical *robur* combination
		1	2	3	4				
					4	3	2	1	
Possible	1	4	10	16	19	16	10	4	1
Actual	1	4	10	13	18	14	10	4	1

The number of combinations which can appear in a population sample is determined by the variability of the population sampled and the sample size. However, quite a small sample (15-20 specimens) is likely to show the range of combination classes present in the population. A general picture of the variability in Scottish oakwoods is conveniently presented in terms of the range and frequency of these combination classes.

If obvious plantations are excluded a majority of the woods sampled fall into category A below; aff. *petraea* forms predominate, while aff. *robur* forms (Classes VIII & IX) are absent. Intermediate forms (Classes III-VII) dominated 15 woods (category B), two of them plantations. Only 8 woods fell in category C (*robur* woods) and 4 of these were obvious plantations; collectively they included a much higher proportion of intermediate classes than the *petraea* woods. The mixed woods (category D) totalled 7; they were distinctive in having both aff. *robur* and aff. *petraea* forms but without a complete series of linking intermediate classes. One of them (Knockman Wood, Galloway) was a rather poor plantation of *robur*

TABLE 3

Representative population samples classified on the range and frequency of their component secondary character combination classes

General category	*Wood sampled*	*O.S. Grid square*	*Combination classes – no. of specimens*									
			I	II	III	IV	V	VI	VII	VIII	IX	*Total*
A. *petraea*-dominated woods	Glentrool	NX	20	6								26
	Elgin	NJ	4	3	2							9
	Spean Bridge	NN	5	6	4	3						18
	Loch Sunart	NM	4	2	3	2	2					13
	Ptarmigan	NN	8	8	8	1	2	2	1			30
B. Dominated by intermediates	Kirkwood	NY			1	7	2	1	2	2		15
	Loch Katrine	NN		2	3	2	3	4	1	1		16
	Dalkeith	NT	1	1	3	9	6	12	9	7	2	50
C. *robur*-dominated woods	Erchless	NH				2	1	2	1	3	3	12
	Gourdie	NO					1	3	3	1	2	10
	Fearnoch	NM						2		3	1	6
D. Mixed woods	Aikieside	NT	9	2						1		12
	Tore of Troup	NJ	2	1		2		3	1	2	2	13
	Springkell	NY	3				1	5	5	2	4	20
Totals			56	31	24	28	18	34	23	22	14	250
Other population samples			122	103	58	57	66	37	58	49	21	571
All population samples			178	134	82	85	84	71	81	71	35	821

affinity bounded by a wall beyond which were a few remnant *petraea;* the few good *petraea* in the plantation may well have been natural seedlings. Another (Aikieside, Berwickshire) consisted mainly of good *petraea* derived from coppice, with scattered aff. *robur* trees which were probably planted in gaps at the same time as a neighbouring *robur* plantation was established.

The next step was the introduction of the primary characters, used as co-ordinates of scatter diagrams, to discover whether the TSTs themselves were discretely differentiated entities.

Fig. 1 shows that they are not; the distribution of values for each is strongly directional with a marked trend towards the concentration centre of values for the other TST and slight overlap. Classes II and VIII showed the same trend more strongly and the overlap was greater. There is in fact a fairly regular gradation right through from Class I (TST *petraea*) to Class IX (TST *robur*) when judged from the mean values for each class (see Fig. 1).

The combination classes are, of course, artificial aggregates of individuals drawn from many rather different types of population. It will only be possible to formulate ' normal ' limits of variation for either species in Scotland if populations can be found which exhibit them. The final test therefore lies in analysis of variation within populations. For this purpose pictorialized scatter-diagrams were used; they allow simultaneous appraisal of all the variables and the population samples do not need to be large or identical in size. The secondary characters were represented by the symbols shown in Table 4 below.

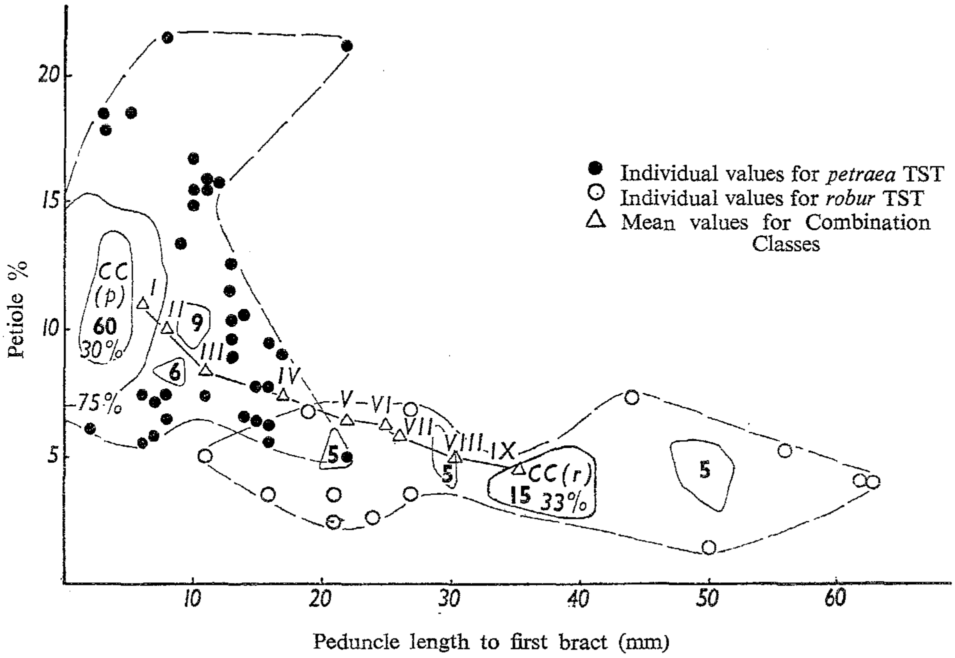


Fig. 1. Scatter diagram of combined petiole % and peduncle length values for all specimens classified as Theoretical Species Types (TSTs). Continuous lines enclose Concentration Centres (CC) for *petraea* (*p*) and *robur* (*r*). Broken lines outline the limits of variation of each TST.

Figures 2-7 show examples covering the range of woodland types. As might be expected from the analyses above, the greater the number of secondary character combinations in the sample, the wider is the scatter. The important observation here is that this principle applies also to the scatter of TST values. *If the TSTs from the more heterogeneous samples had been excluded in preparing Fig. 1 then they would have appeared as discretely differentiated entities.* The most homogeneous samples from *petraea*-dominated woods all include some individuals differing from the TST in one degree (Class II combinations) and all four possible variants occur. There are no equivalent samples from *robur*-dominated woods.

Discussion

These findings cannot be reconciled with the view Jones (1959) has expressed about the current status of *robur* and *petraea* in Britain. If they are acceptable taxa then these data show that the proportion of hybrids in Scotland is at least 50% and probably 75%. Alternatives which have not been seriously countenanced for a long time are (a) that the two taxa are not discrete entities and (b) that a third taxon, intermediate between *robur* and *petraea*, is involved. In spite of intensive collecting in reputed *robur* woods and plantations during 1961 the amount of *robur* material is only just adequate to demonstrate a concentration centre for combined petiole and peduncle values of the *robur* TST. Nevertheless it is fairly clear that two, and only two, taxa are involved in these data.

Introgressive hybridization (or simply 'introgression') was defined by Anderson (1949) as a natural process of gene exchange arising from repeated back-crossing between hybrids and the parent species. 'Introgression' is used here in the same sense, though the process is unnatural to the extent that it has been unintentionally accelerated by Man's activities. The variation described in Scottish oak populations is so exactly what would be

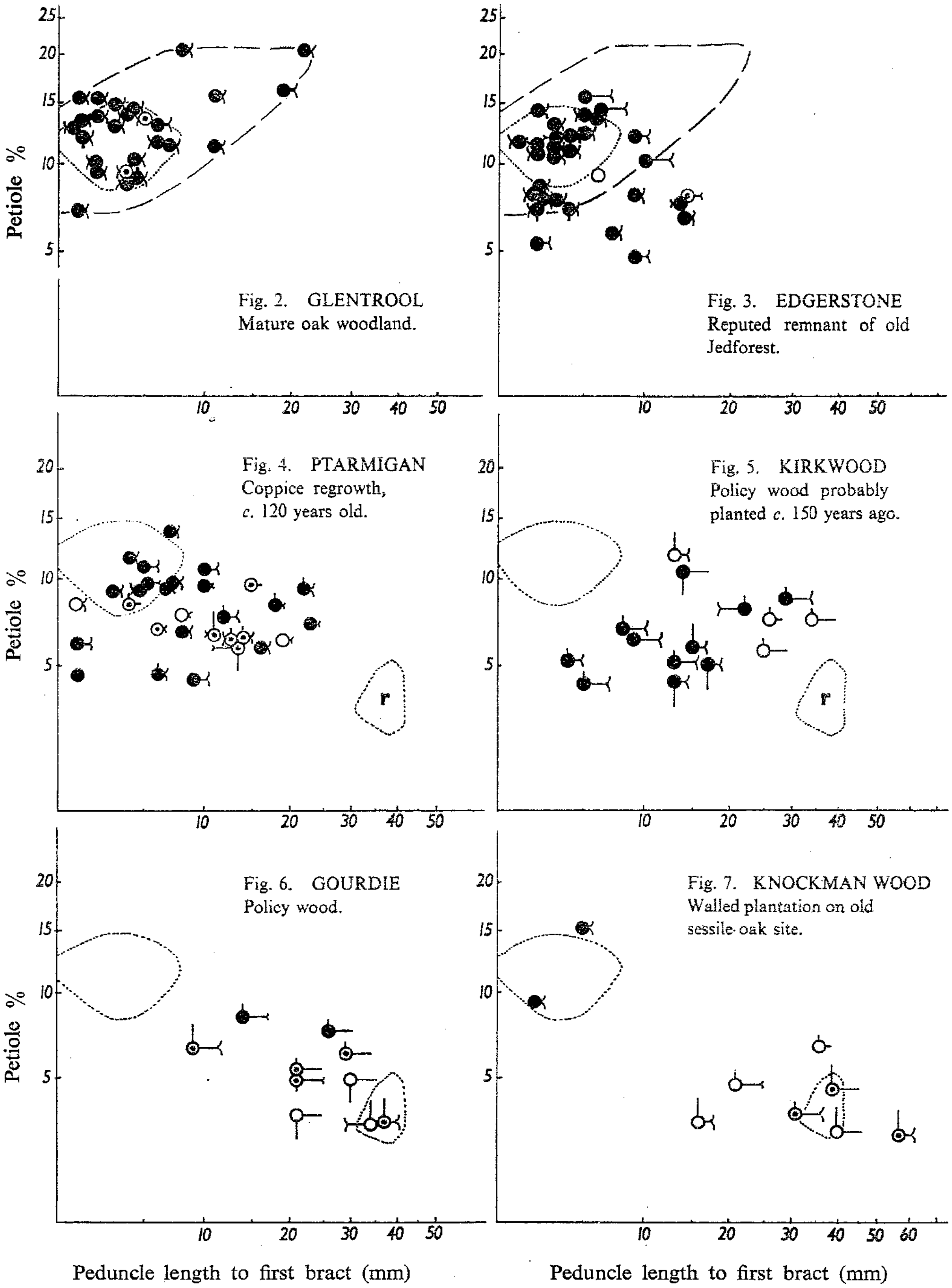
TABLE 4

The diagnostic ranges for secondary characters with symbols*

Character	*Diagnosis*		*Symbol*
1. ABAXIAL STELLATE PUBESCENCE Recorded separately for the small prostrate trichomes on the lamina and large erect trichomes beside the midrib.	Both types abundant	*petraea*	
	One type absent or one or both sparse	indeterminate	
	Both types absent	*robur*	
2. AURICLE TYPE Based on (a) the development of the basal lobes which in the extreme *robur* form overlap the petiole and (b) the sharpness of the reflexion of the lamina where it joins the petiole	Lobes weak (or nil); lamina not sharply reflexed	*petraea*	
	Medium lobes not reaching the petiole; lamina sharply reflexed	indeterminate	
	Lobes well developed reaching the petiole on at least one leaf; lamina sharply reflexed	*robur*	
3. PEDUNCLE DIAMETER Measured by gauge (cut to 1 mm, 1·5 mm and 2 mm) at the narrowest point below first bract	Stout 2 mm diam. or over	*petraea*	
	Intermediate *c.* 1·5 mm	indeterminate	
	Slender 1 mm diam. or less	*robur*	
4. PEDUNCLE PUBESCENCE Caducous pubescence lost by about mid-June. Persistent pubescence tending to rub off on all except very short peduncles	Very pubescent or pubescent at least on protected parts of peduncle	*petraea*	
	Trace of pubescence	indeterminate	
	Glabrous	*robur*	
Theoretical Species Combination		*petraea* TST	
Theoretical Species Combination		*robur* TST	

expected of two mutually introgressing species that conflicting evidence should be critically examined. The fertility barrier between the species demonstrated by Pyatnitski and Dengler is the only serious problem. This may be either not as important or not as generally applicable as workers in this field have assumed. Experimental crosses need to be made in other parts of the range of the two species and, possibly more important still, the success of back-crosses needs investigation.

* For a more detailed description of these characters with illustrations of auricle types see Cousens (1962)



Figs. 2-7. Scatter diagrams for six oak populations. Concentration Centres for *petraea* (from Fig. 10) and *robur* (from Fig. 1) are shown by dotted lines.

As Stebbins (1950) has pointed out oaks are long-lived and form more or less closed communities : interspecific hybrids becoming established in such communities will tend to be isolated among many individuals of the parent species and back-crosses rather than interhybrid crosses will be the rule : furthermore one hybrid is potentially capable of producing an enormous number of back-cross progeny during its lifetime. The interspecific fertility barrier may be relatively unimportant if the hybrids are fully fertile with either parent. Numerous examples of introgession in American oakwoods have already been cited (see Tucker & Muller 1958, Cottam, Tucker & Drobnik 1959, Tucker 1960 and Tucker 1961 for some recent examples).

The historical facts point to widespread and extensive planting activity with a strong preference for *robur* planting stock. *Q. robur* must have been introduced in this way into many areas where *petraea* dominated the natural woodland and the chances of the cross *robur* ♀ × *petraea* ♂ appearing must have been very high. Collection of acorns from these *robur* nuclei would have given the hybrids very favourable chances of becoming established as crop trees in new plantings, particularly if a proportion of them exhibited hybrid vigour (refs. in Dengler 1941). Reasons will be put forward below for believing that the F1 hybrid bears a strong superficial resemblance to *robur;* collection of acorns from such hybrids may frequently have been made in the mistaken belief that they were good *robur.*

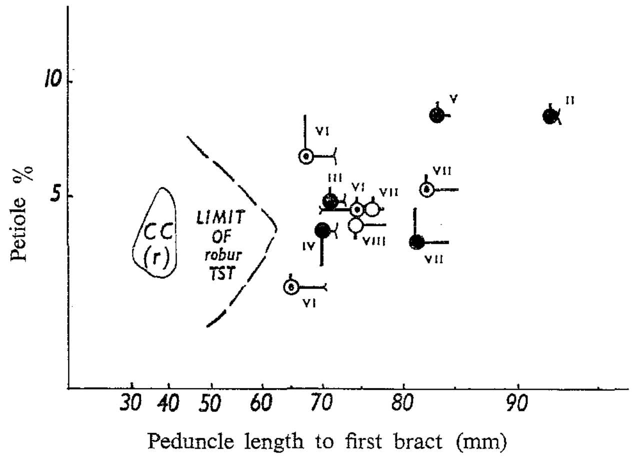


Fig. 8. Specimens with abnormally long peduncles.

The only suggestion of hybrid vigour in these data lies in eleven values for peduncle length to first bract beyond the range of the *robur* TST. They include 10 different secondary character combinations and every class from II to VIII is represented (Fig. 8).

The numbers of specimens recorded in the intermediate combination classes (III to VII) happen to be of similar magnitude (see Table 3). It seemed that analysis of the frequency with which *robur*, *petraea* and indeterminate characters appeared among these putative

TABLE 5

Frequency (%) of secondary characters in intermediate combinations

Character	*Auricle type*	*Abaxial pubescence*	*Peduncle diameter*	*Peduncle pubescence*
petraea	23	**40**	19	**48**
Indeterminate	**52**	31	28	36
robur	25	29	**53**	16

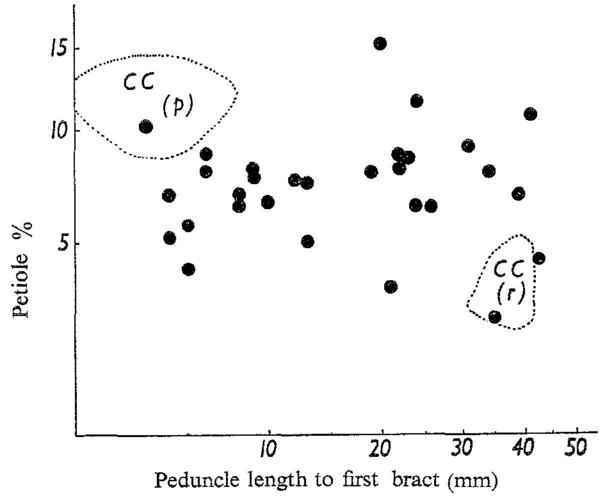


Fig. 9. All values for ? an F.1. hybrid

hybrids might yield significant results. Only auricle type shows a maximum in the indeterminate range, the expectation if the character is under polygene control. The other three characters appear to exhibit partial dominance for *petraea* pubescence of leaf and peduncle and *robur* slenderness of peduncle. If these conclusions are valid the interspecific hybrid will consist mainly of forms with medium auricles, well-developed abaxial pubescence and slender pubescent peduncles. This combination is in fact the most frequent one in these combination classes and provides the only example of an intermediate combination dominating a population sample (*viz.* Kirkwood – see also Table 3 and Fig. 5). Figure 9 is a scatter-diagram for all specimens showing this combination : it will be seen that they show extremely wide scatter in the zone between the concentration centres for the TSTs. This combination is also found in a form described as *Q. robur* subsp. *puberula* (Lasch) Weim. by Weimarck (1947) who noted several ' aberrant forms ' – a f. *brevipedunculata* and a f. *petiolaris* (suggesting that petiole-peduncle values for the sub species would also show very wide scatter) and a f. *longipedunculata* (for which an equivalent did not occur in these data though it might correspond to the forms tentatively suggested above as due to hybrid vigour). *Q. robur* subsp. *puberula* is reported from Norway (Risdal 1955) and is said to become more and more frequent eastwards through Scandinavia; it is also reported as fully fertile (Weimarck 1947). It is interesting to note that Høeg (1929) described the most easily recognisable interspecific hybrid as resembling *robur* but with abaxial stellate pubescence on the leaves.

On the question of hybrid fertility the data offer a little evidence through a comparison of fertile and non-fertile specimens in certain collections. All are from *petraea*-dominated woods (category A of Table 3). The above collections were all made in 1961 when fertile material, particularly of aff. *robur* forms, was less plentiful than in the unusually good fruiting years 1959 and 1960. The proportion of possible hybrids in the collections rises from 42% (22/52) to 57% (49/86) if infertile material is included. Consideration of fertile material alone will lead to an underestimate of hybridity.

It is strange that none of the samples from plantations proved to consist of good *robur* forms, for many of them must have been established with stock raised from the many large consignments of acorns known to have been imported from England and the Continent. Could it be that all importations of acorns have included a high proportion of introgressed stock ? Or was the late Professor Anderson correct in his contention that *robur* is not native in Scotland and that hybrids thrive better here than good *robur* ? Maxwell (1900)

TABLE 6
Percentage fertility by combination classes of auricle type and abaxial pubescence

	Ptarmigan		*Ross Wood*		*Loch Ard*		*Combined*		
	Total	*Fertile*	*Total*	*Fertile*	*Total*	*Fertile*	*Total*	*Fertile*	%
TST (*petraea*)	19	16	13	9	5	5	37	30	81
1 difference	12	6	3	1	8	5	23	12	52
2 difference	12	6	2	—	2	1	16	7	44
3 difference	7	2	—	—	1	1	8	3	37
4 difference	—	—	1	—	1	—	2	—	—
Totals	50	30	19	10	17	12	86	52	60

claimed that both *petraea* and hybrids were much superior to *robur* for planting in Scotland. Only one observation can be offered in this context, namely, that several old *petraea* woods are growing on very heavy clays where *robur* might have been expected if it were native.

The wider implications of the introgression hypothesis extend into the realms of pure speculation. Widespread planting of oaks in the past would have accelerated any introgression that was in progress, but has there been enough time (perhaps nine centuries) for planting to be held completely responsible ? One of Tucker's examples of introgression (Cottam, Tucker & Drobnik 1959) is traced back to the Miocene era. In Scotland introgression could not date back much before the Climatic Optimum some 5,000 years ago. It is possible that *robur* reached Scotland naturally in the more favourable climate of those times.

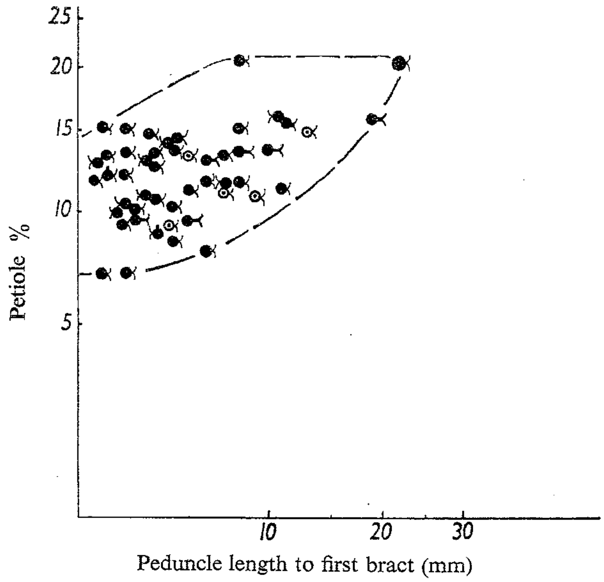


Fig. 10. Scatter diagram for the four most homogeneous *petraea* samples combined.

CONCLUSIONS

Q. robur and *Q. petraea* seem likely to be good taxa but they are very hard to define in Scotland, mainly because there are no obvious natural populations in which to assess the normal ranges of variation of the species. Striking variation patterns are found in Scottish oakwoods but practically all the variation can be completely accounted for by postulating (a) limited interspecific hybridization and (b) extensive introgression initiated or accelerated by Man's planting activities.

TABLE 7

Variation recorded in the most homogeneous samples from *petraea* woods in Scotland‡

		Glentrool SW Galloway	*Aikieside*† *SE Coastal*	*Cheviot SE Borders*	*Menstrie E. Central Ochils*	*Combined Totals*
Elevation		*c.* 250 ft (75 m)	*c.* 200 ft (60 m)	*c.* 600 ft (180 m)	*c.* 500 ft (150 m)	
No. of specimens		26	11	6	6	49
Leaf-length[+] (cm)	range	8·5–15·2	7·5–14·7	7·4–11·3	8·4–10·4	7·4–15·2
	mean	11·4	10·6	9·6	9·9	10·8
Petiole-length[+] (mm)	range	7·5–32·0	8·0–19·0	7·0–17·0	9·0–14·0	7·0–32·0
	mean	14·2	12·6	12·3	11·8	13·3
Petiole %[+]	range	7·0–21·5	7·0–16·0	9·5–15·2	9·7–13·8	7·0–21·5
	mean	12·6	11·5	12·3	11·8	12·2
Pairs of lobes[+]	range	4·3–7·0	4·3–5·8	4·0–6·0	4·0–7·0	4·0–7·0
	mean	5·5	5·0	5·2	5·4	5·3
Lobe depth %[+]	range	29–57	27–44	24–59	34–60	24–60
	mean	38	35	44	43	38·7
No. with deficient abaxial pubescence		2	2	1	—	5
Auricle type	nil	24	4	10	6	44
	weak	26	18	2	6	52
	medium	2	—	—	—	2
Peduncle[×] total length (mm)	range	3–48	6–34	9–34	2–21	2–48
	mean	14·4	17·5	21·0	9·7	15·3
Peduncle[×] length to first bract (mm)	range	1–22	3–11	2–13	1–10	1–22
	mean	5·3	5·8	5·7	4·3	5·3
No. with peduncle[×] diameter intermediate		2	—	1	3*	6
No. with only trace of peduncle pubescence		—	—	—	—	—

* a rather early collection   + mean for two mid-shoot leaves   × longest peduncle on specimens

†ignoring the one obviously non-*petraea* individual

‡ For illustrations showing the range of leaf variation in these samples see Cousens (1962)

Six homotypic characters have been tentatively defined. All are independent variables judging from the high proportion (93%) of the possible character combinations occurring. For each one normal variation in certain directions is indistinguishable from that due to introgression and all six characters appear to be needed to define the taxa. In terms of these characters there are a few woods for which the population samples are reasonably homogeneous and without an introgressive trend in their scatter-diagrams (Fig. 10). They are all *petraea* woods; variation in them is summarized in Table 7. They provide the best material available in these data on which to base a description of *petraea* in Scotland.

There seems little prospect of getting similar material in Scotland for *robur*.

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