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Variation of morphological and chemical characteristics of acorns from populations of *Quercus petraea* (Matt.) Liebl., *Q. robur* L. and their hybrids

P. C. BROOKES* and D. L. WIGSTON†

Department of Biological Studies, Lanchester Polytechnic, Coventry

ABSTRACT

Variation of morphology and inorganic nutrient content within and between natural populations and individuals of *Quercus petraea* (Matt.) Liebl., *Q. robur* L. and *Q. petraea* × *Q. robur* (*Q.* × *rosacea* Bechst.) is described. It is concluded that acorn shape and size are unreliable discriminants between the two oak species, and also between them and their hybrids. No significant differences in N, P, K, Ca, Mg and Na content of *Q. petraea* and *Q. robur* were detected, although the usually smaller acorns of *Q. petraea* clearly illustrate the tendency of both species to have higher concentrations of elements in acorns below 0·2 g cotyledon dry-weight. No regularity in the occurrence of years of high acorn productivity ('mast' years) and little or no productivity ('blank' years) was discovered.

INTRODUCTION

The acorn is the fruit of the oak—a nut which is partially enveloped by a cup formed at the base. In the literature on the native species of oak, *Quercus petraea* (Matt.) Liebl. and *Q. robur* L., reference is made to variability in form and production of acorns, but the nature and extent of this variability is rarely defined. Acorn fall and viability have been examined (e.g. Ovington & Murray 1964, Shaw 1968a, 1968b) and also subsequent seedling establishment and regeneration potential (e.g. Jarvis 1963, Shaw 1968a). These reports refer to *Q. petraea*; little attention has been paid to *Q. robur*, which is surprising considering that *Q. robur* acorns have been favoured for planting in the past (Jones 1959) although today *Q. petraea* is preferred (Penistan 1974). Rushton (1977) distinguished between acorns collected from natural populations and artificially produced acorns from crossing experiments. He pointed out that differences recorded by him in acorn shape between the parent species and F_1 hybrids from controlled crossing experiments were consistent with published accounts, whereas those recorded by Wigston (1971) from field collections might be attributed to differential growth markedly influenced by external factors.

In this paper the following characters of acorns are examined:

1. development and fall,
2. fresh-weight/dry-weight relationships,
3. size and shape,
4. nutrient content (cotyledon potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), nitrogen (N), sodium (Na)).

Variation in these characters is examined at the following 'levels':

A. between acorns of a single tree,
B. between different trees of the same population,
C. between different populations from the same local area,
D. between different populations from different regions of the British Isles.

Each of A–D is considered both within a single year and between years.

* Present address: Soils and Plant Nutrition Department, Rothamstead Experimental Station.
† Present address: School of Environmental Sciences, Plymouth Polytechnic.

TABLE 1. ACORN PRODUCTION IN SAMPLE SITES

Site	Period of observation	Acorn production
(a) Sites on acid peat among granite clitter, Dartmoor, (*Q. robur*)		
Wistman's Wood, GR 20/613.773, v.c. 3	1965–69	1965 & 69; early seed development aborted by autumn
		1966 & 68; no seed production or development
		1967 ; moderate crop of small acorns
	1971–74	1971 ; moderate crop of small acorns
		1972 ; no seed production or development
		1973 ; early seed development aborted by autumn
		1974 ; poor crop of very small acorns
Higher Hisley, GR 20/781.800, v.c. 3	1965–68	1965 ; moderate crop of small acorns
		1966 & 68; poor crop of small acorns
		1967 ; good crop of small acorns
	1972–74	1972 ; poor crop of small acorns
		1973 & 74; good crop of smallish acorns
(b) Mixed woods with hybrids on the margins of the Dartmoor granite		
Dean Wood, GR 20/705.646, v.c. 3	1969	1969 ; moderate crop of variable acorns
Meldon Wood, GR 20/ 564.923, v.c. 4	1969	1969 ; moderate crop of variable acorns
(c) Largely *Q. petraea* woods on the margins of the Dartmoor granite		
Steps Bridge, GR 20/804.886, v. c. 3	1965–67	1965 ; poor crop of normal-sized acorns
		1966 & 67; moderate crop of normal-sized acorns
	1972–74	1972 ; no seed production or development
		1973 ; poor crop of normal-sized acorns
		1974 ; moderate crop of normal-sized acorns
Yarner Wood National Nature Reserve, GR 20/777.808, v.c. 3	1972–74	1972 & 73; no seed production or development
		1974 ; good crop of normal-sized acorns
(d) *Q. robur* wood on abandoned coal waste, Warks.		
Alvecote Pools Nature Reserve, GR 43/255.045, v.c. 38	1972–74	1972 & 74; good crop of normal-sized acorns
		1973 ; good crop including very large acorns
(e) Mixed Wood including hybrids, Staffs.		
Leek Nature Reserve, GR 43/005.525, v.c. 39	1973–74	1973 ; moderate crop of normal-sized acorns
		1974 ; very little seed production or development

TABLE 2. COMPARISON OF FIVE ADJACENT TREES, *Q. ROBUR*, ALVECOTE POOLS NATURE RESERVE

Tree	Acorn size range (g) 1973	Acorn size range (g) 1974	Acorn shape range 1973	Acorn shape range 1974
15	No crop	0·50–3·0	No crop	1·60–2·20
15a	(3–4·5) 6·0–12·0	0·10–3·05	1·30–1·75	1·00–1·40
15b	2·5–5·5	No crop	1·20–1·50	No crop
15c	3·0–6·0	No crop	(1·15-)1·40–1·70	No crop
15d	3·0–8·5	0·5–4·5	1·15–1·55	1·05–1·40

SITES, MATERIALS AND METHODS

Acorns were collected from sites in N. and S. Devon, v.c. 3 & 4, Warks., v.c. 38, and Staffs., v.c. 39, between 1965 and 1974 (Table 1). Populations and individual trees were identified by leaf character analysis (Wigston 1975). In 1973 and 1974 it was possible to pick acorns from individual trees at Alvecote Pools Nature Reserve, but in all other years and for all other populations acorns had fallen prior to collection.

The acorns were collected for seedling growth trials (Wigston 1971, Brookes 1976) and thus observations were made on fresh material. However, nutrient and dry-matter analysis of seedling growth required destructive sampling, and *estimates* of initial cotyledon dry-weight and nutrient content are required. Acorns, like most fruits and seeds, lose moisture until ripe; extreme desiccation leads to loss of acorn viability, particularly if they 'chit' (showing pre-dormancy radicle emergence). Acorns were therefore collected at or as soon after acorn fall as possible, and stored in damp absorbent material. Damp *Sphagnum* and vermiculite are suitable, and partially dried acorns quickly regain moisture and retain viability (Wigston 1971).

Dry-weight was determined after heating at 105°C to constant weight. The nutrient content of cotyledon pairs was determined by dry-ashing at 450°C, dissolving the residue in 0·6N HCl prior to suitable dilution (Brookes 1976). Cotyledon K, Ca, Mg and Na were determined by atomic absorption spectrometry (Price 1972). P was determined colorimetrically (Olsen & Dean 1965) and N by Kjeldahl digest (Bremner 1965) followed by ammonia probe measurement (Brookes 1976).

ACORN PRODUCTION

The term 'mast' is a general term for fruit of the Fagaceae, especially implying 'pannage'–food for swine. In the literature on native oak, 'mast years' are referred to, when acorns are produced in substantial quantities. Conversely 'blank years', such as 1972, are reported, when acorn production is low or non-existent throughout much of Great Britain (Penistan 1974). Rushton (1977) attributed different success rates of artificial crossing in 1969–71 to different amounts of acorn production between years. Some authors refer to 'cycles' of mast and blank years (e.g. Jones 1959, Penistan 1974) implying *regular* alternation of acorn production and non-production.

The data of Table 1 show that for the sites investigated mast and blank years do occur, but these are not necessarily the same for different populations and differences occur between *Q. petraea* and *Q. robur* populations. There is no indication of 'cycles' of acorn production. Also a distinction must be made between blank years with no initial acorn development and those where a substantial number of developing acorns abort. Acorn crops also vary between trees of the same species in homogeneous populations. A group of five adjacent trees at Alvecote Pools Nature Reserve showed considerable differences between each other in acorn production and morphology in 1973 and 1974 (Table 2).

FRESH-WEIGHT/DRY-WEIGHT RELATIONSHIPS

Fresh-weight/dry-weight relationships for *Q. petraea* and *Q. robur* acorns (treated to avoid desiccation) show good correlation between the two variables. Fig. 1 is a scatter diagram illustrating this for 1973. The two species differ in size range, but the proportions of water content are the same. However, exceptionally small *Q. robur* acorns obtained from Wistman's Wood in 1974 gave a much higher water content per unit cotyledon weight than acorns in normal size ranges. This appears to be due to testas which are relatively thick compared with the cotyledons.

It is necessary to establish this fresh-weight/dry-weight correlation in order to *estimate* the initial cotyledon *dry*-weight from total *fresh*-weight in seedling growth trials.

ACORN MORPHOLOGY

Q. robur is stated to have large elongate acorns, whereas those of *Q. petraea* are smaller and rounded (Jones 1959).

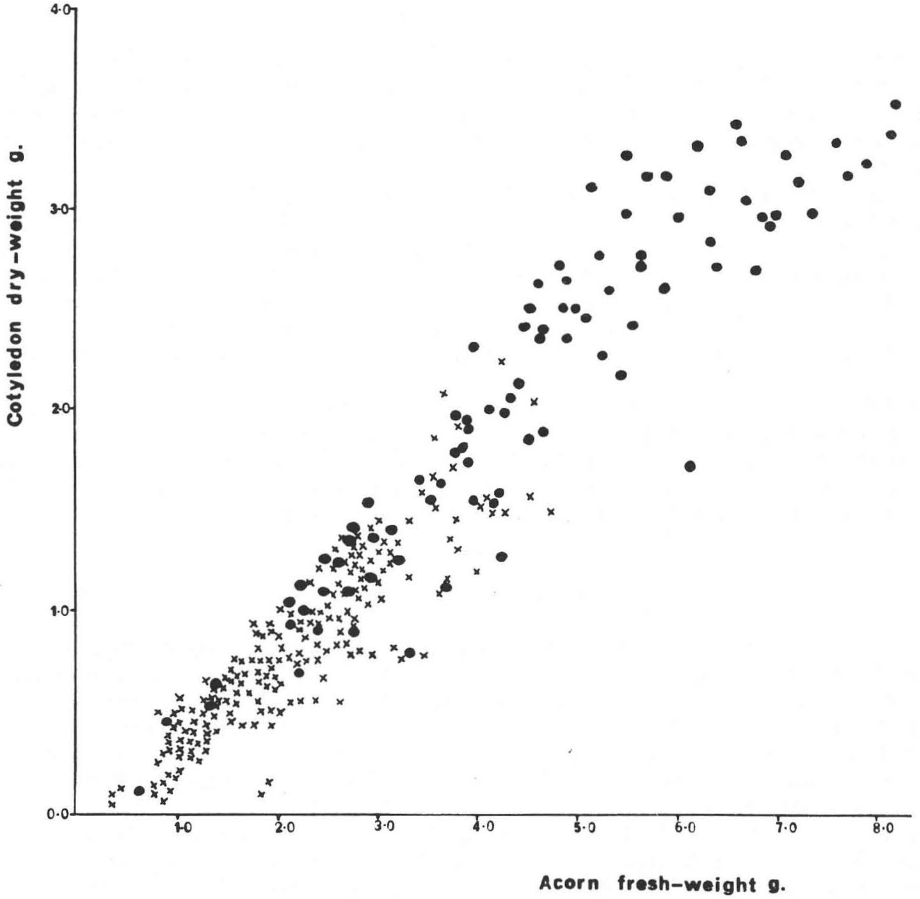

FIGURE 1. Scatter diagram of fresh-weight/dry-weight, 1973; circles – *Q. robur*, crosses – *Q. petraea*.

Figure 2 shows frequency distributions of acorn fresh-weights for *Q. petraea* and *Q. robur* populations sampled in 1973. Although the modal values are distinct there is much overlap. The acorn sizes of most populations are normally-distributed (Wigston 1971) but some have 'skew' distributions. For example, some trees at Alvecote Pools Nature Reserve in 1973 produced exceptionally large acorns (Table 2). The high-level oakwoods of the Dartmoor granite rarely produce good acorn crops, the many blank years being often due to abortion of developing acorns; when acorn crops are produced, the acorns are usually very small (Fig. 3A) and of low viability. These very small Dartmoor *Q. robur* acorns are rounded (wider than long) – a shape diagnostic for *Q. petraea* (Fig. 3B). This could suggest that acorn shape is more a function of size than a reflection of genetic differences.

In populations dominated by trees of hybrid status, such as Dean Wood and Meldon (Table 1), intermediate and bimodal size and shape distributions are obtained. In artificial crosses Rushton (1977) reported that the acorn shape of hybrids fell midway between that of *Q. petraea* and *Q. robur*, but was very variable and considerably overlapped the ranges shown by the parent species. The hybrid acorns were generally smaller than either species. Experimental crosses have low fertility (Rushton 1977) but trees diagnosed as hybrids on morphological characters can produce substantial crops of acorns (Wigston 1971, 1974).

As with other taxonomic characters (Jones 1959), acorn shape is more variable in *Q. robur* than *Q. petraea*, but so also is the size range.

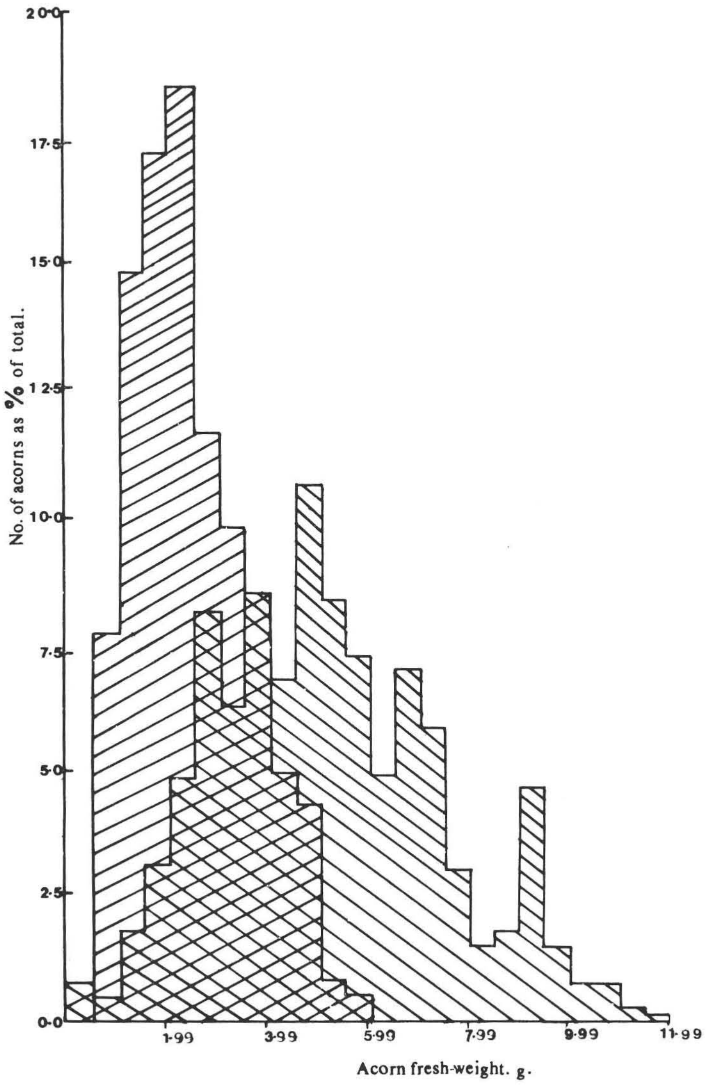

FIGURE 2. Acorn fresh-weight distributions, 1973; right-hand peak – *Q. robur*, left-hand peak – *Q. petraea*.

VARIATION WITHIN POPULATIONS

Table 2 shows data for five adjacent trees at Alvecote Pools Nature Reserve for 1973 and 1974. The remarkably large acorns produced by trees 15a and 15d in 1973 did not occur in 1974 (Fig. 4). Trees 15b and 15c produced similar frequency ranges of normal-sized acorns in 1973, but those of 15c were much more elongate than those of 15b. The crop for tree 15 in 1974 had remarkably elongate acorns for their size, which was at the lower end of the normal *Q. robur* range.

Table 3 shows 1973 data for five areas at Steps Bridge which differ in aspect, exposure, slope and soil-type. Although within the normal ranges for *Q. petraea*, the five samples show considerable variation between each other in size and shape.

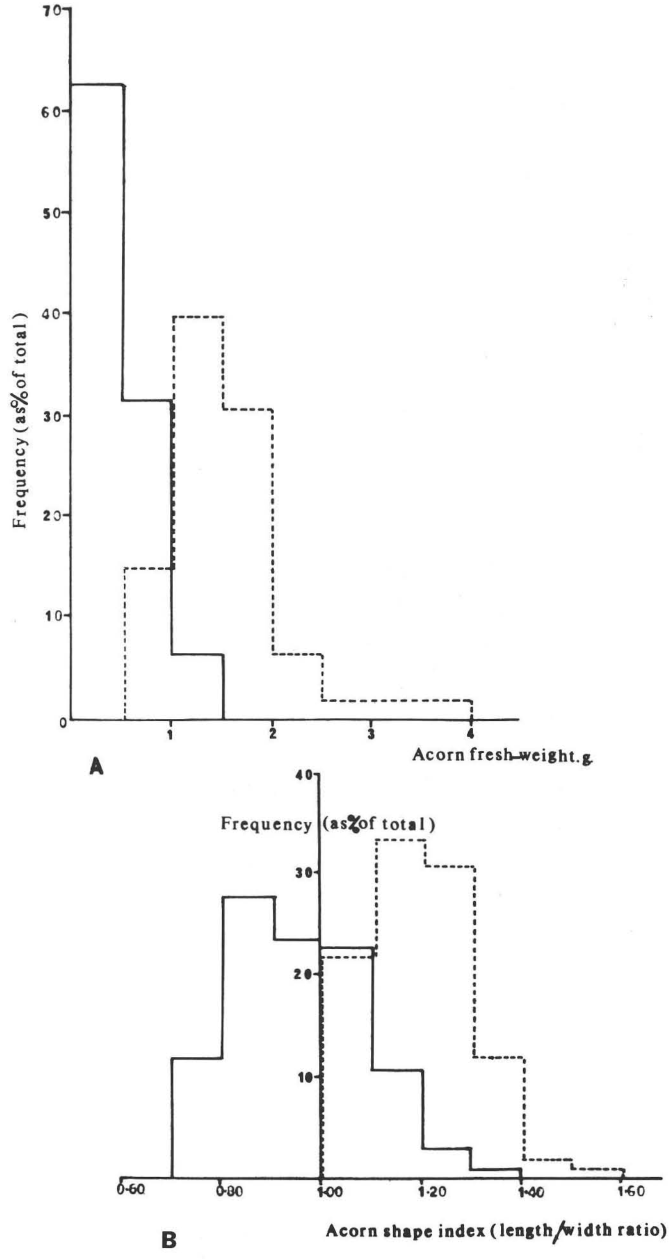

FIGURE 3. A. Acorn weight distributions; B. Acorn shape distributions. Dotted line – Wistman's Wood 1967, solid line – Wistman's Wood 1974.

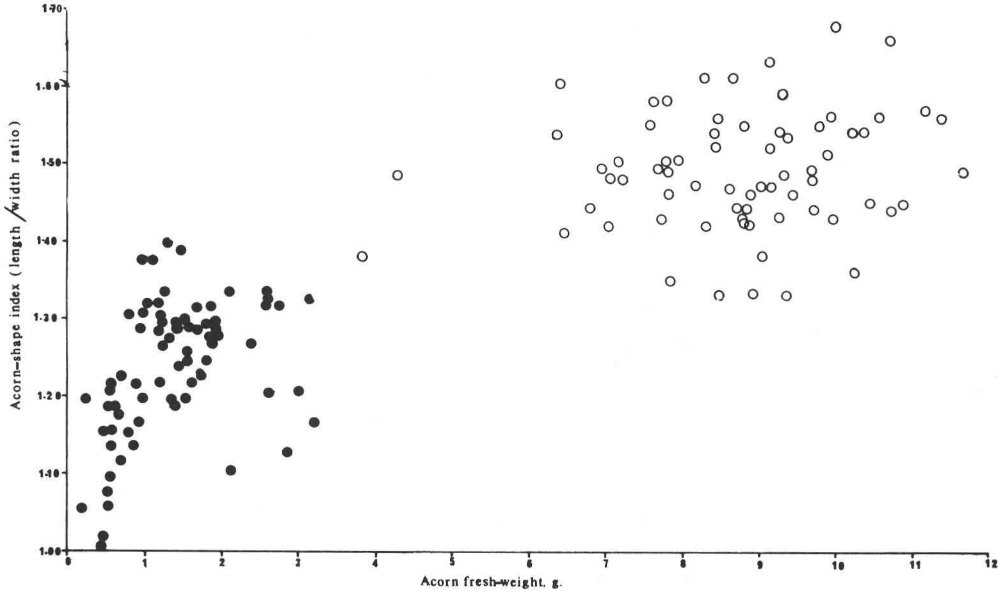

FIGURE 4. Alvecote Pools Nature Reserve, tree 15a (*Q. robur*). Scatter diagram of acorn shape/acorn fresh-weight; closed circles – 1974, open circles – 1973.

TABLE 3. COMPARISON OF FIVE AREAS AT STEPS BRIDGE, *Q. PETRAEA*, 1973

Area	Acorn size range (g)	Acorn shape range
1. Mid-valley bottom (roadside)	0·5–6·0	1·00–1·60 (-1·80)
2. Lower valley, steep north-facing slope	0·1–5·0	1·00–1·80
3. Level area between upper and lower steep north-facing slopes	0·1–4·5	1·00–1·75 (-1·85)
4. Upper valley, steep north-facing slope	0·1–3·0 (3·5–4·5)	1·00–1·80
5. Valley bottom	1·5–6·0	1·05–1·50

TABLE 4. MEAN ACORN NUTRIENT CONCENTRATIONS AND RANGES (mg nutrient g^{-1} cotyledon), ALL POPULATIONS, 1973

	Q. robur	*Q. petraea*
N	15·3, 9·4–21·4	12·6, 8·5–17·7
P	1·60, 0·81–2·45	1·65, 0·56–2·04
K	11·70, 5·14–16·17	9·57, 6·50–21·30
Ca	0·79, 0·35–1·56	2·27, 0·42–3·40
Mg	0·79, 0·39–0·98	0·83, 0·46–1·58
Na	0·34, 0·14–1·11	0·17, 0·11–1·07

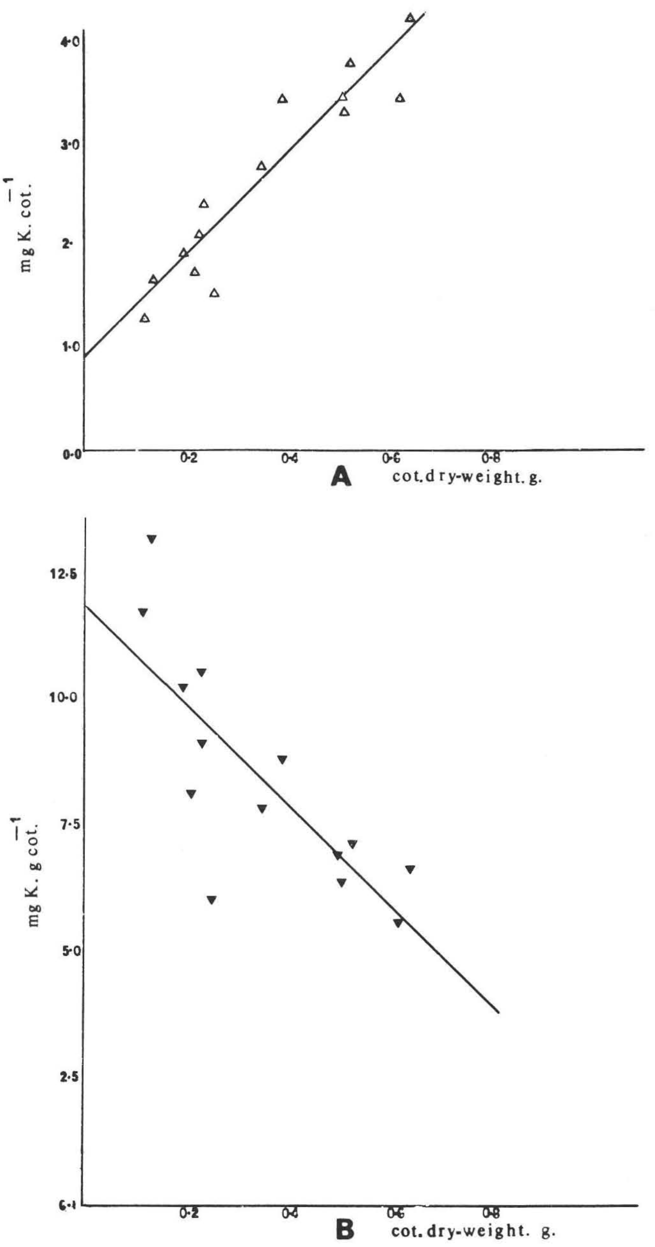

FIGURE 5. Cotyledon K content of *Q. petraea* from Yarner Wood. A: mg K. cotyledon^{-1} against cotyledon dry-weight, $r = 0{\cdot}94$, $p < 0{\cdot}05$, $y = 5{\cdot}0x + 0{\cdot}92$. B: mg K. g cotyledon^{-1} against cotyledon dry-weight, $r = -0{\cdot}79$, $p < 0{\cdot}05$, $y = 11{\cdot}96 - 9{\cdot}90x$.

COTYLEDON NUTRIENT RESERVES

Studies of mineral nutrient metabolism of developing seedlings (e.g. Ovington & MacRae 1960, Newnham & Carlisle 1969) have used acorns of very limited provenance and morphology, usually at our level of variation 'A' only. Brookes (1976) carried out determinations of N, P, K, Ca, Mg and Na levels of cotyledon pairs from acorns from a range of sites, prior to trials which examined seedling growth and nutrient metabolism at levels of variation from A to D. Table 4 shows data for the above elements for 1973. High K content is characteristic of both *Q. petraea* and *Q. robur* acorns, but the difference between the two species in mean values and range for all six elements are not significant. As expected, for all elements, with increasing acorn size (expressed as cotyledon dry-weight) total nutrient content increases. Fig. 5A shows this relationship for K in *Q. petraea* acorns. However, the relationship is more variable for Ca and Na in both species.

If the amount of nutrient per unit cotyledon dry-weight is considered (Fig. 5B), the data show that as acorn size *decreases*, the proportions of nutrients *increase*, departing from linearity below cotyledon dry-weight of 0.2 g. This is most marked in the normally smaller acorns of *Q. petraea* (Brookes 1976).

DISCUSSION

Individual trees show marked variation in acorn morphology within and between years, and different trees of the same population may yield acorns substantially different in the same year. Also there are clearly marked differences between acorns from controlled crossing experiments (Rushton 1977) and collections from natural populations (Wigston 1971, Brookes 1976). The reported differences between *Q. petraea* and *Q. robur* acorns in size and shape do appear in this investigation, but there is so much variation within and between populations and individuals of both species and their hybrids that we do not consider acorn morphology to be a reliable discriminant between *Q. petraea* and *Q. robur*, or between them and their hybrids.

Some authors (e.g. Jones 1959, Penistan 1974) refer to cycles of mast and blank years, but their occurrence is in fact irregular, and the term cycle should not be used. Blank years can apply to individual trees within a population where overall acorn production is high (Brookes 1976) or to local populations in a region exhibiting a good mast year (Wigston 1971).

Few differences in acorn nutrient concentrations between *Q. petraea* and *Q. robur* were observed, and in view of the large number of acorns analysed it is likely that there are no significant differences between the two species in this respect. An interesting feature of the data is that acorn nutrient *concentration* is greater in small acorns than large ones for an individual tree or population, although large acorns have greater *amounts* of these nutrients than small ones.

CONCLUSIONS

The purpose of this study of acorn morphological and chemical characteristics was to establish the nature and range of variation within and between populations and individuals of the two British oak species and their hybrids, prior to seedling growth trials. In our opinion, results based on samples of restricted provenance and size (e.g. those obtained by Jarvis 1963, Ovington & MacRae 1960, Newnham & Carlisle 1969) cannot be regarded as providing valid evidence of variation in nutrient reserves and subsequent seedling response, or account for the differences between the growth of *Q. petraea* and *Q. robur* described by Brookes (1976).

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