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'Shake' defects and wood structure variations in British oaks (Quercus SPP.).

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'SHAKE' DEFECTS

AND WOOD STRUCTURE VARIATIONS

IN BRITISH OAKS (*QUERCUS* SPP.).

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A B S T R A C T .

The overall aim was to gain information required for improvement of wood quality in British oaks (Quercus robur and Q. petraea). Specific aims were 1) to investigate the nature and incidence of shake in British oaks; 2) to quantify variations in oak wood structure and properties, identifying which characteristics are under genetic control and which associated with growth rate; 3) to make prescriptions for selection and silviculture of oak, with a view to improving wood quality in future British crops.

Site surveys (including soil analyses) of 42 woodlands were carried out. An index of severity was devised to standardise shake assessment within individual trees. Wood structure was analysed in oaks from shake-prone and sound woodlands. Associations of wood structure and property variations with genotype and growth rate were analysed in oaks from a seed origin trial.

Environmental factors were strongly associated with shake. High shake incidence occurred on sites which gave poor rooting conditions for oak: shallow, nutrient poor soils with low clay content and low calcium availability, and with soil texture and/or site topography leading to seasonal droughtiness or waterlogging. Woodland type (shake-prone or sound) was a stronger influence than tree condition (shaken or sound) on wood structure: oaks from shake-prone woodlands had wider rings, smaller earlywood percentage, larger wide rays and larger earlywood vessel radial diameters. Density, sapwood width, earlywood vessel frequency and proportions of wide rays and of latewood vessels and fibres varied between seed origins; these variables therefore have selection potential for improvement of oak wood quality. Many parameters also varied with growth rate, and earlywood vessel radial diameter was strongly associated with current ring width.

A model of shake development is proposed in which various predispositions (structural weaknesses) and triggers (mechanical stresses) influence a tree over time. It is proposed that predispositions are caused by environmental factors at the time of wood formation, resulting in physiological stress or cambial damage. Genotype may modify response or susceptibility to environment. Predispositions may be extended by secondary weakening. Triggers of shake are thought to be natural internal growth stresses supplemented by the action of external forces (such as wind). Recommendations are made for site choice and silviculture of future British oak crops.

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CHAPTER 1

INTRODUCTION.

1.1. AIMS OF THE RESEARCH.

Wood quality can be controlled by genetic and silvicultural means. Research into its improvement should aim to specify genotypes and growing conditions which will produce wood of the desired quality. Denne and Dodd (1980) stated that "If we wish to control wood quality, we need to be able to predict effects of environment and effects of silvicultural management on wood structure; to make reliable predictions, we need to quantify patterns of variation in wood development in the tree ... ."

The overall aim of the research reported in this thesis was to add to the knowledge required for the improvement of wood quality in British oaks. The investigations concentrated particularly on the major defect 'shake', one of the more important causes of poor quality in British oak. Quantitative studies of variations in wood structure and properties pertinent to the study of shake as well as to wider aspects of wood quality were made.

The specific aims were as follows:

A/ To investigate 'shake' in British oaks:

1/ To assess the importance of the problem and to identify site factors associated with the occurrence of shake.

2/ To quantify variations in wood structure associated with shake.

B/ To study factors controlling oak wood structure and properties:

1/ To quantify variations in wood structure and properties associated with differences in genetic origin of oak.

2/ To assess the influence of growth rate on wood structure and properties.

C/ To draw together the results of the shake investigation and of the wood structure studies, in order to make prescriptions for selection and growth of British oaks, which it is hoped will help to improve the wood quality of future crops.

The background to this research is described below.

1.2. BRITISH OAKS.

The two native species of oak in Britain, are pedunculate oak (Quercus robur L.), and sessile oak (Q. petraea (Mattuschka) Lieblein). These two species furnish virtually all the supplies of home-grown oak timber, and are generally marketed as "English oak". The same species are also known commercially as "white oak" and "European oak".

The earliest known uses of oak in Britain date from Neolithic times, when oak was the predominant tree species in Europe's extensive forests (Godwin and Deacon, 1974). By the early Middle Ages, oak was an important timber for building, shipbuilding, industrial, agricultural and household uses. By the early seventeenth century, demand for timber was beginning to outstrip supply from England's forests (James, 1981), and in 1875, Laslett (Timber Inspector to the Admiralty) recorded that a shortage of home-grown oak was again apparent. Various schemes had recurred over the centuries to protect or restore Britain's timber resource, varying from several Acts of Parliament to the patriotic planting of oak by private landowners after the Napoleonic wars to provide ship timber for the future (James, 1981). However, in the mid 1800s oak imports from the Mediterranean and Eastern Europe removed the incentive to maintain home-production; the amount of oak planted in Britain then decreased steadily until the 1980s (Anon, 1984) although harvesting continued and there were major depletions during the two world wars. The stock in the remaining woodlands is thus heavily weighted to the larger size classes, and as most of the best boles have been selectively removed over the last three centuries, the timber is mostly of poor form and quality. The current standing volume of woodland oak in Britain is just less than 33 000 000 m^3; this, with around 9 000 000 m^3 non-woodland trees, constitutes 17% of the broadleaved timber volume (Locke, 1987).

In 1982, Elliott said that the British broadleaved resource was expected to decline further in quantity and quality. Johnston (1981; quoted in Elliott, 1982) had estimated that only 30% of the current annual increment of British hardwood was suitable for high grade saw timber. In 1987, Thompson calculated that one third of the annual cut of British hardwood was of low quality mining timber grade; also, that the current annual increment of home-grown broadleaf trees exceeded the annual cut, which indicated that the resource included larger volumes of poor quality timber than the market could absorb (Thompson, 1988). Thompson reported results of a survey of TGUK members which suggested that in the five years from 1987, 36% of the harvest of home-grown broadleaves (the largest proportion for any single species) would be oak.

1.3. DEMAND FOR BRITISH OAK.

The United Kingdom consumption of hardwood timber remained static for the ten years 1978 - 1988; one half of the total was supplied by tropical hardwoods and only one quarter by British hardwoods (Thompson, 1988) of which oak would be approximately one third. However, Brazier (1985) forecast that demand for home-grown hardwood will increase as imports of tropical timber decline. In the early 1980s therefore, a need to increase or at least maintain production of homegrown hardwood was apparent. A concurrent concern for the future of broadleaved woodlands in Britain (valued for conservation and amenity but threatened by loss to agriculture or conifer plantation, and neglect) led to the symposium 'Broadleaves in Britain' and the Sherfield Report (from a sub-committee of the House f Lords on "The Scientific Aspects of Forestry"). Consequently, a policy review concerning British broadleaves, and the supply and demand of home-grown timber from them, was reported in a Consultative Paper 'Broadleaves in Britain' produced by the Forestry Commission (Anon, 1984). The policy statement c ntained in this paper advocated maintenance of the broadleaved resource at about its present extent, with improvement of the productivity of broadleaved woodlands. In 19 9, a policy paper produced by the Forestry Commission consolidated the ideas of the consultative paper following feedback from interested bodies: broadleaf afforestation, including native oak species, was strongly encouraged (Forestry Commission, 1989).

1.4. UTILISATION OF BRITISH OAK, AND CURRENT MARKETS FOR THE TIMBER.

Oak has been, and still is, one of the most widely used hardwoods in Britain (Farmer, 1972). Its strength, and stability after seasoning, suit it for building and joinery. Its durability has been exploited in dock and road construction for over two thousand years (Godwin and Deacon, 1974). The importance of oak in ship-building until the 1800's is illustrated by the number of treatises published (e.g. those listed in James, 1981) which detailed silvicultural method or choice of timber provenance to give oak of suitable qualities. The good cleaving properties and durability of oak made it particularly suitable for roofing and fencing, its toughness suits it for bending, its cleavability and impermeability for cooperage (Alexander, 1972), and its figure for cabinet work and panelling. Top grade logs have been sliced for veneer since the early nineteent century. Finally, oak has been important as a fuelwood since Neolithic times (Godwin and Deacon, 1974).

Traditionally, British oak is characterised by superior toughness and strength, compared to European sources of the same species; this is due to its faster growth (FPRL, 1966), in turn influenced by climate and traditional silviculture (Secti ns 2.2.2.3. and 2.2.3.). French and German oak has been managed to produce a 'milder' (less dense) timber of fine texture (narrow rings with little latewood).

In Britain now, the uses which demanded the tough and durable characteristics of oak are decreasing; softwoods have superseded in new building work. Thompson (1986) listed current uses of oak in the UK as: external and internal joinery, fittings, furniture (including veneers), flooring, structural refurbishing, fencing, mining and fire-wood. Other uses of oak include light cooperage and in boat-building (Farmer, 1972).

Until recently, there were many small timber mills in Britain dealing with low grade oak which supplied the markets for sawn mining timber, dunnage, pallets and fencing. However, since the early 1980s the markets for the lower grades of oak (mining timber in particular) have almost disappeared, putting many of these mills out of business; moreover, mining timber now has to conform to a British Standard of quality (Thompson, 1988). These low grade markets are not likely to return or be replaced (Venables, 1985b) and are currently more than satisfied by the home-grown supply of low-grade oak (Thompson, 1988). Venables even predicted that over 80% of the current volume of British oak will be difficult to market, being of inferior grade (Venables, 1985a).

However, there remains a demand in Britain for the high grade qualities suitable for furniture, cabinet work, flooring, panelling and veneer. Despite a 50% drop in the furniture industry in the ten years to 1988 (Thompson, 1988), the market now appears to be stable and joinery and furniture are reported to be the most important end use of oak, both in terms of volume used and in value per unit volume (Venables, 1985b). Forecasting is always difficult, especially when planning long rotation crops such as oak, but it seems that the present type of market is set to continue. Plastics have failed to replace hardwoods for furniture frames (Baggs, 1983) and although oak is rarely used in building construction now except f r restoration work (Venables, 1985a) this market (using medium and high quality oak) is increasing (Thompson, 1988). Furniture blanks made from small diameter oak (by edge-glueing of pieces), are a possible future market for existing crops and thinnings (Thompson, 1986) - but demand for the l wer quality grades is not likely to supersede that for first quality butts.

The home-grown supply of first grade oak cannot meet the demand currently, and the bulk of white oak timber used in Britain is imported from the United States of America (an annual import of over 30 000 MT) (Thompson, 1986); but if a constant supply of high quality home-grown oak can be produced in Britain in the future, it will find markets because of its versatility , attractive figure and general popularity. Poor quality oak will be passed over in favour of the "white woods" (ash, sycamore, birch) which are easy to work, can be altered by various finishes, and fit the uniform specifications for mass-production far better than oak (Venables, 1985a).

1.5. THE FUTURE OF BRITISH OAK.

Over the last fifteen to twenty years, popular concern for the environment has increased greatly. One consequence of this has been a renewed and widened interest in tree planting in Britain. The planting of native broadleaves is being favoured by the decisions of woodland owners and managers whose interest is not purely commercial, also by government policy and Forestry Commission advice (e.g. Forestry Commission, 1989), or through the conditions and incentives attached to planting grants. Amongst these native broadleaves, oak is particularly popular; it is frequently chosen for nature conservation areas because it is long-lived and can produce attractive woodland, groups or single trees; and it appeals to popular imagination because of myths and legends which have surrounded it through Britain's history. This recent increase in planting of native broadleaves represents a future supply of home-grown timber (potentially), much of which is likely to be oak.

It seems therefore that both public preference and government policy will ensure the increased quantity of home-grown broadleaves, and that there will be a demand for high quality home-grown hardwood timber. However, if any of the new generation oak woodlands are to have a long-term future, this must include commercial prospects by which they provide support for the enterprises which planted and/or maintain them (whether with a primary objective of commercial investment, of nature conservation, or of other purpose). The main revenue will come from sale of timber, and so it is essential that the quality should be excellent in order to meet the markets. A bleak future for home-grown oak is forecast, unless a constant supply of high quality timber can be maintained (Anon, 1984; Venables, 1985a).

1.6. THE NEED FOR RESEARCH.

The poor quality of the hardwood produced in Britain has become a matter of great concern (Paterson, 1980; Denne and Dodd, 1982; Anon, 1984; Venables, 1985a). The quality of Britain's oak timber resource has therefore been the subject of many meetings, and means of improving quality in future crops has become the subject of recent research. Evidence of this can be seen in the work of the National Hardwoods Programme (Harris, 1981), the reports of advisory committees (e.g. the Home Grown Timber Advisory Committee), and the interest of the organisation Timber Growers UK Ltd., which represents private woodland owners (more than 90% of broadleaved woodland in Britain is in private ownership; TGUK, 1989).

Shake and epicormics are currently regarded as the major causes of degrade in British oak: in the BIB Consultative Paper (Anon, 1984), the section dealing with timber quality states that "If the incidence of these defects could be reduced this would have an appreciable effect on profitability and meet the market preference for wood of high quality."

1.7. THE TIMBER DEFECT OF SHAKE.

Shake is one of the most important defects in oak timber, yet it is also one of the least understood. Shake is a gross structural defect. Shakes are longitudinal splits inside the wood of the standing tree, and once formed, they cannot be remedied. The separation of the wood does not usually occur until trees are of saw-timber size. The affected tree may meet all other criteria required for a high quality oak bole, but the presence of shake will reduce the utility and value of the timber drastically. The defect is difficult (if not impossible) to detect externally, so the usual British practice of selling timber standing can pose great financial risk to a buyer, who may reduce his offer to the seller in order to cover that risk.

1.8. THE QUALITY REQUIRED IN BRITISH OAK.

The "first quality" required for the furniture and joinery markets in which mass-produced kitchen units and reproduction furniture now dominate, is generally timber of straight grain, free of defect, even in colour and 'character free' (Venables, 1985a). Some users, such as cabinet makers who exploit variations in structure and properties, remind those marketing the timber that wood often regarded as waste, can be 'prime' for particular uses (Garvey, 1983), but these uses represent relatively small volumes.

The criteria to be met in producing high quality timber from British oak are: a) good timber length, form and diameter, b) freedom from major defects - shake, rot and large knots, then c) straightness of grain and d) narrowness of sapwood (which affects the usable volume) (Graham, 1985; Venables, 1985a). Lesser defects than shake and rot (for example epicormic twigs and traces, or mineral stain and other colour variations which affect the aesthetic value of the timber) vary in importance depending on the end uses expected for the timber; they would be very important defects in veneer timber, fairly important in oak for mass-produced joinery work, and not important in construction timber. Other finer points of quality such as texture and mildness will vary in importance similarly.

1.9. IMPROVING THE QUALITY OF OAK TIMBER.

It is not certain whether the poor quality of the mature oaks which remain in Britain is due to purely genotypic influence, or is phenotypic: the best boles have been creamed off from existing woodlands, but also the lands growing the best oak may not have been continued under woodland as they were often the most desirable agricultural land. The usual method of re-stocking in Britain is by planting of selected stock, rather than reliance on natural regeneration (Harley, 1982) so control of quality in future crops can be achieved by manipulation of both genetics and environment.

In summary, the main aims of the research reported in this thesis were:

A) to investigate the defect of shake in British oaks, and the growing conditions associated with shaken and sound trees.

B) to gain quantified information on factors controlling wood structure and therefore wood properties of British oak timber.

These aims work towards the improvement of quality in future crops f British oak.

CHAPTER 2

REVIEW OF LITERATURE.

2.1. OAK - THE TREE AND ITS TIMBER.

2.1.1. THE BIOLOGY OF OAK.

2.1.1.1. TAXONOMY AND DISTRIBUTION.

The oaks belong to the Fagaceae, a large family of broadleaved trees and shrubs, comprising six genera and represented in Europe by three genera: Fagus (beech), Castanea (chestnut) and Quercus (aks).

Mitchell (1978) stated that over 800 species of oak, includin numerous hybrids, have been described. Their distribution is over a large geographical range in the Northern hemisphere, from temperate, through sub-tropical to tropical-mountain areas. Within the genus there is a large range f tree, leaf and acorn form, ecology, physiology and wood structure. The majority of temperate oaks are deciduous, though some are evergreen (e.g. Q. ilex). Almost all are large trees of wide-branching habit and long life. The genus is sub-divided on the basis of leaf, wood and fruit characteristics: Williams (1939) described two groups, Erythrobalanus ("red oaks") and Leucobalanus ("white oaks"). Metcalfe and Chalk (1950) gave each of these groups sub-genus status. This treatment still holds, but Gasson described a lack of agreement between authors in allocating the various evergreen species to one or other of these groups, and noted that additional sub-genera have been described by some authors working on oriental species (Gasson, 1984). The species with which this thesis is concerned, are both white oaks.

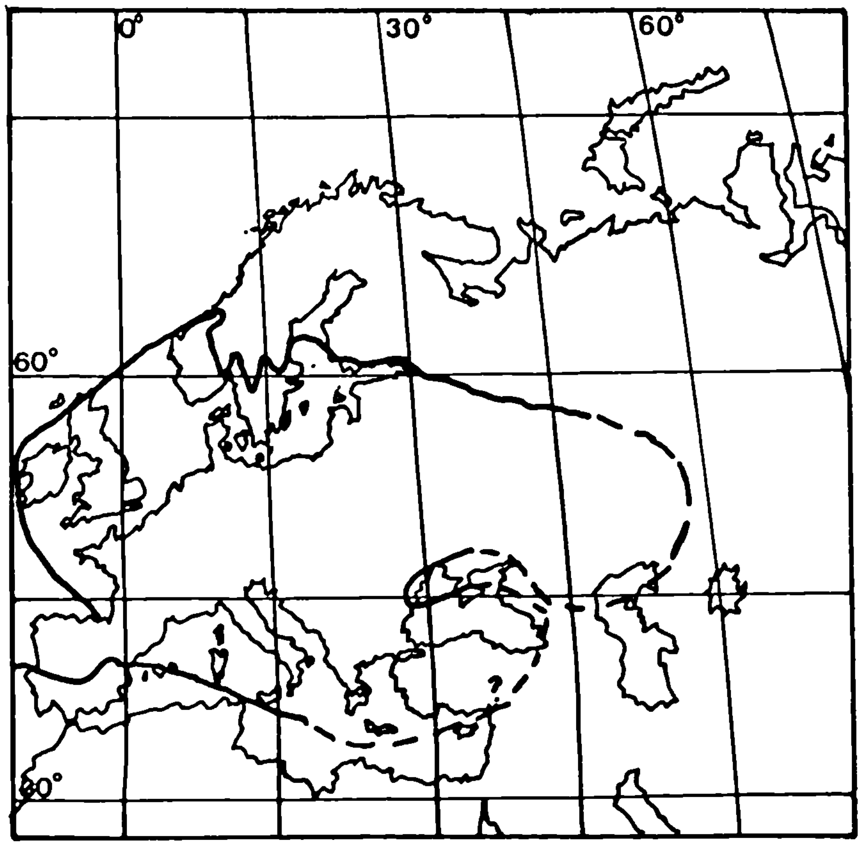


Figure 2.1.a. Geographical distribution of Quercus robur L. (from maps and text of Jones (1959)).

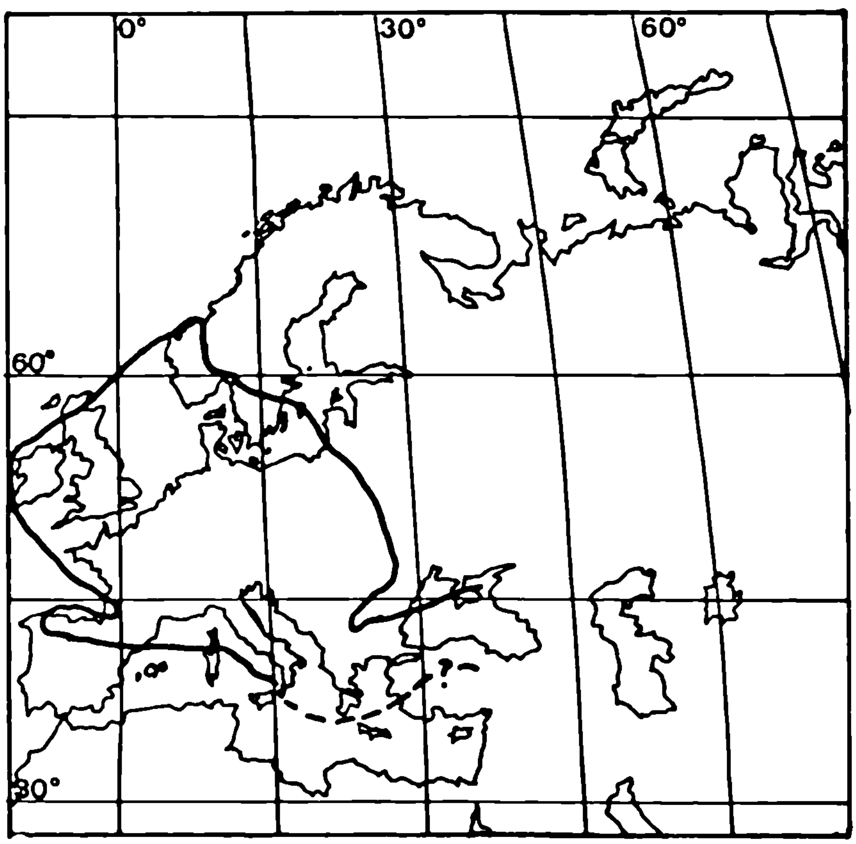


Figure 2.1.b. Geographical distribution of Quercus petraea (Matt.) Liebl. (source as above).

2.1.1.2. SESSILE AND PEDUNCULATE OAK.

The two oak species native to Britain are pedunculate oak - Quercus robur L., and sessile oak - Q. petraea (Matt.)Liebl. The synonyms Q. pedunculata Ehrh. and Q. sessiliflora Salisb. are still used for the two species occasionally; Gardiner (1974) described the history of this taxonomy. Pedunculate and sessile oak in the British Isles, are reported to be near the North and West extremes of their geographical ranges, although they occur naturally as far as 63° North on the West coast of Norway. Figure 2.1. illustrates the geographical distribution of the two species. In the Mediterranean basin, they occur in the montane regions. Jones (1959) wrote a monograph on Quercus L. in Britain, from which most of the botanical notes in the following descriptions are taken; tree form, leaf, fruit and bark characteristics of pedunculate and sessile oak have also been described by Cousens (1965), Kissling (19), and Sigaud (1986) for purposes of species identification.

B th pedunculate and sessile oak are large, deciduous trees (up to about thirty metres in height), valued for their timber. There is high intra-specific variability in all characteristics of both species, but especially of pedunculate oak (e.g. morphology: Elwes & Henry, 1906; Jones, 1959; timber properties: Laslett, 1894; Nepveu, 1984b). The differences seem to be heritable to a certain extent, such that ecotypes can be said to exist, though no geographical races nor even clines can be distinguished (Jones, 1959); the following descriptions are those considered by the various authors to represent the pure type.

Quercus robur typically has a broad crown and, when open-grown, a heavy-branching habit with wide angles between branches and bole. The bark is brownish-grey and deeply fissured. The glabrous leaves have short petioles, an obovate outline and an irregularly lobed lamina with a strongly reflexed margin each side of the petiole (auricles). The 'cups' holding the acorns are borne on long peduncles (2 - 9 cm). Terminal buds are small and obtuse (Jones, 1959). The natural distribution of pedunculate oak in Britain tends towards more frequent occurrence on moister, heavier soils from North Scotland (Sutherland) southwards; it is rare in the extreme West and above 300 m altitude. There are differing views on the extent to which man has influenced this distribution (Jones, 1959; Gardiner, 1974; Wigston, 1974; Paterson, 1980).

Quercus petraea has a similar appearance to Q. robur, though the branching tends to be more straight and steeply angled, with the bole persisting through the crown; this gives a better form for timber production. The bark can be thinner and less deeply fissured than that of Q. robur; the leaf has a longer petiole and the lamina has no (or poorly expressed) auricles and its abaxial surface is more or less pubescent (stellate hairs being the usual form). The lobes of the leaf lamina are more numerous and less deeply cut than those of pedunculate oak. The fruit peduncles are short (0 - 1 cm). Terminal buds are large and acute. Sessile oak in Britain is more frequent on lighter, more acid soils, and can be found on higher and more difficult ground than that colonised by pedunculate oak.

Both species grow vigorously on deep, non-waterlogged soils, but the importance of water table seems to vary with stage in development as well as with species. The classic concept, based on observations of distribution, is that Q. robur thrives best on moist, deep, fertile soils , whereas Q. petraea 'prefers' lighter, drier soils which are usually on valley sides (Tansley, 1939; Anderson, 1950; reports summarised in Jones, 1959; Ietswaart and Feij, 1989), but some authors qualify this. Harley (1982) describes Q. petraea as being "less exacting" in its requirements, growing well on soils lighter, sandier and drier than those needed for Q. robur. Jones (1959) reported that there is no evidence of soil preference in the two oak species when they grow together in the typically 'Sessile' regions of the West; experiments by Tansley (1939) suggested that sessile oak seedlings were more tolerant of waterlogging than pedunculate. However, recent experiments in France have shown that Q. robur appears to withstand water-logging better than Q. petraea at germination, seedling and juvenile stages, while in adult trees, Q. robur is more sensitive to extremes of both water-logging and drought, Q. petraea performing better under such conditions (Levy et al., 1986; Becker and Levy, 1986). Becker and Levy also concluded that Q. robur is less able than Q. petraea to adapt to permanent changes, such as drainage of a wet site; and that older trees (over 100 years) of either species adapt poorly to such changes, being unable to alter root systems as easily as younger trees. Sigaud (1986) stressed the importance of recognising and understanding these differences between the two species (and Q. pubescens in France) in order to make use of their different performances on different sites. Q. robur is described as 'hygrophilic' by Sigaud, and its restriction to damp sites is recommended.

nly a few authors have attempted to distinguish the wood anatomy of the two species (Hartig, 1894; Huber et al.,1941 quoted in Walker and Fletcher, 1978; Walker and Fletcher, 197 ; the distinction is not easy. There has been little economic incentive to make a distinction, because timber users treat the two woods as identical (e.g. FPRL, 1966; Farmer, 1972) and many are unaware of the existence of a species difference. Most dendrochronologists also treat the two species together (Trenard, 1982).

Attempts to identify the two species from any leaf, fruit or wood structural characteristics (macro- or microscopic) are complicated by apparent hybridisation of populations.

2.1.1.3. HYBRIDISATION OF SESSILE AND PEDUNCULATE OAK.

The degree to which hybridisation of sessile and pedunculate oak occurs, is much debated. Individual trees exhibiting combinations of supposed type-characteristics of both species, occur in many oak populations, suggesting hybridisation yet perhaps being ecotypes of a 'pure' species (Jones, 1959).

In tests of the success of controlled sessile-pedunculate crosses, Rushton had less than 1% mean success rates with inter-specific hybrids, and Jones reported 2 - 15% success from his own and others' work (Jones, 1959; Rushton, 1977). The hybrids were often of low fertility. Despite these results, both Jones and Rushton concluded from concurrent observations and site studies that mixed oak populations exhibit such variety that there must be a certain amount of natural hybridisation occurring. Gathy (1969) concluded from studies on progeny of pure and hybrid oak mother trees, that natural hybridisations exist but are very rare, and that introgression (the successive back-crossing of hybrids with a parent) ccurs only on a very small scale; he found that hybrid characters were fixed and occurred in progenies.

While accepting that a small amount of hybridisation did occur naturally, Jones (1959) and Gathy (1969) believed that hybridisation was too often assumed when high intra-specific variability was encountered in single-species populations. Cousens (1965) suggested that confusion can arise because _Q. petraea_ populations have a narrow range of clearly distinguishable characteristics, while _Q. robur_ has a very large range of 'types'. However, Rushton (1977) found that _Q. robur_ mother-trees were more successful in hybridisation; this may explain the apparently more discrete characteristics of _Q. petraea_ populations, and Cousens' observed variability of _Q. robur_ types may be due after all, to various degrees of introgression of sessile oak into these populations.

Several authors believe that introgression is a more common consequence of hybridisation than are hybrid swarms (Cousens, 1962; Becker, 1972; Wigston, 1974). Aebischer (1987) discussed other theories concerning hybrid populations: 'morphology-viability linkage' of genes resulting in hybrid populations strongly resembling one parent; and a 'multi-species' concept in which species are not reproductively isolated (i.e. interbreeding is possible) but populations are usually kept separate by environment because of adaptation of different gene types to different conditions.

Studies of hybridisation and introgression have been based on analysis of a variety of morphological characteristics. Cousens (1962) quantified leaf and acorn characters in sessile and pedunculate oaks from Scotland and used Pictorial Scatter Diagrams to illustrate the existence of pure and intermediate types. Wigston (1974) described six techniques which had been devised by various authors for investigating the amount and type of hybridisation between populations. He demonstrated the techniques on oak populations of South-West England: using two woods with pure populations of sessile and pedunculate oak as references, he illustrated woodlands which showed a mix of pure species, intermediate stages of introgression, and residual introgression. Aebischer (1987) reviewed the work of several other authors who have used leaf morphology to denonstrate the existence of intermediates.

Becker (1972) investigated intermediate forms of oak in the forest of Charmes, France, by using vegetative and wood characteristics.

Deret-Varcin (1983) tested the wood properties of French _Q. robur_ and _Q. petraea_ and of types classed as intermediate on the basis of leaf characters. The pattern she observed was similar to that seen by Cousens in vegetative characters: _Q. petraea_ had very discrete results, significantly different from _Q. robur_ and the intermediate types, but the intermediates were never significantly different from Q. robur.

Olsson (1975) studied mixed sessile and pedunculate oak populations in South Sweden. He described four "phenotypic" groups, separated by assessments of leaf petiole percentage and fruit peduncle length. These were sessile, pedunculate and "similar to" sessile or pedunculate oaks. Olsson felt that a taxonomic review of the two species was needed.

Kissling (1980) produced triangular population diagrams based on leaf pubescence for sessile, pedunculate and pubescent (Q. pubescens) oaks because he said that "In the morphological continuum of the middle european oaks, it is as difficult to distinguish the species, as to place the intermediate forms." Kissling demonstrated that these diagrams were also good phytosociological and ecological indicators; for example, the balance between sessile and pubescent oak populations related to a scale of temperature, and the balance between sessile and pedunculate populations related to hydrological regimes (pedunculate types occurring on sites with greater availability of water).

Ietswaart and Feij (1989) also demonstrated the phytosociological usefulness of introgression studies, as they showed a gradient in a natural oak population, from pedunculate oak on moist lowlands, to sessile on the drier, higher land; elsewhere, hybridisation and introgression were considered partly due to artificial planting of pedunculate oak.

Unfortunately, the methods of morphological assessment which have been used are not always consistent. This makes comparisons between studies difficult. Moreover, few authors seem confident of having found populations of 'pure' species to provide accepted types. Cousens (1965) quantified as 'pure' reference populations, Q. petraea from Ireland and Q. robur from Hungary (he assumed that the Q. robur could not hybridise with the *Q. cerris* growing in the same forests, but Kissling (1980) found that there is a rare influence of *Q. cerris* in european white oak populations in France).

2.1.1.4 PHENOLOGY OF SESSILE AND PEDUNCULATE OAK.

Sessile and pedunculate oak are deciduous. In the British Isles they flush from about mid-April to late May; shoot elongation continues until about mid-June and some trees (particularly in moist summers) may produce 'lammas shoots' from July onwards; shoot elongation is normally finished by October and leaf senescence complete by end of November (Longman and Coutts, 1974; Denne, 1976; Harmer, 1990).

There is considerable variation in flushing time of oaks, but it appears to be genetically controlled, with individuals or populations being consistent in their relative times of bud-burst (Riedacker, 1968; Crawley and Akhteruzzaman, 1988) Sessile oak has been reported to flush earlier than pedunculate (Woolsey, 1920), though the opposite has also been reported (Long, unpubl.). Jones (1959) described other conflicting reports: in some, site differences affected the relative timing of the two species, in others, there were no consistent differences even though the species were in mixed populations. He concluded that intraspecific variation greatly exceeded any possible interspecific variation, while noting that "probably no *Q. petraea* is ever as late as the latest *Q. robur*". However, occasional populations are so very different that they become regarded as separate varieties of the species e.g. the "June oak" (*Q. robur* var. *tardissima*), a very late-flushing form found in NE France, Germany and Eastern Europe (Hesmer, 1955 - quoted in Jones, 1959; Riedacker, 1968). Riedacker (*op. cit.*) reported that flushing in typical pedunculate oak and in the June oak was regulated by cumulative temperature (laboratory experiments with temperature and photoperiod had been carried out).

As a consequence of such variation, certain types may escape damage from late spring frosts, others from defoliator attack. Evidence for this is given by Koloszár (1987); however, Crawley and Akhteruzzaman (1988) found that certain individuals in a group of oaks were prone to attack in consecutive years, but that this was not related to flushing time. Other work concerning this is noted in section 2.1.1.5. below.

2.1.1.5. PATHOLOGY OF SESSILE AND PEDUNCULATE OAK.

The longevity of these two oak species is legendary. Although no fatal disease of oak is epidemic in the British Isles there are certain important pests and pathogens to note. Defoliating larvae of two moth species, Tortrix viridana L. (oak leaf roller moth) and Operophtera brumata L. (winter moth), can cause severe defoliation in certain 'plague' years. Such attacks may affect a stand of trees for two or three years in succession, then moth numbers will decline rapidly again. Leaves are stripped soon after flushing, and complete defoliation can occur by early June; wood production (as indicated by ring width) that season can be markedly reduced (Winter, 1985) because both canopy loss and mobilisation of reserves for production of new leaves decrease the substances available for wood and fruit production (Speight, 1985). Successive severe attacks will debilitate the tree, but never directly cause death of the oak. Tortrix are reported to attack pedunculate oak more readily than sessile oak (Smith, 1891 quoted in Elwes and Henry, 1906; Osmaston, 1927). Satchell (1962) investigated this in two woodlands and confirmed the suspicions of the above authors, that early-flushing oaks avoided attack by defoliators; sessile oak tended to flush earlier than pedunculate in all these woodlands, but flushing time varies considerably within the species (section 2.1.1.4.) and so is more important than species in this context. The leaves of oaks which flush some time before the moth-larvae hatch, are too tough and unpalatable for the emerging larvae to feed on (Speight, 1985). Very late flushing oaks also tend to escape defoliation, as earlier-hatching larvae are unable to enter the bud.

The only damaging foliage pathogen of oak in Britain is mildew (the fungus Microsphaera alphitoides (Murray, 1974); seedling oak, lammas shoots of defoliated trees and coppice shoots are particularly prone to attack. Mildew does not kill oaks, but can damage the affected leaves very badly thus reducing the health of the tree - resulting in reduced growth, reduced acorn crops, and susceptibility to attack by secondary parasites (Murray, 1974). Q. petraea is regarded as less susceptible to mildew than Q. robur.

The honey fungus Armillaria mellea is present in the majority of oak sites (Murray, 1974); it can kill oaks, but such severe attacks are rare: usually only those oaks severely debilitated by other pathogens or adverse growing conditions succumb. Incidences of attack of dominant and suppressed oaks by the fungus are equal, but invasion success is much greater in suppressed trees (Davidson and Rishbeth, 1988). Soil type also affects susceptibility to infection, with higher incidences on acid sands, moderate incidences on loams and alkaline sands, and no cases found on acid peats or alkaline clays (Redfern, 1978). It has often been suspected that oak decline in Britain and on the Continent has been due to invasion by honey fungus following damage to roots by drought years (Robinson, 1927; Macaire, 1984), waterlogging (Guillaumin, 1983) or debilitation of the tree by succession of drought, defoliation and mildew attack (Robinson, 1927). Wargo (1972) said that defoliation, drought, lightning strike and waterlogging all increase the concentration of reducing sugars in forest trees, and these favour growth of A. mellea (though stimulation of fungal attack is due to amino acids secreted by roots).

Another fungal pathogen which can kill oak, is Heterobasidion annosum; although not typical of oak woodlands, it can infect oak planted on old conifer sites or in mixes with conifers, when the conifers are removed and stumps are left (Murray, 1974). Murray describes other root pathogens of oak which are less well known, and so not generally regarded as important.

Pathogens causing decay of standing oaks are described by Murray (1974); of these, the most important are Laetiporus sulphureus (cuboidal brown rot of heartwood), Stereum gausapatum (pipe rot), and Fistulina hepatica (which in its early stages causes discolouration, giving the 'brown oak' heartwood sought after by many timber merchants). These rots are all important to the timber grower, but are not as threatening to the tree as are the root pathogens. Stereum causes 'palm-and-finger' pattern rot, eventually leading to severe pipe rot; it enters high in the tree through dead branch stubs and has very fast longitudinal spread in the rings ass ciated with the branch by which the rot entered; its incidence was strongly correlated with altitude of site and with shall w soils by Day and Peace (1947).

Two other important natural agents of damage to British oaks are frost and drought. Severe frost can cause leaf-kill even in large trees, and can damage the cambium (Day & Peace, 1946). Dujesiefken & Liese (1986) report retarded development of heartwood due to wounds suffered during frost spells .

Drought causes reduction in radial wood formation, and both oak species in Britain are limited at times by water stress (Pilcher & Gray, 1982). Mortality due to a single season's drought is said to be rare in oak - but Young (1965) described dieback of Q. robur in Norfolk as primarily due to drought, while noting that Q. petraea was not affected. Similarly, Becker and Lévy (1986) recorded high mortality in Q. robur in France after the 1975/6 drought years; Q. petraea appeared to be more resistant. Drought has been associated frequently with oak decline in forests on shallow soils over difficult subsoils (Day and Peace, 1947); Robinson, 1927; Macaire, 1984; Guillaumin et al. 1985), but the agent of decline has usually been fungal attack following reduced resistance in the trees debilitated by drought.

2.1.2. THE ANATOMY OF OAK STEM WOOD.

2.1.2.1. FINE STRUCTURE.

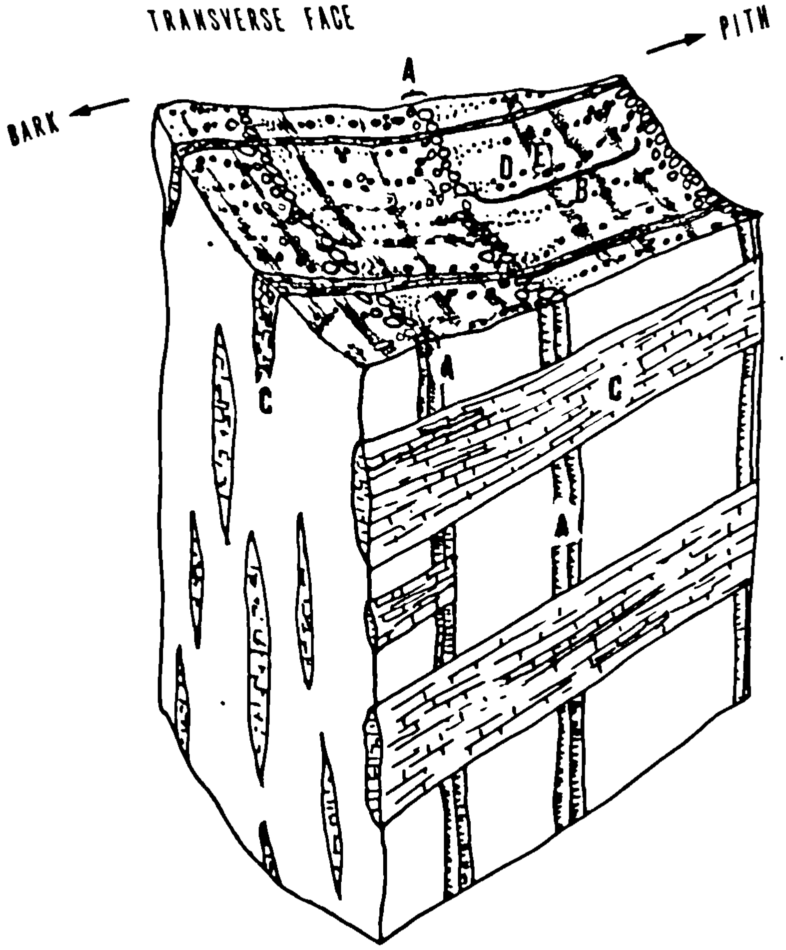
Oak wood has a complex structure, incorporating most of the cell types found in hardwoods: vessels, tracheids, libriform fibres, fibre-tracheids, axial parenchyma and ray parenchyma. Most oak species have a ring-porous wood structure pattern which is characteristic of the genus; the 'evergreen oaks' are an exception e.g. *Q. ilex*) (Wilson & White, 1986). Figure 2.2 illustrates diagrammatically the typical stem wood structure of oak.

Ring porous oaks have one to five tangential rows of large solitary vessels in the earlywood of the annual ring. The change from earlywood to latewood is abrupt, with a marked reduction in vessel size; at the same time, vessel arrangement changes from tangential bands to radial or slightly oblique lines, surrounded by tracheids and axial parenchyma (Wilson & White, 1986). This tissue appears as wedges or "flames" in the dense fibre matrix of the latewood. The flames may be ribbon-like or fan or fork towards the end of the ring (Fletcher, 1978).

Rays of two distinct sizes are found in almost all oak species. The narrow rays are 'weak' (i.e. tending to be deflected during expansion of adjacent earlywood vessels (Wilson and White, 1986)). The wide rays distinguish oaks from other members of the family Fagaceae, being particularly large (up to 400 um wide, and about 4 cm high (Wilson & White, 1986)). Frequency and width of both ray types is very variable, within and between oak species, but there are normally several narrow rays between every two wide ones, and the total volume is reported to be more or less constant. Maeglin (1974) believed that the similarity in total ray volume extends between many hardwood species, temperate and tropical, although Myer (1922) concluded that Quercus spp. have the largest ray volumes of any species.

Axial parenchyma in oak is scattered and infrequent in the earlywood; in latewood it is predominantly apotracheal, occurring in diffuse aggregates in tangential bands between the rays (Desch and Dinwoodie, 1981).

The above cell arrangements lie within a matrix of librif rm fibres. Libriform fibres with a thickened layer replacing the normal S-2 layer of the cell wall (the gelatin us or g-layer) occur frequently in oak . Blocks of such fibres are characteristic of tension wood in many hardw d species, when the g-layer is generally unlignified; normal frequencies of other cell types within the fibre matrix are reduced in areas of g-fibres (Taylor, 1968; Panshin and deZeeuw, 198). In oak, g-fibres may or may not be associated with tensi n wood; they occur as scattered cells or bands of cells in the late wood (Cano-Capri & Burkart, 1974), and the g-layer is said to be lignified to a greater or lesser extent (Casperson, 1967).



A Large vessels of earlywood.

B Vessel 'flame' in latewood.

C Wide rays.

D Libriform fibres form blocks in latewood.

E Axial parenchyma cells in latewood, in tangential bands of variable width and number.

Not shown: uniseriate rays, not visible to naked eye, run parallel to wide rays.

Figure 2.2. Diagrammatic representation of a block of white oak stem wood. (x 4 approx.).

2.1.2.2 GROSS STRUCTURE.

Larger scale structure patterns occur across the rings from bark to pith. The difference between sapwood and heartwood is more a physiological than an anatomical difference, but it is macroscopically identified in oak by a definite colour change.

The pale coloured outer rings of a mature oak stem remain physiologically active for a number of years after formation. This 'sapwood' acts as a pathway for translocation of water and minerals, maintains metabolic processes and stores food (Bauch 1980). The food reserves are mostly starch deposits in axial parenchyma and rays; the reserves decrease during leaf production early in the year and may be totally depleted in trees suffering successive defoliator attacks during one growing season.

The sapwood surrounds the heartwood which in oak is rich br wn in colour; the shade of brown varies markedly between trees C urtoisier, 1976). Heartwood develops during the dormant season in oak, when cambial activity ceases. Biochemical activity in the rays results in the decrease of sugar, starch and ATP from bark to pith. Wardell and Hart (1973 rep rted a radial decrease in potassium, phosphor us, calcium, magnesium and manganese from sap- to heart-wood of Quercus sp., though Bauch (1980) noted that re-deposition of minerals may occur later. Before heartwood forms, the amount of living parenchyma decreases, and food reserves are removed or converted to typical heartwood substances - organic extractives such as flavonoids and terpenoids. The moisture content of the wood decreases in the transition from sap- to heart-wood; though it may increase again in mature heartwood.

There is some debate as to the function of heartwood. Stewart (1966) believed it to be a repository for toxic metabolic by-products e.g. polyphenols). Bamber (1976) viewed it less as a passive development, but rather as a regulation mechanism, which keeps the sapwood level at an optimum for its role in the tree. He therefore claimed that the principal controlling factor in heartwood development is the requirement of, and provision for, food reserves. The evidence of other authors supports this: Bauch, although proposing that the sap/heart ratio is genetically determined, said that heartwood formation is retarded by wounds (when reserves of metabolites are required for protection and healing (McGinnes and Shigo, 1975)) and that climate and soil conditions may cause individual trees to "regulate" the sap/heart ratio (Bauch, 1980).

Genetic determination of the ratio of heartwood to sapwood probably reflects the typical habit and physiology of the genotype and is therefore part of the overall regulating mechanism. Deret-Varcin (1983) showed a genetic influence on the heartwood of oak, where the process was "delayed" in Q. petraea compared to Q. robur. She speculated that this was a compensating mechanism for the lower sap conductivity potential of Q. petraea earlywood (following Bamber's idea of the regulating role of heartwood formation on the storage and conduction functions of sapwood), having shown that the frequency of earlywood vessels was lower in the samples of Q. petraea.

Bamber and Fukazawa (1985) reviewed sapwood and heartwood studies and concluded that the sapwood width depends on the growth rate of the tree, and will therefore be influenced by species, age, site, and all other controls of growth. Milsom (1979) studied the sapwood of Q. petraea; he found that width varied greatly within and between trees, but found no significant correlation between sapwood width and tree age, cambial age of the sapwood, or mean ring width. He did find that the more vigorous the tree the wider the sapwood, but the fewer the rings of sapwood.

The common impression that heartwood is dead wood, with a sole function of mechanical support, is challenged by Shigo (1984). Experiments on heartwood decay in Q. rubra, showed that "micro-elements" were translocated far into the heartwood after injury to the tree. Shigo removed initial uncertainty as to whether this is due to active or passive movement, or even to concentration of elements by pioneer invading bacteria (Shigo and Shortle, 1979), with the evidence that spread of decay within a living tree was ordered, whereas in cut timber it was quite random. That this might be the result of growth habit in the different fungi which invade living and dead wood is possible, but Shigo and others have shown many instances of decay-stopping 'boundaries' forming in an ordered manner in the heartwood of living trees (Shigo and Marx, 1977; Shigo and Tippett, 1981). Therefore it seems that the mechanism of micro-element translocation is an active one, implying that heartwood should not be regarded as dead, but as physiologically inactive most of the time.

Tylosis formation is characteristic in the earlywood vessels of white oak heartwood (their abundance varies with species (Jane, 1970)). The tyloses do not form necessarily in association with the heartwood transition, but may follow earlier embolism of vessels (common in the very wide earlywood vessels of oak (Longman and Coutts, 1974)), or may be a trauma response in sapwood. Their presence prevents the conduction of liquid along the vessels and discourages the longitudinal spread of fungal hyphae (Wilson and White, 1986).

2.1.2.3. THE WOOD STRUCTURE OF QUERCUS ROBUR AND Q. PETRAEA.

The wood structure of the two native British oaks follows the characteristic white oak pattern. Transverse sections from stem wood of both species are shown in Chapter 5 (Plates 5.2 to 5.5). They illustrate the strongly ring-porous nature of these woods. Growth rings correspond to annual increment, and the large vessels of the earlywood are easily visible to the naked eye. In the first ring from the pith of oak, the vessels are very small and grouped, and their diameter increases with progression across the ring (Vikhrov and

Perelygin, 1949 - Q. robur; Gasson, 1984 - Q. robur and Q. petraea). Gasson termed this ring alone 'juvenile'. During years 2 - 22 from the pith, the pattern becomes steadily more ring porous, with increasingly large earlywood vessels. Greater differences in vessel diameter between earlywood and latewood occur quite early. The earlywood vessel pattern changes from the grouping seen in the first 5 - 10 years (Vikhrov and Perelygin, 1949; Gasson, 1984) to a complete tangential band. Gasson termed this 'immature wood', though 'juvenile wood' is more usually used for all rings not exhibiting typical mature wood characteristics (Wilson and White, 1986).

The cambial age (ring number from pith) at which the wood becomes 'mature' varies with annual height growth and with crown depth. FPRL (1936) said that mature wood in oak occurs after about 30 years; Hartig, that earlywood vessel proportion increases until 40 rings from the pith (reported in Desch, 1932). Vikhrov and Perelygin (1949) stated seven to eight years from pith as the age of mature character in Q. robur, but their trees were only ten years old! Gasson gave an age of at least 25 years from pith, for mature wood - but said that the wood structure pattern is not a reliable indicator of cambial age unless it is obviously juvenile, because the diameter ranges of earlywood vessels in sessile and pedunculate oak are so large.

In mature wood, earlywood forms between 4% and 95% of the annual ring. Vasicentric tracheids surround the earlywood vessels, and are associated with the radial lines of latewood vessels, along with axial parenchyma (identification of individual cells surrounding vessels in latewood flames is often impossible in T.S. however (Gasson, 1984)). Tyloses are present in the earlywood vessels of heartwood. The tyloses of Q. robur are two-layered structures, one layer being suberised (Pearce, 1982). A recurrent feature is the dense tangential band of wood, entirely composed of libriform fibres, which occurs at the earlywood/latewood boundary within a ring

(Milsom, 1979). In the earlywood, axial parenchyma is rarely distinguishable from the vasicentric tracheids; in the mid latewood, complete or broken uniseriate bands of apotracheal axial parenchyma occur, crossing the fibre blocks tangentially (Gasson, 1984). Rays are of the two characteristic types in oaks: frequent narrow (uniseriate) rays, and fewer wide (multiseriate) rays. Seen in T.S., the wide rays swell typically at the ring boundary; such 'noding' of rays is described for other hardwood species (Tilia and Aesculus) by Wilson and White (1986).

Differences in structure or related properties between the two oak species are rarely recognised by timber merchants and those working the wood. Choice of timber for particular qualities is more often based on experience of oaks of different geographical origin (Laslett, 1894; Venet, 1967a; Farmer, 1972). FPRL (1936) stated that "there is no known method of separating the two by examination of their wood, and, other things being equal, there is probably nothing to be gained by differentiating between them in practice.". However, some researchers have attempted to separate the two on the basis of structural characteristics.

Detailed studies of the nature and formation of wood in Q. robur and Q. petraea were carried out by Hartig (1847). Subsequent wood structure studies of these two species, although thorough, have usually been confined to a small number of trees of one or other species, and have concentrated on within-tree variation (e.g. Gasson, 1984). Huber et al. (1941), reported in Fletcher and Walker, 1978) were the first to distinguish the two species by characteristics that could be measured quickly and easily. Studying oak from a site in Germany, they identified two quantitative characters (number of earlywood vessel (EWV) rows, and the earlywood proportion of the growth ring) and two qualitative characters (EWV shape and latewood 'flame' shape) as distinctive. They recognised the highly variable nature of oaks, and that presence of all four of the above features in their species-characteristic form would be rare in a single tree; however, the presence of three out of the four in a sample gave 90% success in allocating samples to the correct species.

Fletcher (1978) and Walker (1978) modified Huber's system (Table 2.1 overleaf) and Walker correctly identified twelve out of thirteen oaks from a single site by this means. Walker (1978) distinguished Q. robur as having more oval earlywood vessels (EWVs) than Q. petraea (i.e. tangential:radial diameter ratio (T:R) of less than 1.0). Their system is only successful in rings of medium width in undamaged wood, and the need for caution in its use is emphasised by the results of part of Gasson's study (Gasson, 1984). He found that EWV T:R ratios of 0.5 - 1.9 (i.e. from radially flattened, through perfect, to tangentially flattened circles) occurred in Q. robur alone, and concluded that the range was so wide, that EWV shape could not be a useful diagnostic character of Q. robur; furthermore, he re-worked the data of Huber et al. to produce comparable T:R ratios and found that the range for pedunculate oak overlapped that for sessile at both extremes, and that within three different ring width classes, the mean sessile shape was more oval than the mean pedunculate. Courtois et al. (1964) found that within ring-width classes, eccentricity of EWV shape in Q. petraea always exceeded that in Q. robur; more generally, eccentricity of EWVs was influenced by growth rate (ring width), a pattern also reported by Gasson (1984).

The reliability of earlywood vessel shape as a diagnostic feature in these two oaks thus seems uncertain. Deret-Varcin (1983) found that there were fewer rows of EWVs in Quercus petraea than Q. robur, which supports another of the criteria of Walker's definition. There was no significant difference in EWV size (seen in TS); but for frequency of EWVs around the ring (Walker's 'crowding'), she found a highly significant difference between the two species (vessels in all earlywood vessel rows per ring were counted). In Q. petraea there was a mean of 17.6 EWVs/5 mm of ring tangent, and in Q. robur a mean of 23.9 EWVs/5 mm. She commented that ".. a full investigation comparing the wood structure of the two species *Q. robur* and *Q. petraea* involving quantification of the different elements has never been undertaken, to our knowledge. There is the opportunity there for an 'in depth' study ...".

Feature	*Q. robur*	*Q.petraea*
EWV (earlywood vessel) shape	CLEARLY OVAL or CROWDED AND DISTORTED	Approximately circular uncrowded
Number of EWV rows in rings >2 mm wide and beyond year 5 from pith	3 or more	1 OR 2, EXCEPTIONALLY AS MANY AS 3
In such rings, ratio of EWV zone to total ring width	Over 0.25 predominantly	UNDER 0.25 PREDOMINANTLY
Appearance of latewood vessel groups called "flames"	Wide, broadening towards the end of the year; if not, bifurcation frequent.	Narrow and strap-like bifurcation, if present, is weak
Transition from earlywood to latewood in rings >2 mm	Gradual	Abrupt

Table 2.1. Separation of *Q. robur* and *Q. petraea* by wood structural characteristics (from Walker, 1978).

Correct diagnosis is regarded as highly likely if there are at least four of the species characteristics present, and these include the essential ones (in CAPITALS).

WOOD STRUCTURE CHARACTERISTICS		AUTHOR
Q. robur	Q. petraea	
GENERAL:		
Wood anatomy not distinguishable		FPRL (1936) Jane (1970) Farmer (1972)
Sapwood narrower (mean width = 2.9cm at 250 years old)	Sapwood wider (mean width = 3.6cm at 250 years old)	*Deret-Varcin (1983)
Sapwood rings fewer (mean = 18.8)	Sapwood rings more numerous (mean = 22.2)	" "
Mean growth rate: no significant difference		*Courtoisier (1976) *Deret-Varcin (1983)
Mean annual increment greater up to 90 - 100 years old	Mean annual increment greater after 90 - 100 years old	Krzysik (1975)
Bark thicker (not significant difference)	Bark thinner	*Courtoisier (1976)

Table 2.2. Wood structure differences between *Q. robur* and *Q. petraea*, given in the literature.

EWV = earlywood vessel; LWV = latewood vessel. * = results from studies where both species were growing on the same site. N.B.: 1) Courtoisier (1976) notes that all trees in her study were grown on a site favouring growth of *Q. robur*. 2) For qualification of Walker's data, see page 30.

Table continued overleaf.

WOOD STRUCTURE CHARACTERISTICS		AUTHOR
Q. robur	*Q. petraea*	
GENERAL:		
Bark thickness: no significant difference		*Deret-Varcin (1983)
Rays higher	Rays less high ("partial lack of silver grain")	Elwes & Henry (1906)
Earlywood/latewood transition gradual	EW/LW transition abrupt	Beauverie (1910) *Walker (1978)
EW:ring width ratio > 0.25	EW:ring width ratio < 0.25	" "
VESSELS:		
EWVs clearly oval or crowded	EWVs approx. circular, uncrowded	*Walker (1978)
Growth rate has a stronger influence on EWV shape, than any species difference between sessile and pedunculate oaks.		Gasson (1984)
EWV rows in mature wood = 3+	EWV rows in mature wood = 1 - 2 (-3)	*Walker (1978)
Radial diameter of EWVs: no significant difference		Courtois *et al*(1964)
Mean size (area) of EWVs: no difference		*Deret-Varcin (1983)

Table 2.2. continued. Wood structure differences between *Q. robur* and *Q. petraea*, given in the literature. (see notes on first page of table). Table continued on next page.

WOOD STRUCTURE CHARACTERISTICS		AUTHOR
Q. robur	*Q. petraea*	
VESSELS:		
Number of vessels in EW significantly higher (24 / 5 mm TS of ring)	Number of vessels in EW significantly lower (18 / 5 mm)	*Deret-Varcin (1983)
LWV flames widen and bifurcate	LWV flames strap-like	Beauverie (1910) *Walker (1978)

Table 2.2. continued. Wood structure differences between *Q. robur* and *Q. petraea*, given in the literature. (See notes on first page of table).

Differences in sapwood and heartwood proportions in the two species have been recorded. Deret-Varcin found Q. petraea to have a wider sapwood than Q. robur (dimensions given in Table 2.2 above). However, Milsom (1979) found a range of 18 - 54 rings (or 0.5 - 4.1cm range in width) in sapwood of Q. petraea from natural oak woodland, and he estimated a mean sapwood amount for mature oak, of 34 +/- 7 rings by summarising several British and European studies.

Table 2.2 summarises references in the literature to differences in structure of the two species. In the general appraisal of any wood structure differences between Q. robur and Q. petraea, Polge (1984) was of the opinion that the effects of silviculture, site and introgressive hybridisation masked any easily detected species differences. There are often 'transitions' in type of wood structure, as well as 'intermediate' types of oak as defined by leaf and fruit characters. Polge (1984) and Courtois et al. (1964) did however note certain textural and other wood property differences, despite recording no consistently different structural characteristics. Wood properties are described further in Section 2.1.3. below.

2.1.3. WOOD PROPERTIES OF OAK.

European White Oak timber is generally described as having medium to high density and strength properties (e.g. Beauverie, 1910; FPRL, 1936; Farmer, 1972; Desch and Dinwoodie, 1981). It is characteristically tough, hard, tangentially shear resistant, easily cleaved radially and a good bending wood. Thompson (1986) noted that the commonly accepted density and strength properties of oak tend to exaggerate its performance when compared to its actual properties (most of its strength properties, for example, are only slightly higher than those of Scots Pine and Douglas Fir; they are slightly lower than beech timber (Farmer, 1972; Desch and Dinwoodie, 1981)). Mathieu (1897) also recognised this, but commented that "The wood of oak is not of the first rank for any of the properties which distinguish woody material; ...., but it combines all these qualities to a certain extent ... [and] it can reach such dimensions that it is without doubt the most precious of all those which our forests produce.".

Thus the value of oak timber is that it combines a variety of working qualities and aesthetic advantages, with levels of durability and strength not found in many of the woods which are considered suitable for joinery or decorative work. This versatility is due to the great variation in properties which exists between trees and between populations of oak (FPRL, 1936; Farmer, 1972; Polge, 1984). Causes of such variation are reported in section 2.2.2.

The density of oak is about middle of the range for all timbers; mean densities of the air-dry timber, of 460 - 720 g/dm^3 have been reported (FPRL, 1936; Krzysik, 1975; Farmer, 1972; Polge, 1973; Mourey, 1979; Desch and Dinwoodie, 1982 ; Deret-Varcin, 1983).

The heartwood of white oak is classed as durable (5 - 25 years); the sapwood is not durable but, being permeable to liquids, it can be treated (as long as tyloses have not formed).

Oak takes most surface finishes (other than paint) well, and glues satisfactorily; nails and screws hold well in the timber, but ferrous metals are corroded rapidly and cause staining (Desch and Dinwoodie, 1981). Corrosion of iron is due to high tannin content, which can be 5 - 7% of the wood dry weight (Beauverie, 1910).

The main drawbacks of oak as a timber for high grade uses are difficulties in seasoning, due to slowness of drying and to anisotropy of shrinkage on drying. Boards of 3 cm thickness can take five to six months to air-dry, and the wood tends to split and check on drying (Farmer, 1972; Desch and Dinwoodie, 1981). Movement in seasoning is generally described as 'medium' (e.g. Farmer, 1972; Desch and Dinwoodie, 1981), but shrinkage is related to density of the wood (Polge and Keller, 1973; Courtoisier, 1976; Nepveu, 1984b), and consequently movement varies considerably. Tangential shrinkage is generally greater than radial, in the same piece; ranges of reported shrinkage values from green to air-dry state are 5.5 - 9.0% for tangential shrinkage, and 2.6 - 4.3% for radial shrinkage (FPRL, 1936; Polge, 1972; Farmer, 1972; Mourey, 1979). This anisotropy of shrinkage is the cause of seasoning problems when drying rate is uncontrolled.

The 'figure' of radially cut oak (due to the pattern of the wide rays) gives the timber a high decorative value. Best quality logs are therefore prized for radially sliced veneer, which is easily cut if the wood is steamed or boiled (Venet, 1967a).

In the past, knowledge of provenances has guided choice of oak timber for desired properties and therefore end-uses. Provenance names were generally based on port of export (Laslett, 1894; Beauverie, 1910). Appendix Table 2.1 summarises the oak provenances listed by these two authors. Provenance differences would be due in part to species differences (generally sessile or pedunculate), yet timber merchants and woodworkers rarely distinguish between sessile and pedunculate oak when considering wood qualities (e.g. Venet, 1967a). Recently however, interest in species differences is increasing because of the need (and improving ability) to improve genetic stock of oak, and breed for desired qualities. Reported differences in properties of sessile and pedunculate oak are summarised in Table 2.3 below.

WOOD PROPERTIES		AUTHOR
Q. robur	*Q. petraea*	
Maximum density significantly lower (622 & 842g/dm³ in juv. & mature wood)	Max. density significantly higher (808 & 902g/dm³ juvenile & mature)	*Courtoisier (1976)
Mean density significantly lower in mature wood (approx. 150 yrs) 485g/dm³	Mean density higher in mature wood 661g/dm³	" "
Minimum density: no significant difference		" "
Less dense (means of 468 - 524 g/dm³) (significant in certain zones only)	More dense (mean density: 498 - 532 g/dm³)	*Deret-Varcin (1983)
Specific gravity significantly lower SG = 420 - 451	Specific gravity significantly higher SG = 456 - 495	" "
SG lower (mean of 22 clones = 561 cambial age = 16 - 22 years)	SG higher (mean of 30 clones = 595 cambial age = 18 - 24 years)	Nepveu (1984b)

Table 2.3. Wood property differences between *Q. robur* and *Q. petraea*, given in the literature.

* = results from studies where both species were growing on the same site. N.B.: 1) Courtoisier (1976) notes that all trees in her study were grown on a site favouring growth of *Q. robur*. 2) Reports of "density" values are from studies using X-ray densitometry; specific gravities were calculated by gravimetric methods; values derived from samples from the same trees can differ greatly between the two methods, but there is a strong correlation between the two (Courtoisier, (1976); Deret-Varcin, (1983).

Table continued overleaf.

WOOD PROPERTIES		AUTHOR
Q. robur	Q. petraea	
Hardness: No consistent difference		FPRL (1936)
Less hard (torsion torque = 170 cm/kg (not significant difference)	Harder (torsion torque = 178 cm/kg (difference n.s.)	*Courtoisier (1976)
Shrinkage lower (not significant difference) from wet to air-dry		" "
Shrinkage (tangential and volumetric) from wet to oven-dry was lower (n.s.)	Shrinkage higher (not significant diff.)	*Deret-Varcin (1983)
Anisotropy of shrinkage lower	Anisotropy of shrinkage higher	" "

Table 2.3. continued. Wood property differences between _Q. robur_ and _Q. petraea_, given in the literature. (See notes on first page of table).

2.2. THE CONTROL OF WOOD QUALITY IN OAK.

The concept of timber quality depends on the desired end-use. FPRL (1936) stated that oak "should be judged by different standards of quality according to the various intended uses".

As outlined in Chapter 1, timber quality in oak is affected by :

a) tree size and form

b) gross structural defects which over-ride any finer aspects of quality; these could be rot, shake (section 2.3) or severe seasoning degrade.

c) the combined, overall properties of the wood. These are related to anatomical characteristics (section 2.2.1).

d) other defects such as staining, epicormics, and colour variations. These may not diminish structural qualities (though epicormic shoots are unacceptable in veneer butts), but they can affect appearance sufficiently to decrease value substantially. These defects have been studied by other authors e.g. Shigo, (1976) - staining; Wignall and Browning (1988) - epicormics; Venet (1967a) and Courtoisier (1976) - colour.

Therefore, timber quality can be controlled (to a certain extent) by manipulation of wood structure development and reduction of extrinsic causes of defect.

2.2.1. THE INFLUENCE OF STRUCTURE ON WOOD PROPERTIES OF OAK.

The structure of timber has a direct influence on its properties. Specific gravity is considered to be one of the best criteria to use as a general guide to relative strength properties of different timbers, because it reflects the overall structure of the wood (a combination of tissue proportions and cell wall thicknesses) which give it its characteristic properties (Desch and Dinwoodie, 1981). However, the value of density as an indicator of quality in hardwoods has been disputed because their complex wood structures lead to great variation in the possible combinations of woody tissues, and thus in the related properties (FPRL, 1936; Polge and Keller, 1970). The study of wood structure is therefore essential in the investigation of the control of wood quality in oak.

In the following sections which deal with structure/property relationships in oak, only whole-wood properties are included; characteristics relevant to pulp and paper-making are not addressed.

2.2.1.1. THE INFLUENCE OF TISSUE PROPORTIONS AND CELL DIMENSIONS ON OAK WOOD PROPERTIES.

Increased fibre and decreased vessel production generally lead to increased density (Polge and Keller, 1970; Marchal, 1983). However, Taylor and Wooten (1973) and Leclerq (1980: work on beech) pointed out the additional effect of variations in fibre cell size and wall thickness. Density also depends on the amount of latewood vessel in oak. Fletcher and Hughes (1970) showed this relationship to be clear, and sensitive enough to use as a climatological indicator.

Ray proportion is significantly positively correlated with density in many hardwoods (Myer, 1922; Taylor, 1969 and 1975). Myer used ray volume calculations and figures from wood density tables to show the variation between species, and believed that the wood elements associated with the rays were implicated in the density increase. Taylor (1975) and Polge (1984) showed the same correlation within species, but demonstrated that it was the rays themselves which were denser. In oak, the rays become heavily lignified during heartwood formation (Bamber and Fukuzawa, 1985). Hardness and compression strength perpendicular to the grain are positively correlated with ray proportion in oak (Myer, 1922; Deret-Varcin, 1983); shear parallel to the grain is negatively correlated. "Hard" and "semi-hard" oak gave volumetric shrinkage figures of 16% and 14% respectively (Nepveu, 1984b), and shrinkage has also been linked positively to wide ray proportion (McIntosh, 1955).

Tissue proportions can affect colour. Darker wood (much latewood fibre in wide rings) has traditionally been chosen for tough strong ship timber (Venet, 1967a). Courtoisier (1976) found that "yellow" oak had a higher lignin content than "pink", but could find no significant differences in associated wood structure.

Textural properties of oak are most affected by vessel diameter and ring width: large vessels produce a coarse texture, and the varied proportions of vessels across rings of different width produces a variable texture (Marchal, 1983).

Vessel dimensions and conditions may also be important in the natural durability of the timber. Large lumens can provide pathways for biodegrading organisms, but tylosed vessels would be less vulnerable.

Most of the above wood structure characteristics are dependent to an extent on growth rate and ring width (section 2.2.2. reports work on the relative importances of site and genotype in control of wood structure). Ring width is quickly and easily measured, therefore much of the work on structure/property correlations in oak has been in relation to ring width, and is reviewed in section 2.2.1.2. below.

2.2.1.2. THE INFLUENCE OF RING WIDTH ON OAK WOOD PROPERTIES.

INFLUENCE OF RING WIDTH ON DENSITY. Rings in oak can be divided into earlywood and latewood portions (section 2.1.2.). The earlywood is of low density, being dominated by large vessels, while the latewood is of relatively higher density due to its larger proportions of libriform fibres. The width of the earlywood is relatively constant, but that of the latewood varies from year to year depending on growing conditions (section 2.2.2.2). Consequently, the proportions of dense and less dense wood vary with growth rate, and the common generalisation for sessile and pedunculate oaks is that wood composed of wider rings, has denser wood.

The 'wider-rings/denser wood' rule was confirmed as an overall trend for oak by Polge and Keller (1973) and Polge, (1973). However, they qualified this by demonstrating that within any one population of oak, there was a small percentage (about 2 - 3%) of individual trees within which wood density was consistently low, even in very wide rings. Polge (1984) illustrated examples; the low densities of the latewood were due either to the large diameter or abundance of the vessels, or to the scarcity of blocks of libriform fibres. Krzysik (1975) found that density increased with increasing ring width in rings of 0.7 - 2.5 mm, but that the trend then reversed in rings wider than 2.5 mm (both sessile and pedunculate oak were studied, but not separated in these results).

These findings illustrate the complexity of ring-width/density patterns, which arise from varying widths and structure patterns of the latewood. Venet (1967a) believed that latewood density was much higher in Continental than in Western Oceanic provenances of oak - but he made no distinction between sessile and pedunculate oak, as the study was based on harvested timber and there was "no sure method of distinguishing between the timbers of these two species.". The widening of latewood flames through the latewood of pedunculate oak (described by Walker (1978): section 2.1.2.) could be expected to result in a lower mean density for very wide rings of this species than for rings of medium width. Nepveu (1984b) studied clonal material of sessile, pedunculate and red oak; he found significant correlations between mean ring width and specific gravity for sessile oak only (the most important source of the variation was genotype). Similar results were obtained by Deret-Varcin (1983), though the correlation was also significant for pedunculate oaks of narrow mean ring width (i.e. where vessel flames would still be narrow and low-density latewood would be minimal).

INFLUENCE OF RING WIDTH ON TEXTURE. Ring width, by affecting the percentage of latewood in a ring, also affects even-ness of texture: wide rings in ring-porous wood produce uneven texture (Desch and Dinwoodie, 1981). High quality oak is often cut radially, to exploit the figure produced by the wide rays, and texture becomes particularly important. Both uneven and coarse textures are characteristics disliked by veneer merchants (Marchal, 1983).

INFLUENCE OF RING WIDTH ON TIMBER STRENGTH. Ring width and bending strength are positively correlated up to a maximum strength at ring widths of 2.0 - 2.5 mm (Szappanos and Tanka, 1966; Krzysik, 1975) or 3mm after which strength is variable depending on tissue proportions in the late wood (FPRL, 1936). These figures reflect the close correlation of bending strength with density of timber.

The APECF (1983 - quoted in Nepveu (1984c) gave a summary of strength figures at different ring widths for European oak (Q. robur and Q. petraea) which suggested that the trend of increasing strength with increasing ring width continues, even in ring widths above 3 mm (differences in results from those above may be because some studies test strength of individual rings of known width, and others test blocks of rings categorised by mean width). The summary is given in Table 2.4 below:

RESISTANCE TO BREAKING (mega pascals) at:	MEAN RING WIDTH 3 mm (max. 5 mm)	MEAN RING WIDTH 7 mm (min. 5 mm)
Axial compression	40 - 50	50 - 60
Static bending (parallel to grain)	90 - 100	100 - 120
Tension	4	5
Shear (parallel to grain)	11	14

Table 2.4. Influence of ring width on strength of oak timber. (after APECF, 1983).

INFLUENCE OF RING WIDTH ON SHRINKAGE OF OAK. Several authors have demonstrated correlations between ring width and shrinkage of oak. Nepveu (1984b) quoted a mean volumetric shrinkage for European oak of 4.2% for rings less than 5 mm and 7.2% - almost double - for rings over 5 mm wide. Deret-Varcin (1983) found tangential and volumetric shrinkage in Q. petraea to have a significant positive correlation with ring width in the outer heartwood, but not the inner. Significant negative correlations of axial shrinkage with ring width have been reported (Deret-Varcin, 1983) but with the exception of tension wood, axial shrinkage of oak is reported to be minimal and has no economic importance. Venet (1967a) reported that wood with low ring width was favoured for veneer partly because of the reduced warp and shrinkage.

2.2.1.3. INFLUENCE OF TENSION WOOD ON OAK WOOD PROPERTIES.

The presence of tension wood reduces quality of oak timber for virtually all end uses. Density increases with increase in amount of tension wood, because of the typically reduced proportions and sizes of vessels and axial parenchyma (Wahlgren, 1957; Panshin and deZeeuw, 1980). Shrinkage and associated seasoning defects are increased compared to normal wood. Compression strength parallel to the grain, is reduced (Clarke, 1937).

2.2.2. CONTROL OF OAK WOOD QUALITY BY CONTROL OF WOOD STRUCTURE AND PROPERTIES.

Control of wood quality involves control of tree form and branching, control of wood structure and control of defect. Wood structure is determined by the activity of the cambial layer (cambium and adjacent differentiating tissues) which is regulated by relative levels of a number of growth substances. This in turn depends on the position in the tree of any part of the cambial layer, also on the genotype of the tree, and on environmental influences. The effects are compounded, though each may have a stronger influence on some aspects of wood structure than others.

Studies of the contribution of individual factors have been made in various ways. For example, by following within-tree variations through different ring sequences (e.g. Duff and Nolan, 1953); by comparing different and similar genetic types grown under equal conditions (e.g. Nepveu, 1984a); and by analyses of several genotype/environment/structure correlations, which aim to assign different percentages of the variation to known factors (e.g. Pilcher and Gray, 1982). Denne and Dodd (1981) describe the complex interactions of the various environmental controls of wood formation, and review studies of individual factors.

2.2.2.1. GENETIC CONTROL OF WOOD STRUCTURE AND PROPERTIES IN OAK.

Sections 2.1.2 and 2.1.3 describe wood structure and property differences reported between sessile and pedunculate oak (see also Tables 2.2 and 2.3 in those sections). Polge (1972) and Keller _et al_. (1980) also made comparisons of pedunculate oak and red oak (_Q. rubra_).

If genetic variation is to be exploited for selection of stock of a required quality, then the amount of variation within a species is of interest. Large variance between trees within a species has the advantage that breeding programmes are more likely to succeed (Panshin and deZeeuw, 1980). The larger the range of tree types exhibiting the desired wood characteristics, the greater the chance that they are not all linked to undesirable characteristics: for example, Brazier (1985) stated the general rule that "the techniques for enhancing vigour of growth rate are not necessarily those most desirable for enhancing wood quality" - yet Polge found that in 2 - 3% of trees within each oak provenance he was studying, low density wood was characteristic, even in fast-grown wood (section 2.2.1.2.). However, there was still a drawback in this case: the trees which produced low density wood without loss of vigour (potentially useful for production of high quality oak in faster rotations than at present) had a texture and colour which spoiled their quality for veneer timber.

There are numerous references in the literature, to the variability between and within populations of oak; this should be promising for breeding programmes. Krahl-Urban (1957) found greater phenological differences between provenances of sessile and pedunculate oak than between the averages for the two species. Greater differences between trees than between provenance or site have been found in oak wood structure by Farmer and Nance (1969) and Maeglin (1974). Farmer and Nance concluded that field selection of breeding material should be from individual trees. Polge concluded that the reason that comparisons within and between species are often inconclusive may be due to the level at which they are viewed (Polge, 1973). The low-density types of oaks he discovered within populations only became apparent when he examined variations of oaks **within** trial plots of seed from different forests. Comparisons between plots had revealed no significant differences.

Provenance trials have demonstrated that many of such variations within and between populations are, to an extent, heritable (e.g. Krahl-Urban, 1957). This is also important if genetic variation is to be exploited in future crops. More recent tests of heritability in oak have been made by Nepveu (1982, 1984b) and Castera (1983). Nepveu (1982) measured a broad sense heritability of 0.65 for specific gravity in 19 one-year-old clones of sessile oak. Castera (1983) found a strong narrow sense heritability for specific gravity in two year-old Q. rubra. Nepveu (1984b) tested heritability of various wood properties in late juvenile wood of clones of sessile, pedunculate and red oak. Within each of the three species there was a significant difference between clones for specific gravity, tangential and volumetric shrinkages; mean ring width and radial shrinkage were significantly different between clones in sessile and in pedunculate oak. Heritability values for clones within each of the three species were highest for specific gravity, then for tangential shrinkage, then for volumetric shrinkage.

Nepveu (1984a) investigated variation due to genotype and year, of various wood structure characters in pedunculate oak. He measured widths of earlywood and latewood, percentage of vessels in earlywood, and percentage of fibres in latewood, in five rings of 14 clones of pedunculate oak. There were significant differences between trees within clones at the 1% or 5% level for all characters. The effect of year was highly significant for all characters except the width of the earlywood, which was not significantly different between years. In this material, Nepveu showed that genetic variation between clones accounted for 41% of variation in the width of the earlywood, 14% of variation in the latewood, 23% of variation in earlywood vessel percentage of earlywood, and 11% of variation in percentage of fibres in latewood.

The time taken to test heritability and the results of breeding programmes can be extremely long in species like oak, where the mature wood characteristics are not confirmed until at least 15 - 20 years old. It is very useful therefore to know which wood structures and properties show a good juvenile-adult correlation, and can therefore be assessed at an early stage. Polge (1973) found that density of juvenile oak "pre-figured" that of wood at fifty years of age. Other studies of oak within and between sites, have shown good juvenile-adult correlations of mean maximum and mean minimum density and specific gravity (Courtoisier, 1976; Deret-Varcin, 1983).

Sometimes genetic differences will be expressed phenotypically: Enkova and Shirnin (1970) showed genetic differences between two varieties of pedunculate oak (Q. robur vars. praecox and tardissima) to have an indirect effect on wood properties; which variety produced the 'best' timber, depended on the soil type and whether it favoured the growth of that variety. Similarly, Koloszár (1984) found that 'Slav' oak (Q. robur var. tardissima) was more productive than 'common oak' (typical Q. robur)on poor sites, where it would be recommended for planting on account of its superior wood qualities (lower shrinkage and higher static bending strength); common oak was more suitable for planting on fertile sites.

Genotypic variation can be exploited in ways other than selection for breeding. In Eastern Europe, where there are still large resources of primary oak woodland to exploit for timber, many authors have tried to define associations between external tree characteristics (morphological and phenological) and wood structure or properties (Vihrov and Enkova, 1952).

Phenological differences may simply reflect genetic varieties, or in addition may influence wood structure indirectly (via lengths of growing season, or avoidance of defoliator attack for example). Kostov _et al_. (1980) found no link between morphological features of _Q. cerris_ leaves, and wood properties. Although bark-type, flushing time and retention of senescent leaves have all been associated with wood quality in the tree, they concluded that none of these was well enough correlated to use as a selection criterion. Babos (1976) however, found differences in wood properties of two _Q. cerris_ varieties, across eleven different sites. Nikolov _et al_. (1981) described four forms of the 'Vardim' oak (_Q. robur_ from Vardim island in the Danube) in which combinations of flushing-time and bark type were linked to wood quality. In Western Europe also, there is a large resource of timber to be used before the results of recent work on selection and breeding of preferred types of oak can be made use of, and the new crops grown: Savill and Mather (1990) have demonstrated a link between flushing times and mean size of early wood vessels in oak (later-flushing trees within a population tended to have larger vessels); such a linkage could be used for selecting out trees with undesirable wood structure, without need for testing by damaging and time-consuming coring.

2.2.2.2. ENVIRONMENTAL CONTROL OF OAK WOOD STRUCTURE AND PROPERTIES.

Environmental control of wood structure operates a) by influencing growth substance production and cell response (temperature and photoperiod effects), b) by regulating availability of nutrients and water, and c) by pathological interruptions of 'normal' growth. Environmental effects are discrete and easily observed when they become the limiting factor at any stage in the growth of a tree. Water availability is usually considered to be the most common limiting factor in tree growth, with temperature perhaps as inportant in controlling ring width (Dobbs, 1953; Sutcliffe, 1979).

CLIMATIC INFLUENCES ON WOOD STRUCTURE IN OAK. Nearly all early interest in tree rings was in their correlation with climate - especially rainfall. Dobbs (1953) reviewed the evolution of dendrochronological and dendroclimatological studies, and their viability. Trenard (1982) reviewed the whole subject of dendrochronology.

The climatic factors of any year are an important influence on the structure of that annual ring. Milsom (1979) found that between 43% and 71% of ring width and density variation in sessile oak was related to current climate and prior ring width, while 32 - 66% of variation could be attributed to climate alone. Huber (1982) attributed the following amounts of variation to climate in studies of 36 annual rings per tree in sessile and pedunculate oak: earlywood (EW) width - 12%; latewood (LW) width - 34%; vessel proportion in EW - 14%; fibre proportion in LW - 10%. Nepveu (1984a) tested the same characteristics over 5 rings in 14 clones of pedunculate oak, and found the following amounts of variation due to year (including that due to interaction of clone and year): EW width - 7%; LW width - 30%; percentage of vessels in EW - 2%; and percentage of fibres in LW - 10%. Eckstein and Frisse (1979) found that climate influenced annual variation in vessel size of beech and oak, more than it influenced ring width.

The climatic factors of previous years also influence the structure of any annual ring if they markedly alter the food reserves of the tree. For example Kostov (1985) found that the effects of severe drought in Bulgarian oak 40 - 55 years old persisted in ring patterns for three to four years. Myer (1922) found that any decrease in growth season or vigour of oak resulted in reduction of tissue reserved for storage (over-riding any genetic differences).

More specific influences of climatic factors on wood structure which have been demonstrated are as follows:

a) **RAINFALL.** Pilcher and Gray (1982) showed that high rainfall in the growing season was correlated with increased ring width in sessile and pedunculate oak. Reduced rainfall resulted in increased vessel proportion because of reduced latewood (Knigge and Shulz, 1961). Doley and Leyton (1968) suggested that water stress reduced wood production by causing marked reduction in water potential of the tree, which resulted in decreased cambial division and expansion. Under severe drought conditions, cell wall thickness of Pinus radiata was reduced and zones of collapsed cells occurred; similar reaction tissue in young Q. petraea was caused by severe frost damage (Day and Peace, 1934).

b) **TEMPERATURE.** High temperature early in the growing season is reported to supplement the effect of high rainfall and result in increased wood production. Q. robur is said to be particularly responsive to temperature increase (Pilcher and Gray, 1982). Unusually high winter temperature can maintain green leaves on oak through the dormant season (Jones, 1959). Even if less extreme, high winter temperature may maintain a high respiration rate in the tree which depletes food reserves and which is apparently the cause of reduced early wood production the following season (Pilcher and Gray, 1982). Low winter temperature in temperate hardwoods is important for induction of dormancy and normal wood production in the following season (Huber, 1984).

The effect of frost on wood production depends on timing. Late spring frosts damage and kill buds, twigs and even branches, if severe, and cause formation of a 'frost ring' in the wood. Day and Peace (1934) made experimental studies of the effects of frosting in young (two to five year old) sessile oak. They found great variability between trees in the temperature sensitivity of oak, regardless of amount of leafing out; but the critical temperatures reported for injury were -4 to -6° C in early summer, falling to about -8° C at the end of the growing season. The duration of frosting which caused damage could be as little as half an hour. The type of abnormal tissue which developed after freezing was to an extent controlled by the stage of development of the cambium at the time of damage. Day and Peace stated that early spring frosts may produce only a few collapsed cells and a small amount of abnormal tissue (Day and Peace, 1934). Later frosts (during the growing season) caused a marked frost ring.

Frost rings are essentially similar in conifers and hardwoods (Day and Peace, 1934); they are described by Glerum and Farrar (1966) for conifers, and by Harris (1934) for broadleaves. Frost rings observed in these studies were a tangential band of altered tissue within an annual growth ring, and were composed of two distinct zones. The first zone, formed from cells dividing at the time of freezing, was composed of parenchymatous cells, often collapsed, which had unlignified walls. The second zone was of lignified parenchyma cells of abnormal shape (isodiametric) which graded via more normal parenchyma into normal wood. Rays 'passed through' the frost ring and formed part of the undifferentiated parenchymatous tissue, resuming their normal course and structure after the frost ring. Gummosis was also associated with severe frost rings in oak. Autumn damage, after end of late wood formation, could cause apparent spring-frost damage in the subsequent year's ring because over-wintering xylem mother cells were damaged.

Day and Peace (1946) described frost injury to old wood. Tree trunks were less susceptible than branches and twigs because the bark was thicker, but the temperatures would be lower at the base than the top of the tree. They stated that the cambium could be killed, resulting in cankers, or injured resulting in typical frost rings. They collated reports on the severe frosts of 1935/36, and found that oaks showed much greater variability in susceptibility than did other tree species.

Day and Peace (1934) noted the Continental experience that sessile oak was hardier in winter cold, but they found no difference between the two species in experiments of spring frosting.

Other forms of variation in oak wood structure can result from seasons of severe cold weather. Bands of included sapwood called 'moon rings' (or 'double' or 'false' sapwood) can occur in oak heartwood, and have been attributed for nearly a century to extreme winter cold (Jones, 1959). Recent work by Dujesiefken and Liese (1986) showed that the damage which prevented sapwood from changing to heartwood, but allowed normal heartwood formation in rings formed in subsequent years, was due to branches broken during the cold weather. The cambium and last-formed ring were not damaged, but the low temperature prevented compartmentalisation of the damage. Air entered the older sapwood and killed the parenchymatous tissues which would normally be involved in tylosis formation and production of heartwood extractives. Sessile oak seemed more frequently affected than pedunculate, but no link was found between moon rings and site, topography, or stand quality.

c) LIGHT. Hartig (1894) and Weinstein (1926) reported higher ray proportions in oak grown in full light (10 - 12%), than in shaded trees (4 - 8% wide ray). Denne and Dodd (1980) showed that in sycamore and ash, increased light intensity at any level in the tree resulted in increased cambial activity (measured as fibre production) in branches at that level; and Denne (1976) suggested that a similar effect may occur in oak.

INFLUENCE OF SITE ON WOOD STRUCTURE AND PROPERTIES OF OAK.
Reports of the influence of site vary, depending on whether the site factors have been studied separately, or in combination as 'site index'. Zahner (1971) said that site quality probably has a measurable effect on the proportion of vessels in hardwoods, and certainly has a significant effect

on the size of vessels. Zasada and Zahner (1969) found that current site conditions had a "minor and subtle" influence on earlywood vessel parameters, but a strong influence on fibrous latewood of rings in red oak. Neusser _et al_. (1975) showed that both density and wood structure were strongly influenced by site.

Courtoisier (1976) reported marked differences with site in density, shrinkage and static bending strength of mixed sessile and pedunculate oak, but no significant correlation between site and axial compression, hardness or shock resistance. It seems that much of the 'site effect' was due to the silvicultural regime superimposed, as the three sites which produced the 'best' quality timber had very different soils but identical silvicultural systems; however, the timber of poorest quality came from sites with waterlogged anoxic soil.

Kostov _et al_. (1980) found that wood quality of _Q. cerris_ varied more with site than with genetic type. Yet Enkova and Shirnin (1970) found that the interaction of site and genetic effect was important (section 2.2.2.1). This interaction is evident also in the recommendations of Anderson (1950) Koloszár (1984) and Sigaud (1986) that the differing performances of species and varieties of European white oaks on different sites be borne in mind when choosing oak for a particular area.

a) SITE INDEX. Zasada (1968) found that site index influenced the radial diameter of earlywood vessels in red oak (increasing from 250 um to 300 um over a site index range of 38 to 80), but that the factors controlling tangential diameter were relatively independent of site conditions.

Site index explained less than 50% on average (but up to a maximum of 75%) of variation in vessel proportion in a study of red oak (_Q. rubra_) in America (Maeglin, 1974). A mean of 42% of variation in all tissue proportions was explained by site index (Maeglin, 1976). Maeglin found a significantly negative correlation of site index with vessel proportion in red oak, and a significantly positive correlation with fibre. There was a non-significant negative correlation of site index with axial parenchyma and ray proportion (Maeglin, 1974).

b) SOIL TYPE. Soil type is assessed in a number of studies of site effect on wood structure of oak. Moisture retention is important. Evelyn (1729) observed that moist soils produced tougher, less shake-prone timber. Laslett (1894) stated that dry, rocky soil produces hard, compact wood, and that swampy sites give wood of a "soft, spongy texture". Brown et al. (1949) reported this latter effect in the butt wood of American swamp-grown hardwoods: rings with wide latewood had thin-walled cells which conferred reduced specific gravity and strength on the timber. Pryor (1939) attributed the development of thin-walled cells in fast-grown rings, to an abundance of nitrogen in soils of moist, fertile sites. Low nitrogen availability is said to result in over-abundant carbohydrate production and thicker cell walls (Transeau, in Pryor, 1939). Pryor cited as examples, the mild oak grown on the fertile Appalachian slopes, and the "poor quality" hard timber from the low-nitrogen, leached soils of the Southern Lowlands. Zahner (1971) discussed the theoretical effects on wood structure and density of American upland hardwoods, and summarised these in a table, part of which is given overleaf (Table 2.5.).

Myer (1922) found no variation in ray proportions of red and white oak with soil type, but Williams (1942) found that oak from dry sites had broader rays than that from wet sites.

Some influences of soil texture on oak quality are reported. Evelyn (1729) said that 'smoother grained' oak was grown on light sands; this was probably the result of slow growth on constantly dry sites. Venet (1967b) reported that compacted clay causes black veining patterns in veneer of oak.

Nikolov *et al*. (1982) recommend shallow, concave or even slopes, with shady aspect and leached cinnamon forest soils of light texture, for growing veneer quality oak with a low susceptibility to "cracking defects".

RING POROUS WOODS

Wood type	Earlywood production	Latewood production
Good site produces wide annual ring; moderate to high density wood.	Brief period; narrow zone with high proportion of vessels; thin-walled fibres.	Extended period; wide zone, fibres with large lumens; high proportion of storage parenchyma.
Intermediate site produces moderately wide annual ring; high density wood.	Brief period; narrow zone with moderate proportion of vessels; fibres of moderate lumen size.	Moderate period; moderately wide zone of thick-walled fibres.
Poor site produces narrow annual ring moderate to low density wood.	Brief period; narrow zone with moderate proportion of vessels; fibres of moderate lumen size.	Brief period; narrow zone; fibres with small lumen; low proportion of storage parenchyma.

Table 2.5. Summary of theoretical effects of site on annual ring production and wood density in American upland hardwoods. From Zahner (1971).

c) **ASPECT/ALTITUDE/LATITUDE.** In Maeglin's (1974) study of *Q. rubra*, aspect accounted for 30 - 45% of variation in vessel percentage. A study of *Quercus* spp. from different altitudinal belts suggested that altitude affects both macro- and micro-structure of the wood (Novruzova, 1964). Maeglin (1974) found no consistent trends in tissue proportions of *Q. rubra* over many sites across a wide latitudinal range.

d) POLLUTION. Eckstein and Liese (1979) found that pollution effect on xylem production often resembles that of drought. They believed that such changes may be considered as an adaptation by the tree to an unfavourable environment, in the same way that it is suggested that small vessels resist drought stress (Carlquist, 1982; Aloni and Zimmerman, 1984).

2.2.2.3. THE INFLUENCE OF BIOTIC FACTORS ON WOOD STRUCTURE AND QUALITY OF OAK.

The influence of other living organisms on wood structure of oak can be transitory (usually traumatic, e.g. defoliation of tree) or medium to long term (e.g. fungal attack, competition of tree with neighbours).

DEFOLIATION. Sessile and pedunculate oak in Britain are subject to attack by defoliators (section 2.1.1.5.). Severe attacks can cause a reduction in the amount of late wood produced (Winter, 1985), and Wargo (1972) showed that starch depletion was marked in years of severe defoliation. In extreme cases an easily identified ring can develop in which latewood vessels are unusually large (due to changes in levels of hormones following removal of influence of mature leaves) giving the appearance of extra rows of earlywood vessels, and latewood width is markedly reduced (Huber, 1982).

Experimental defoliation of four year-old oak has shown that altered wood anatomy can result when defoliation is total; xylem production throughout the season was of the earlywood type, with no reduction in vessel size, and low proportions of fibres; lesser degrees of defoliation produced morphological changes in the tree, but no major anatomical differences (Hilton *et al.*, 1987).

FUNGAL ATTACK. Schoeneweiss (1959) has shown that in American oak, resistance to attack by *Ceratocystis fagaceae* (a fungus which causes wilt by blocking early wood vessels) is achieved by the tree producing a sharp line of very small cells before the production of large vessels resumes. Mullick (1977) explained that automatic defence against pathogens invading the bark is non-specific and follows a set pattern of cell restoration and chemical defence (see 'Wounding').

WOUNDING. Mechanical damage which penetrates the bark, disrupting the cambium and exposing the wood, can alter wood formation temporarily or for a number of years. To generalise from the work of Shigo and Marx (1977), Pearce (1982) and Shigo (1984): the gross structure of the wood around a healed wound is an inroll of newly formed wood from the cambium at the edges of the damaged area. When the growing edges of new wood meet across the wound-exposed wood, the cambium once again becomes a continuous layer, but it may take some years before the wood forming over and adjacent to the wound returns to normal.

Surface infection is inevitable when a wound removes the protection of the bark, but immediately following the wound, a mass of undifferentiated, parenchymatous tissue develops (large, thin-walled cells). Pearce (1982) has shown that the walls of these cells in pedunculate oak are suberised, and thus resist fungal invasion. This tangential band of reaction tissue was termed the "barrier zone" by Shigo and Larson (1969); it forms wall-4 of the model of "compartmentalisation of decay in trees" (CODIT) (Shigo and Marx, 1977). The other three CODIT walls result from secondary changes in the existing wood (e.g. deposition of phenolics).

The extent of the barrier zone beyond the wound edges varies. In hybrid poplar, maple and birch, its tangential and axial extents appear to be genetically controlled; thus some genotypes are more successful than others in containing rot fungi invading through wounds (Shigo, *et al.*, 1977; Eckstein *et al.*, 1979; Shigo *et al.*, 1983). The barrier zone in British oak species has been observed to extend some distance above and below the causative wound, but not much further than the wound itself, transversely (Pearce, 1984, pers. comm.).

Barrier zones have been shown to form far from wounds, in response to infection from those wounds. Shigo and Tippett (1981) demonstrated this response to infection by the root pathogen Armillaria mellea; Schoenweiss (1959) described a similar response of oak to infection by oak-wilt fungus.

As cell differentiation resumes outside the barrier zone, small regeneration vessels form (Aloni and Zimmerman, 1984). In oak, the number of vessels per unit area in this zone was much less than in pre-wound tissue. Rays have been observed to return as uniseriate only, and gradually aggregate before normal wide ray structure is resumed (Bailey, 1910). Wood structure may remain abnormal for some years following the wound: increases in ray tissue, in number and diameter of vessels (Bauch, 1980) and in amount of axial parenchyma (Bauch, 1980; Tippett and Shigo, 1981) have been recorded. McGinnes et al. (1977) found that many gelatinous-fibres were formed in the year following injury of red oak, and earlywood vessels had infolded walls and contained traumatic tyloses.

Secondary changes in wood structure due to biotic factors have been examined by Bauch (1980), and in ultrastructure by Wilcox (1970). Wilcox summarises the action of rot types: brown rots (mostly in Gymnosperms and felled timber; e.g. Poria monticola) remove carbohydrate from the wood, and white rots (e.g. Armillaria mellea) remove carbohydrate and lignin. White rots were said to colonise vessels and rays, and as they move from the lumens, the first symptoms are radial cracks in the cell walls; they also destroy the middle lamella. A third group, the soft rots (usually non-hymenomycetes and colonisers of felled wood, e.g. Penicillium) are reported to first make use of stored foods in the wood, then attack cell walls. Bacteria were said to act mostly on the ray parenchyma. Work on bacterial degradation in standing trees is noted in Section 2.3.3.4.

2.2.2.4. SILVICULTURAL CONTROL OF WOOD STRUCTURE AND PROPERTIES.

Silvicultural practices exploit species differences and environmental effects on tree growth to achieve particular volume production and wood of a desired quality. Site choice and crop protection, as well as planting, spacing and thinning régimes, are relevant practices. Rendle (1936) stressed the importance of "good" silviculture to get the best out of species and site and said that unsuitable treatment of plantations on what were originally good oak soils showed that "silvicultural methods constitute a factor of the first importance in the production of good quality oak".

In oak, because wood structure varies across the ring and properties can be influenced by altering tissue proportions, control of ring width has been the primary objective of the silviculturalist (Venet, 1967b). The balance of height and diameter growth is also important however: in the 15th Century, oak was commonly raised at very close spacing; this produced straight-grained oak, suitable for posts and cleaving. In the 16th and 17th Centuries, coppice-with-standards was a usual method of raising oak: the more open-grown trees were valued for ship timber, and the coppice yielded tan-bark and wood for charcoal. The wood of open-grown pollard oaks was sought after for its variable, rough grain which was considered ideal for mill machinery, and trees with twisted grain were preferred for piles or posts under compression (Evelyn, 1729).

In recent decades the variety of oak timber-types required in Britain has diminished, and recent silvicultural innovations have aimed to reduce rotations of trees for sawtimber. The slow (and costly) establishment of oak can be reduced by the use of translucent plastic tree shelters (Tuley, 1983); this method has been so successful that it is now in widespread use (Frearson and Weiss, 1987), despite the fact that long term effects on tree health and wood structure are still being tested. Following establishment, the 'free growth' method of oak silviculture described by Jobling and Pearce (1977) keeps trees at conventional spacing until pole stage, then opens the canopy with early selection and pruning of dominants for final crop trees. The crowns are then kept from competing, by regular crown thinning, with the aim that a yield class six plantation will reach sawlog size by 70 years instead of the usual 150 years or more.

Venet (1967b), Pardé (1978), Oswald, (1981), Polge (1984) and Evans (1984) have summarised the recommended silvicultural methods for modern requirements of European oak timber.

2.3. SHAKE AND SPLITTING IN TIMBER.

2.3.1. IDENTIFICATION OF SHAKE.

The term 'shake' describes splitting faults within the structure of wood or rock. In timber, the term generally applies to fresh wood of standing trees, though once present, it will be found in the seasoned timber also. The defect of shake, its prevalence on certain soils and its importance to timber quality of oak, has been recognised for centuries (Evelyn, 1729; White, 1788; Laslett, 1894; James, 1939). However, its cause has never been understood and it has often been confused with various seasoning defects which develop in felled timber. Laslett describes "....other defects, also expressed by radiating fissures which look very similar to the rest [seasoning defects], to the inexperienced eye, but which are due to quite other causes, often operating while the tree is standing in the forest.". Clearer definitions of the defect are given in more recent timber texts (e.g. Erteld _et al._,1964; Jane, 1970). Even then, some fail to separate seasoned and standing timber, and attribute cause of shake to post-felling events (Corkhill, 1948).

The simplest general definition of shake in timber is that given by Panshin and deZeeuw (1980), "...longitudinal separations of wood in the standing tree.". Appendix Table 2.2. gives the British Standards list of definitions and illustrates the range adopted by other authors.

Shakes are described by their appearance in the cross section of the log. "Ring shakes" are tangential splits within or between growth rings. "Star shakes" split the wood in a radial direction from the pith, and may be few or numerous at any one level in the stem (Butin and Volger, 1982). Both ring and star shake are more frequently found in the lower part of the stem only, but if found higher in the tree they will also be at the base. The axial extent of shakes can be from below ground level, and up to 10 m up the bole (Kandeel and McGinnes, 1970), but can sometimes be less than 1 m in the butt only (Garfitt, 1983, pers. comm.). Shakes are very rarely found in trees of smaller diameter (below about 35 - 30 cm diameter) (Kubler, 1987), irrespective of age.

In oak, frost-cracks are an exacerbated form of shake. Their origins have been demonstrated to be the same as shakes (Butin and Volger, 1982) and they are therefore included with shakes in the following sections on associated growing conditions. Morphological studies of frost cracks are described in Section 2.3.6.

"Felling cracks" and "tension splitting" may give a similar appearance to shake in timber. Felling damage in eucalypts has been shown to produce clean ring shakes along a structurally weak but previously intact ring (Barnacle and Něcessaný, 1972); and James (1939) said that the shock of felling is said to produce star shake. He also stated that "The liability to shake is again held by certain authorities to be less in winter-felled timber than in summer-felled, and less in axe-felled than in sawn-felled timber.". The defect of "tension-splitting", attributed to growth stresses in

Eucalyptus spp. and Fagus sylvatica, is not regarded as a true shake as it develops with growth stress release on felling or during conversion, i.e. the splits are not present in the standing tree (section 2.3.7).

Identification of shake in the standing tree, although attempted by some merchants buying standing timber, is reported to be unreliable (James, 1939; Garfitt, 1983, pers. comm.). Ribs and shallow grooves in the bark of an oak are supposed to indicate a shaken interior (Evelyn, 1729; James, 1939), but these can be due to damage of the outer wood which is not associated with shake (James, 1939). Moreover, shake is often found in stems which outwardly appear sound and of excellent form (Rol, 1948).

Shake (ring, star or both) is found in a variety of tree species, temperate and tropical, angiosperms and gymnosperms. Depending n species, the form of the shakes varies. They may have typical organic or inorganic deposits associated, which are n t normal heartwood extractives (Bauch, 1980), and which are the result, not the cause of the shakes (Kubler, 1987).

In Britain, shake is commonly found in the hardwoods sweet chestnut (Castanea sativa) and oak (Quercus petraea and Q. robur), and in one gymnosperm - yew (Taxus baccata). No reports of shake occurring in ash (Fraxinus excelsior), another common British ring-porous hardwood, have been found; some state positively that it never occurs in this species (Garfitt, 1983, pers. comm.). Early literature mentioning shake in Great Britain described the macroscopic appearance of shake in the cross section and referred to counties or soils associated with its incidence (Evelyn, 1729; White, 1788; Laslett, 1894; Davy, 1936).

James (1939), writing specifically on the subject, described the occurrence of shake in British timber and speculated on its causes. He collated his own observations and reports of shake incidence in various species (predominantly sweet chestnut and oak, but occasionally also elm, willows, poplar, horse chestnut, beech and lime). Site conditions and stand history were examined, but not the structure of the timber itself. James concluded that "The appearance of 'shake' in timber is evidence that there is 'something wrong', ..." and that "the root of most of the trouble, is the planting of the species [which shake] on sites which are unsuited to them.". James suggested that species may be unsuited to sites because they are frost-tender and planted in frost-hollows, not wind-firm and planted on exposed sites without provision of shelter, naturally deep-rooted but planted on shallow soils, etc.. The affected trees are therefore less able to cope with the agents causing shake, which James listed as: soil conditions unsuitable to the growth of the species, frost, wind, injury, and perhaps felling shock.

2.3.2. SHAKE IN OAK.

2.3.2.1. INCIDENCE OF SHAKE IN OAK.

In Britain, a survey of World War II fellings in 92 oak stands more than 100 years old in England and Wales, suggested 54% of these stands were "appreciably" affected by shake; "appreciably" seemed to average 38% of butts badly affected. (Brown, 1945).

In Europe, Galoux (1978) reported that red oak (Q. rubra) planted on three sites in Belgium, yielded 2% of trees with ring shake and 34% with star shake. The figures were higher for sessile and pedunculate ("European") oak: 27% ring shaken and 41% star shaken on some soils and a total of 31% shaken on others. Thill (1980), also in Belgium, reported a survey of 5068 red and white oak logs over 80 cm diameter: 18.3% of red oak and 4.9% of white oak were star shaken and 8.3% of white oak were ring shaken. These studies illustrate the great variation in severity of shake between stands.

In the USA, a survey at nine timber mills in South Central Missouri found that 29% of oak logs were shaken; red oak was more prone to shake than white, and ring shake was the most frequent form (McGinnes, 1965).

2.3.2.2. THE ECONOMIC IMPORTANCE OF SHAKE IN OAK.

Laslett (1894) said that timber merchants regarded shake as second only in importance to the problem of major rots. In the Missouri survey reported by McGinnes (1965), ring shake was considered the more severe form of shake in terms of loss on conversion. However, there will be significant loss on conversion even if only a few radial splits are evident in the butt, because the plane in which the splits lie further up the tree may be quite different (Laslett, 1894; Volkert, 1940 quoted in Kubler, 1987); conversion through the splits at the butt may therefore be no solution. Similarly, such butts are unusable for sliced or peeled veneer.

There are few figures to back the general opinion that shake is an economically important defect, but it is accepted that shake is a serious down-grading factor in timber quality (Paterson, 1980; Denne and Dodd, 1982; Anon, 1984), and this inevitably affects the financial interests of both growers and millers of timber. Shigo points out that shake defects can be more serious than decay, because decayed wood is often compartmentalised by the tree, and high quality timber can be cut from round it - whereas star shakes, once started, extend continuously towards the bark (Shigo, 1972). The relative importance of rot and shake are likely to vary however, depending on location, age and history of stands: a sawmill survey of volume loss of oak in the Tennessee Valley (USA), found that on average rot was most important (1.2% of total volume produced), then poor form, then shake at 0.1% volume loss (Tennessee Valley Authority, 1956); volume loss due to shake increased very slightly over log diameters of 30 - 45 cm, but volume loss due to rot increased fifteen-fold over log diameters 20 - 45 cm.

2.3.3. PROPOSED CAUSES OF SHAKE.

Some factors are associated with both forms of shake. These will be addressed first; those factors which appear to be associated specifically with ring or star shake are noted separately in the following sub-sections.

2.3.3.1. ENVIRONMENTAL FACTORS ASSOCIATED WITH SHAKE.

S il conditions have long been associated with incidence of shake (Plot and Bobart, 1684; James, 1939). Acid sands, gravels and soils with much stone (even clay with flints) have been linked with high incidences of both forms of shake in oak, whereas deep loams and good clays have been linked with low incidences of shake (Evelyn, 1729; White, 1788; Laslett, 1894; Davy, 1936; James, 1939). James suggested that shallow or compacted soils and those with "unsuitable mineral composition" produce shaky trees; and Anderson (1950) associated occasionally droughty soil with ring shake in sweet chestnut.

In France, Lachaussée (1953) found that low calcium, and high iron levels characterised the only shake-prone soil out of three different soils growing Q. robur on otherwise comparable sites (the soil was also compacted and leached). The only American work investigating the possibility of a shake/site correlation, is McGinnes' (1968) study of walnut, in which he concluded that there was no large scale geographical link with the amount of shake in 10 500 butt logs of Missouri walnut!

Denisov (1980) showed that the incidence of 'frost crack' in oak of the Eastern Russian plain, was greater on sites of low site-class; the incidence of the defect was also influenced by the Continental climate of the area, and increased with increases in tree diameter (age-related), and decreases in stand density. Retention of underwood was recommended in order to reduce frost-crack; however, presumably this is proposed in order to reduce the effect of cold on stems, in which case only the external expression of internal shakes would be controlled, and the basis of the problem would not be solved (see Section 2.3.6. for the explanation of frost-crack formation given by Butin and Shigo (1981)).

Shake in American red and white oaks, elms and cottonwood has been associated with 'bacterial heartwood' (Section 2.3.3.4.) which is most prevalent in trees grown on waterlogged sites (Ward et al., 1969; Ward, 1982); infected trees usually showed root or root-collar injury also; red oaks were more prone than white, with the latter only affected in the most swampy areas.

2.3.3.2. ASSOCIATION OF WOUNDING WITH DEVELOPMENT OF SHAKE

In an article which summarised twelve years' work on decay in living trees of a number of species, and drew particularly on a study of 23 oaks (dissections of trunk, butt and roots of Q. rubra and Q. alba), Shigo (1972) concluded that "All shakes were associated with wounds ..... But all wounds did not lead to shakes." In reference to ring shakes, he stated that "The wall of altered cells [which form subsequent to wounding], and the changes in the tissues on the inner side of it, are the keys to understanding shakes." The causes of wounding which lead to the structural weaknesses said to cause ring shake and star shake are detailed in sections 2.3.4. and 2.3.5. below.

2.3.3.3. WOOD STRUCTURE PATTERNS CHARACTERISTIC OF SHAKEN TREES.

Savill (1986) analysed the overall character of the wood of shaken and unshaken oaks (Quercus robur and Q. petraea); ring and star shake were treated together. He found that of six wood structure characteristics measured, only the diameter of earlywood vessels was significantly correlated with the presence of shake (the other characteristics measured were earlywood width, earlywood vessel frequency, ring width, mean width of wide rays, and percentage of wide ray). The trees with the larger diameter earlywood vessels were more likely to be shaken.

Cinotti (1987) studied wood structure patterns in frost-cracked oaks (Q. robur and Q. petraea), and found a significantly lower percentage of earlywood, and significantly larger mean areas of individual earlywood vessels, in cracked trees compared to sound trees. He found no significant differences in percentage of latewood fibre (despite differences in specific gravity), vessel percentage in earlywood, or ring width.

Wood structure patterns peculiar to shake zones are described separately in Sections 2.3.4. and 2.3.5.

2.3.3.4. MICROBIOLOGY OF SHAKES.

American researchers have isolated anaerobic and facultative anaerobic bacteria from shake surfaces, in particular the anaerobes Clostridium spp. (Ward et al., 1969; McGinnes et al., 1971). Ward et al. made consistent isolations of anaerobic bacteria from the root, root-collar and lower bole heartwood of apparently healthy oak, elm and poplar trees which contained shakes. Ward and Shedd (1979) found that no ring shake they examined in black oak (Q. velutina) was without bacterial colonies; the usual niche of the bacteria was the bordered pits between vessels or between early wood tracheids and vessels. Any fungi were regarded as secondary colonisers. The bacteria caused a sour smell (fatty acids) (Ward et al., 1969; Ward and Zeikus, 1980).

McGinnes (et al.. 1974) isolated bacteria and non-hymenomycetous fungi from shake surfaces in oak; they and Ward et al.(1972) suggested that shakes develop in wood which has been weakened by bacterial degradation of the middle-lamella between cells.

It is believed that these bacteria invade the wood when the tree is wounded and probably are the cause of 'wetwood' formation. Wetwood is a condition where some or all of the heartwood develops a high moisture content and alkalinity; it is n t decayed by fungi, but is mainly colonised by bacteria. Discolouration of the wood, and biochemical changes (most noticeably presence of fatty acids) characterise this wood (McGinnes and Wu, 1973; Ward and Zeikus, 1980).

Schink et al. (1981) described wetwood in American elms and cottonwoods as being part of an "anaerobic microbial ecosystem composed mainly of fermentive Clostridium, Bacteroides, Erwinia, Edwardsiella, Klebsiella and Lactobacillus species." They stated that their work did not prove a role for bacteria in wetwood formation, but described activities of bacteria found in association with wetwood. A prevalent bacterium in all wetwoods examined was a pectinolytic Clostridium species (the obligative anaerobe C. butyricum), and pectin decomposition was the "most dynamic metabolic activity expressed by the microbial population" associated with wetwood in hardwoods. This pectinolytic activity involves degradation of the middle-lamella between cells, and of the torus of bordered-pit membranes between sapwood vessels and rays (Schink et al.), 1981; Owen and Wilcox, 1982). Schink et al. noted that middle-lamella degradation due to pectinolytic activity may explain the tendency of wetwood to develop shake and frost-cracks in standing trees, and checking defects in seasoning timber. Wetwood without the strong pectinolytic bacteria will not develop shake and honey-comb (Boone and Ward, 1977), and Ward (1983) said that although not all trees with wetwood have shake, all trees with shake have wetwood.

Some authors believe that the secondary weakening by bacteria aggravates the initial weakness of wound-reaction tissue, because ring shakes develop later in the weak zone (Kandeel and McGinnes, 1970; Chang, 1971; McGinnes *et al.*, 1974). Shigo (1984) stated that boundaried wood round wounds is the primary point of micro-organism attack in wood products; and McGinnes (1968) found that stained ring shake (i.e. bacterially colonised) in walnut had a far greater longitudinal extent than unstained, implying bacterial aggravation of the weakened areas. In conifers however, various authors have found middle lamella breakdown to be the sole weakness associated with ring shake, in the absence of any other structural modification of the wood (Schroeder and Kozlik, 1972 - Western hemlock; Ward and Zeikus, 1980; Owen and Wilcox, 1982).

Ward and Zeikus (1980) stated that wetwood bacteria remove hemicelluloses from between the microfibrils of the cell walls, and thus cause a reduction in specific gravity of the wood. They explained the dark stain of wetwood as being due to oxidation of bacterial by-products, the actual colour depending on bacterial type. However, Schink *et al.* found that microbial degradation of the structural polymers (lignin and cellulose) was not part of the wetwood 'syndrome' (Schink et al., 1981). Ward and Pong (1980) made a thorough review of the nature of wetwood and the implications for timber production.

Wetwood bacteria can invade via stem wounds or root damage (branch wounds seem a less likely route, even though branch wounds are the entry point for many rot fungi, because shake nearly always develops at the tree base and extends upwards). Stem wounds can have a number of causes: mechanical damage during silvicultural operations, animal damage, fire, or other disruption of the bark allowing entry of pathogens to the wood. Root damage could result from abrasion, die-back of debilitated roots in anoxic soils, drought or toxic conditions, or from lesions caused by root pathogens such as honey-fungus (which attack more successfully those trees stressed by drought or defoliation) (Rishbeth, 1980).

The alterations caused by wetwood bacteria may enlighten some un-explained observations in the literature. Evelyn (1729) advised against "stumping back" of seedling oak because the wood which develops is red in colour and not favoured by timber merchants; this technique was used to improve vigour of sl w-to-establish transplants, but represents substantial wounding. Courtoisier (1976) reported that in France the oak with red heartwood which is disliked by French timber merchants had a low lignin content, and that it warped excessively on drying: this ties in with the seasoning degrade observed in 'bacterial oak' which initiated the American research into wetwood.

2.3.3.5. MECHANICS OF SHAKE DEVELOPMENT.

The formation of shakes has been studied from the aspect of mechanics of wood failure by Schirp et al. (1974; experimental freezing of wood), by Leban (1985; in sweet chestnut) and by

Cinotti (1987; in sessile and pedunculate oak). Work implicating the role of growth stresses in shake formation is noted in section 2.3.7.4.

2.3.4. FACTORS ASSOCIATED WITH FORMATION OF RING SHAKE.

Corkhill (1948) suggested that ring shake might be due to cambial damage arising from wounds, lack of nutrients during growth, or termite attack in tropical trees; but no extensive studies were made until the 1960s, since when a number of studies have been carried out in the USA. For example: Shigo, (1963); McGinnes, (1968); Kandeel and McGinnes, (1970); McGinnes _et al._, (1971); Chang, (1971); Ward _et al._, (1972); Shigo, (1972); McGinnes _et al._, (1973); McGinnes _et al._, (1974); Shigo _et al._, (1979). These studies have arisen from research into wound response and pathology of hardwoods; most deal solely with ring shake, and examine the defect in relation to microscopic wood structure, microbiology and wood chemistry.

2.3.4.1. WOOD STRUCTURE ASSOCIATED WITH RING SHAKE.

GROSS WOOD STRUCTURAL ASSOCIATIONS WITH RING SHAKE. Gross structural observations in many studies of ring shake have shown that cambial damage usually occurred somewhere in the tree, in the same annual ring as the ring shake. Various agents of damage have been identified: wounding during forest operations and bark-stripping by animals (Chang, 1971 and 1972; Shigo, 1972; McGinnes _et al._, 1971; Butin and Volger, 1982); and fire scorch (Laslett, 1894; McGinnes _et al._, 1971; Shigo, 1972). Pecking by "sapsuckers" (birds) has been shown to be associated with the face of ring shakes in Eastern hemlock (_Tsuga canadensis_) (Jorgensen and Lecznar, 1964). Shigo demonstrated an association between sapsucker injury and ring shake in eastern hemlock, birches, maples and beech

(*Fagus grandifolia*); he found that the extent of the ring shakes beyond the points of injury was far greater in the hemlock than in the hardwoods (Shigo, 1963).

Loss or breakage of branches near to the bole, allowing invasion of microorganisms, has also been proposed as a cause of ring shake, following gross anatomical observations (Laslett, 1894; Shigo, *et al.*, 1979); Hartig (1894b) describes the formation of rot defects within rings, resulting in ring separations in pines and spruces, due to the invasion of *Trametes pini* through breakages of live branches. In all these cases, the development of the separation is related to, and contained within, the ring structure of the tree.

Arrested heartwood development has been associated with shake: Igmándy (1969) reported a close positive correlation of presence of ring and star shake with presence of false heartwood in *Quercus cerris*; healthy trees with normal heartwood were usually sound. Shigo (1963) reported that ring shakes opened on drying, along the line which was the sap/heartwood boundary at the time of the wounding which caused ring and star shake in the tree.

POSITION WITHIN RINGS, OF RING SHAKE FAILURES. Reports on the positions of ring shakes vary. McGinnes *et al.* (1974) found that ring shakes may develop anywhere within the ring or between rings of red and white oaks and eastern cottonwood (*Populus deltoides*), but that separations within the latewood or along the latewood-earlywood boundary were most usual. Ring shakes have also been observed within the latewood, on the boundary of normal and wound tissue or of false latewood (Chang, 1971; Wu and McGinnes, 1974; McGinnes *et al.*, 1974). Splits at the end of the ring (on the LW/EW boundary) are reported in *Castanea sativa* (Saya, 1962), *Quercus coccinea* (Wu and McGinnes, 1974), and western conifers (Meyer and Leney, 1968). Koehler (1933) reported a separation within the early wood of Western hemlock, and Meyer and Leney (1968) observed the same in other conifers.

Shigo (1972) suggested that the position of the shake depended on the time of year of the causative wounding. Panshin and deZeeuw (1980) said that a ring shake tends to run in the latewood because crack propagation is greater in denser material.

MICROSCOPIC WOOD STRUCTURE OF RING SHAKE ZONES. The ring shake zone is frequently reported to coincide with abnormal patterns of wood structure. The reported patterns are various, and can be due to wounding or to changes in growing conditions; they comprise traumatic tissue, or else changes in size and proportions of normal cell types.

Traumatic parenchyma and increased amounts of normal parenchyma have been observed on the bark-side of the ring failure (Boyd, 195 b; Kandeel and McGinnes, 1970; Wilkes, 19 6). Kandeel and McGinnes (1970) reported higher percentages of gelatinous fibres to the pith side of ring shake in Q. coccinea; yet McGinnes et al. (1971) found gelatinous fibres to be abundant on the bark-side of the shake year in walnut (Juglans nigra), though absent adjacent to the shake separation itself.

Modified vessel type and number are reported in oak (Kandeel and McGinnes, 1970) and in eucalypts (Wilkes, 1986); the type of modification seemed to depend on whether it was due to wound reaction or to environmental conditions. The pattern reported in oak was a decrease in vessel size from the pith-side up to the shake, followed by larger than normal vessels immediately following the shake; it was suggested that this was due to abnormal growing conditions.

Pearce (1982) found that the abnormal wood formed following wounding of pedunculate oak (Quercus robur) comprised layers of parenchymatous cells resembling those reported as associated with shake by American authors; the decay resistance due to suberisation of these cells was very strong, but Pearce points out that "If predisposition to shake is found to be correlated with the resistance of the wall 4 barrier, the resulting loss of timber quality could negate the usefulness of enhanced decay resistance."

ULTRASTRUCTURAL STUDIES OF RING SHAKES. Ultrastructural studies of ring shakes have also been made. The path of a ring shake is most often reported as being between cells, rather than tears across cell walls (Koehler, 1933; Jorgensen and Lecznar, 1964 - Western hemlock; McGinnes, 1968 - *Juglans nigra*; McGinnes *et al*., 1971 - various hardwoods). Kandeel and McGinnes (1970) reported 82% of failures in *Q. coccinea* as being middle lamella separations in tangential walls; they found no trans-wall ruptures in vessels. Meyer and Leney (1968) working on conifers, reported middle lamella separations in latewood, but cell wall tearing in earlywood; and McGinnes *et al*. (1974) found that earlywood vessels of red and white oaks were more often torn across walls than separated at middle lamella. Wilkes (1986) reported trans-wall failures in parenchyma or vessels as the usual path of separation in eucalyptus. In the false latewood of walnut which developed a ring shake, McGinnes *et al.* (1971) found that the middle lamella and S2 layer of the cell wall were of normal structure - but the S1 layer was thin and poor.

2.3.4.2. ENVIRONMENTAL FACTORS ASSOCIATED WITH RING SHAKE.

TRAUMATIC EVENTS. Tree response to traumatic, extrinsic factors results in the wood structure aberrations associated with ring shake formation described above (Section 2.3.4.1.).

EXPOSURE TO WIND. The action of strong winds bending or twisting trees has also been cited as a cause of ring shake. Janes (1939) proposed that the greater manifestation of ring shake in the butt could be due to the action of wind because the leverage exerted by swaying stems would be greatest at the base. Koehler (1933), explains how the mechanics of this are unlikely: a whole tree can only fail in shear if affected by internal stresses, or if it has abnormally low shear strength. Moreover, there is no evidence of peripheral damage or compression failures accompanying ring shakes, which would be expected if wind bending was the cause. Barnacle and Něcessanÿ (1972) discount wind causing shear, on the basis that the effect (if it existed) would operate more at the top of the tree - but the shakes are more common at the base. There may be indirect effects of exposure to wind which increase the risk of ring shake formation; for example, wind causes branch breakage and abrasion and thus barrier zone formation and the predisposition to ring shake.

ASPECT AND SLOPE. Watts (1987) showed that frequency of ring shakes in sweet chestnut (Castanea sativa) in some sites in Britain was greater in the North-West side of trees on a West-facing slope, and the North side of trees on a North facing slope; he concluded that a combination of Northerly aspect and downhill side of the bole were the associations with frequency of shakes within trees. The same study investigated associations between amount of shake and particular annual rings; mean spring temperatures of the years around the shake years were the most strongly correlated factors, and rainfall figures did not seem to be important.

By contrast, Auvray's (1978) study of ring shake in sweet chestnut in South France, suggested that there was a weak tendency towards more shake in trees grown on South-facing, rather than North-facing slopes. Topography was not generally related to incidence of shake, but high incidences occurred in trees grown on terraces.

2.3.4.3. BIOCHEMISTRY, MICROBIOLOGY AND CHEMISTRY OF RING SHAKE ZONES.

Anatomical studies using staining techniques have found the cells of ring-shake zones to be incompletely lignified. Saya (1962) found that the middle lamella of cells in a ring shake zone in Castanea sativa had an unusually low lignin content; lignin in cell walls was low also. Barnett (1976) found that the cells which collapsed and produced a ring shake in Pinus radiata under conditions of severe drought, were thin-walled and unlignified; they had formed false rings in response to spasmodic watering during the drought.

McGinnes et al. (1971) however, showed that the actual lignin content of a shake ring in Juglans nigra was 5% higher than that of a control ring. They also demonstrated that there were higher amounts of a) alcohol-soluble and b) water-soluble extractives in shaken than in unshaken rings of Juglans nigra, which they proposed could be either the products of a) lignin degradation and b) carbohydrate degradation, or the result of a) incomplete lignification and b) "immaturity" of xylem cells. They concluded from combined anatomical and biochemical evidence, that both arrested cell maturation and microbial degradation contributed to weakening of cells in the ring shake zone. McGinnes et al. (1974) confirmed the presence of bacteria and non-hymenomycetous fungi in such zones.

McGinnes and Wu (1973) thought that a change in lignin content of the wood may be associated with wounds, and that such changes may be characterised by a weaker middle lamella between cells; they also showed that there is a difference in lignin content between early- and latewood. They suggested that these facts could explain the usual position of shakes at the earlywood-latewood interface, or at that between normal and wound tissue.

The association of inorganic substances with shake zones is little investigated. McGinnes *et al.* (1971) recorded high levels of calcium, and similar distributions of magnesium and potassium in the vicinity of a ring shake in black walnut.

2.3.4.4. GROWTH RATE AND RING SHAKE.

EXTREMES OF RING WIDTH. Ring shakes have been observed to occur in rings of abnormal width, compared to the surrounding wood. Plot and Bobart (1684) noted that a ring shake will occur between an unusually wide ring, and the following rings. Kandeel and McGinnes (1970) observed this same pattern in scarlet oak (*Q. coccinea*).

TREE VIGOUR. Auvray (1978) and Watts (1987) found no association between incidence or severity of ring shake in sweet chestnut and vigour of the trees (i.e. the diameter at a given age). McGinnes (1968) found no association between ring shake in walnut, and mean growth rate, growth pattern, form or age of the trees.

2.3.4.5. PROPOSED MECHANISMS OF RING SHAKE DEVELOPMENT

Shigo (1972) proposed the following mechanism to explain the association of shake with old wounds. Following wounding, the barrier zone (wall-4 of the tree's compartmentalisation reaction; section 2.2.2.3.) becomes a line of structural weakness where the ring shake forms; microorganisms which entered through the wound colonise behind the barrier zone, degrading and weakening the zone further; then as the tree ages, internal mechanical stresses, perhaps aggravated by wind movement, cause failure of the weak zone: a ring shake. He noted that the time of year of wounding may be of great importance because it influences the speed and strength of the healing and protective responses of the tree. Evidence for such a sequence of events, and refinements of the model have been proposed by McGinnes *et al*. (1971), Phelps *et al*. (1975), Shigo (1984).

Anatomical studies of ring shake in eucalypts (*E. maculata*) suggest that secondary degradation by bacteria is not always a factor in ring shake formation; Wilkes (1986) found ring shake was associated with wounding, but the separation was triggered by drying stresses in the felled tree, and occurred in weak, anatomically abnormal, post-wounding tissues, and not at the usual point of failure (the interface of tissue present at time of wounding, with that formed immediately after).

In sweet chestnut (*Castanea sativa*), the ring shakes are not always due to wounding. A thorough study of chestnut in France by Chanson *et al.* (1989), found that 6% of logs from a wide range of sites and silvicultures had ring shake associated with trauma (wounds or rot), while 18% had ring shake with no associated traumatic wood formation. The majority of the shakes described became apparent some time after felling, or during steaming and conversion. The trauma-associated shakes were attributed to old fire and animal damage and led to major ring defects. The non-traumatic groups of ring shake described by Chanson *et al*., overlap with defects categorised as due to felling and seasoning (i.e. not true shakes) as defined by other authors, but cause ring separations similar to traumatic ring shake in sweet chestnut. The proposed causes of the non-traumatic group of shakes were a) poor radial cohesion between the wood elements (genetic variation was implicated/speculated in this), b) release of severe growth-stresses on felling or conversion, and c) drying stresses, which are exaggerated in large dimension timber where the outside dries more quickly than the core, and anisotropic shrinkage causes the damage.

2.3.5. FACTORS ASSOCIATED WITH FORMATION OF STAR SHAKE.

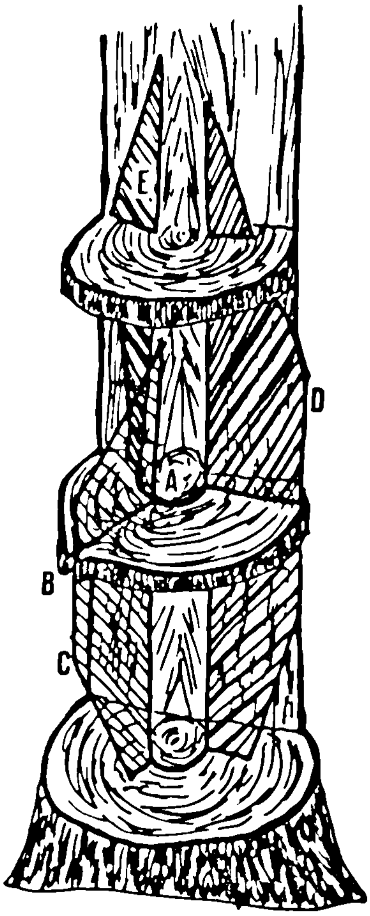
2.3.5.1. WOOD STRUCTURE ASSOCIATED WITH STAR SHAKE.

MACROSTRUCTURE. Hartig (1894b) described three types of radial crack in oak: associated with reaction to sunscorch, and to frost damage, and associated with accelerated growth.

Volkert (1940, quoted in Kubler 1987), said that the direction of the splits of star shake in pine logs depended on eccentricity of the tree and pattern of internal stresses. Thus, in oval stems the main split would lie along the short axis of the cross-section; and in longitudinal view the splits would appear to follow changing radial planes because they follow the (spiral) grain for a certain distance, then "jump back" to the original orientation.

Shigo (1972) found that star shakes were always associated with central pockets of decay resulting from low wounds when the tree was young, or from decayed coppice stubs which had become incorporated in the main stem. A further study of more than forty oaks (Quercus rubra, Q. alba and Q. montana) confirmed these findings (Butin and Shigo, 1981) and added the information that star shakes were invariably associated with ring shakes at some point in the trunk, also.

Butin and Volger (1982) found that in 40% of the 25 oaks they studied in Germany, star shakes began at occluded former bark wounds or arose from the ring shakes caused by these - Figure 2.3. overleaf is taken from their diagram showing the three dimensional layout of three star shakes originating from an earlier wound and ring shake. The remaining 60% of star shakes examined by Butin and Volger, started from the centre of the stem.



A - Original wound and consequent ring shake.

B - Rib formed by healing and re-splitting of primary crack.

C - Primary crack.

D, E - Secondary cracks originating from ring shake.

Figure 2.3. **Three dimensional layout of three star shakes demonstrating origin from an earlier wound and ring shake.** From Butin and Volger (1982).

MICROSTRUCTURE. Amos (1953) studied small radial splits in spruce, Douglas Fir and Pinus radiata. These developed in the earlywood of rings, and although they did not extend into the latewood of those rings, they sometimes extended towards the pith and the boundary with the late wood of the previous ring; longitudinally, they were up to about 30 cm in extent. Amos found that these splits occurred along radial lines of thin-walled earlywood tracheids which had collapsed due to adverse growing conditions during latewood formation of the same year (climatic factors early in the season were not implicated).

Phelps *et al*. (1975) noted that star shakes split between cells, not across cell walls. Butin and Volger (1982) examined the ends of developing star shakes in oak (*Q. robur* and *Q. rubra*) and noted that their tips always showed hairline cracks in the adjacent wood, either in or near the rays. They described tissue breakdown as being in the middle lamella for the most part, with notable colonisation of the walls of the cracks by bacteria; vessels adjacent to the main and hairline cracks were discoloured and tylosed.

2.3.5.2. ENVIRONMENTAL FACTORS ASSOCIATED WITH STAR SHAKE.

The environmental factor most often associated with star shake is soil type (section 2.3.3.1).

Conditions of water stress in the tree were the cause of weakness in wood of conifers exhibiting radial fissures (Amos, 1953); the fissures were worst in particular years, indicating the cause of water stress to be flood (root damage), or drought due to heat or freezing of soil.

2.3.5.3. ASSOCIATION OF BACTERIAL WETWOOD AND STAR SHAKE.

Rishbeth (1980) described the presence of radial cracks in wetwood in British hardwoods. These cracks were said to originate from the centre of the wood usually, and sometimes to extend to the sapwood and bark. The cracks are lined with wetwood, and Rishbeth proposed (after recording pressures inside elms) that they are probably caused by high internal pressure that results from generation of gases such as methane by the bacteria. The pressures he recorded were far below the pressures which wood can withstand without breaking, but could perhaps have augmented other stresses acting on bacterially weakened wood; Rishbeth measured gas pressures of 20 - 25 p.s.i. (pounds per square inch), yet Chafe (1977) measured growth stresses in eucalypts of 400 p.s.i. up to a maximum (in one tree) of 3500 p.s.i., and Mark (1973) concluded from modelling that transverse tangential strength of wood cell walls could withstand a tension of greater than 24 000 p.s.i. This latter parameter would be the direction of stress which would cause ring (not radial) shakes, but illustrates the order of stress size likely to cause longitudinal separations in wood.

2.3.6. FROST CRACKS.

Literature concerning frost cracks has almost always been about oak grown on the Continent (e.g. Rol, 1948; Lachaussée, 1953; Denisov, 1980; Cinotti, 1987), though some older literature in Britain also refers to the phenomenon: for example Plot and Bobart (1684) - who investigated the cracking of oaks following the severe cold winter of 1683, and Hill (1897) who commented that "frost-shake" was common in the Forest of Dean. The term describes splits in the stems of oak which are apparent externally as newly opened or healed cracks; they are reported to appear during severe winters (e.g. 1985, when temperatures in parts of France dropped below -3 ° C), and to be worsened by spells of extreme cold in subsequent years (Cinotti, 1987).

Plot and Bobart (1684) recorded that elm, walnut and ash also split in Britain as a result of the severe frosts; all these trees are ring-porous, and all except ash are species prone to shake. Rol (1948) reported oak, elm, poplar and "certain firs" to be particularly susceptible to frost crack.

Inside frost-cracked stems, further radial splits may be present which do not extend into the sapwood and bark. All the splits are said to be characteristically stained brown, with areas of stain in the adjacent wood also (Butin and Volger, 1982).

The traditional view of frost-crack formation is that cracks form from the bark towards the pith as a result of stem shrinkage in severe cold (e.g. Hartig, 1894b), but Mayer-Wegelin (1955) studied experimental data and doubted that the tensile forces resulting from thermal contraction could be sufficient to be the sole cause such failures of the wood. Rol (1948) said that frost crack was caused and reopened by cold; he also described ring shake as a "close relative" of frost crack, as the two were often found together, in which case the common cause was cold (although he noted that wind action could also cause ring shake, and that both wind and cold caused these defects by acting on weak points of abnormal wood structure).

Butin and Volger (1982) stated that the traditional view of frost crack formation needed revision. Phelps et al. (1975) had suggested that wound-associated star shakes, opened internally by drought, may split to the outside with frost. Butin and Volger (1982) proposed that the stem cracks called 'frost' cracks result from injury or decay of the stem, suffered when the tree was young; that over time the cracks extend to the bark, or recede to become an internal shake as the tree increases in diameter. They attributed the explosive sound of stems cracking in severe cold weather (which has given rise to the belief that the defect is caused by freezing alone), to the failure of existing externally-healed splits, or the opening for the first time of internal shakes; whichever is the case, the effect of the low temperature is said to be secondary to the main cause of the defect (Butin and Volger, 1982). Such a mechanism was in fact suggested by Plot and Bobart in 1684, but was never adopted as a 'traditional view'; they recorded from a questionnaire, and observed, that some trees within each woodland were more susceptible than others to splitting during the 'Great Frost' of 1683. They suggested that "A great part of the cause is supposed to be imperfection in such a tree, ..., which some call wind-shaken, ..., the cause whereof remains yet to be examined, ...".!

The demonstration by Butin and Volger that 'frost crack' and ring and star shake are related defects, with equivalent origin but different expression, perhaps explains the different importance attached to 'shake' and to 'frost crack' in Britain and on the Continent. It seems the differences are a consequence of terminology alone. In Britain, the severe cold which gives rise to explosive cracking of oak stems and external manifestations of the splits is rare, reports describe it as an unusual and extreme phenomenon (Plot and Bobart, 1684). Thus the internal defect "shake", particularly disadvantageous because it can remain undiscovered in the standing tree, is recognised in Britain. On the Continent, where winter temperatures often remain lower over longer periods than in Britain, it seems that the physical stresses resulting from these low temperatures extend the radial splits to the outside of oak stems, forming ribs and splits which continuously open and heal as the tree grows. Thus "frost crack" is the usual nature of the defect on the Continent; exclusively internal shakes ('roulure' and 'schällrisse' - ring shake, and 'fentes' - radial splits) are relatively infrequent (and unseen) in affected woodlands, and so are accorded less interest.

Cinotti (1987) made a thorough review of literature concerning frost-cracks; he covered in particular the mechanics of frost-crack formation, including experimental studies of effects of freezing on behaviour of wood samples.

2.3.7. GROWTH STRESSES IN TREES.

Jacobs (1945) gave a basic definition of growth stresses as "forces found in green woody stems". Kubler (1987) qualified this to omit stresses resulting from crown weight or variations in sap tension. Kubler's own definition was that "growth stresses are autogenerated; they evolve in the growing tree, and are a kind of internal or residual stress, which characteristically exist within a solid body even though no external stress producing force is acting."

Kubler (1987) produced a major review of all work concerning growth stresses in trees; the topics he covered were: growth stress measurement, longitudinal and transverse stresses and strains, origins of growth stresses, silvicultural control of growth stresses, adverse effects of stresses in standing trees - and occurrence, cause and control of resultant defects in sawn timber.

In reference to measured tensions and compressions, Kubler (1987) noted the importance of differentiating between stresses and strains, because strains lend themselves better to evaluations of defects caused by growth stresses: "a given strain is a species-independent measure of the likelihood of wood failure, whereas a given stress affects light woods more than dense woods.".

Growth stresses develop in stems, branches and roots of trees (Jacobs, 1938). Early investigations were made by Martley (1928). Jacobs (1938, 1945, 1965) developed methods of assessing growth stress magnitudes and directions. Extremes of longitudinal tension stress develop in tension wood, (the reaction wood to lean or bending of hardwoods), and help to maintain orientation of stem and crown (Clarke, 1939); though Chafe (1979) points out that the nature of reaction wood is more specialised than development of extreme growth stress alone.

It is now accepted that growth stresses develop as a result of longitudinal cell contraction, but the means by which this occurs is still debated. Two main hypotheses have each been supported by a number of authors; the main hypotheses and proponents are:

a) cell shortening due to lignification (Munch, 1938; Boyd, 1950c, 1972 and 1985)

b) cell shortening due to cellulose crystalisation (Bamber, 1978; Wilkins, 1986; Bamber, 1987). In fact Wilkins, while favouring this latter hypothesis overall, concluded that "a combination of the lignin swelling hypothesis and the cellulose tension hypothesis may go part of the way to providing the necessary explanation."

2.3.7.1. PATTERNS OF GROWTH STRESSES IN TREE STEMS.

Growth stresses occur in three general directions: longitudinally along the grain, and in the tangential and radial directions across the grain. In mature stems, longitudinal stress is tensile at the periphery and compressive at the core. Martley (1928) first described the nature of longitudinal tensions in branches; he also calculated the pressure effects due to weight of crown and bole on the base of conifers and oak, and concluded that these forces (even supplemented by bending in wind) could not be sufficient to cause the brashness observed in the timber from the centre of trees with high growth stresses. Jacobs (1938) studied the extent and significance of longitudinal tension in eucalypts, and proposed that the pressure was exerted by each consecutive cone of wood which formed the tree being laid down in longitudinal tension. This also explained the concurrent radial and tangential tensions and compressions (Jacobs, 1965).

LONGITUDINAL STRESSES. The transition from tensile to compressive longitudinal stress occurs at about a third (Boyd, 195 a - eucalypts; Wilhelmy and Kubler, 1973 - red oak) to one half (Kubler, 1959) of the radius, centripetally.

New bark is said to generate as much longitudinal strain as new wood (Okuyama _et al._, 1981, cited in Kubler, 1987).

TANGENTIAL TRANSVERSE STRESSES. Patterns of transverse stress have been described by Koehler (1933), Jacobs (1945 -

eucalyptus), Ferrand (1982 - beech) and Kubler (1959 - oak). A pattern of compressive transverse stresses at the periphery of a stem, and tensile transverse stresses at the centre was found - confirming the model of Boyd (1950a). Kubler (1959) identified the changeover zone from compression to tension as being at about one third of the radius, centripetally.

The strength of transverse stresses averages only one tenth of longitudinal stresses, but the strength of wood in the transverse direction is lower, so the strains in the transverse direction can be greater than those in the longitudinal direction. Thus, even small transverse stresses can cause splitting in stems, logs or planks (Kubler, 1987).

RADIAL TRANSVERSE STRESSES. Radial growth stresses are tension forces acting from pith to bark, with the greatest levels of stress being at the pith; they occur in reaction to tangential compression at the periphery (Boyd, 1950b). Kubler (1987) describes work investigating radial stresses. Old wood counterbalances the radial forces of the growing wood, and the bark is said to have relatively little force against the expanding wood, so radial growth itself generates little stress.

2.3.7.2. WOOD STRUCTURE AND PROPERTY VARIATIONS ASSOCIATED WITH HIGH LEVELS OF GROWTH STRESS.

Lenz and Strässler (1959) found that beech trees with the most tension-splitting damage contained large amounts of tension wood.

Ferrand (1983) studied wood structure patterns in beech (Fagus sylvatica) with different levels of growth stress. He found that very high numbers of gelatinous fibres, and lower than normal percentages of ray, vessel and normal-fibre were associated with high growth stress.

Bucur (1986) found that beech with high growth stresses was characterised by slightly higher basic density and longitudinal shrinkage than those of normal wood. An increased frequency of large rays in the outer rings was also associated with trees of high growth stress. This latter observation perhaps reflects a change of growing conditions after thinning (Hartig, 1894b; section 2.2.2.2), which would represent the unstable growing conditions which can lead to high growth stress (Kubler, 1987; section 2.3.7.3).

2.3.7.3. CONTROL OF GROWTH STRESSES FOR REASONS OF TIMBER QUALITY.

The damaging effects of growth stresses on timber are worse in broadleaves than in conifers (Wilkins, 1986); the stresses are stronger in broadleaves (Table 1 in Kubler, 1987).

Panshin and deZeeuw (1980) stated that "the system of growth stresses .... is in equilibrium in stems of standing trees, and it is usually too low in magnitude to cause failures in the wood. However, certain conditions can produce characteristic defects that are the result of these growth stresses.". The most commonly reported of these defects are a) brittleheart, an abnormal brittleness of the tree core due to natural compression failures in the fibres, which is commonly found in eucalypts (Dadswell and Langlands, 1938); and b) post-felling splitting defects.

Post-felling defects due to high growth stresses in sound trees occur in the log and during conversion. Such "tension-splitting" was described in detail for beech by Lenz and Strässler (1959). These defects develop before seasoning, and are not due to shrinkage. They have been noted as particularly bad in the economically important timbers of eucalypts, beech and poplar (Jacobs, 1965; Hillis, 1978; Chafe, 1979; Polge, 1981; Ferrand, 1983).

Variations in growth stress are very large within and between trees, and appear to be determined by both genetic and environmental factors (Kubler, 1987). Lenz and Strässler (1959) suggested that genotype was a controlling factor of the very considerable variation observed between trees in a stand of beech. Significant influences of genotype on strain levels in poplars (Waugh, 1972), and on stresses in poplars and beech (Polge, 1982) have been demonstrated.

Longitudinal stresses and tension splitting in *Fagus sylvatica* have been shown to be greater in trees grown at higher altitudes (Lenz and Strässler, 1959; Nikolov, 1967 quoted in Kubler, 1987). Nikolov also suggested that high stresses are associated with poor site 'condition'.

Silvicultural control of growth stress may be possible through means other than stock and site selection. Polge (1981) showed stands of beech growing under four different thinning regimes to have significantly different mean growth stress levels; the lowest growth stresses were associated with heavy thinning of stands. If such an association should hold true for oak also, then the free-growth method of silviculture (Jobling and Pearce, 1977) should be advantageous for the production of oak timber with low stresses. However, Kubler (1987) warned that sudden, delayed thinning may have the opposite effect and induce high growth stresses in trees, because the opening up of closed canopies can result in much re-orientation of the remaining stems. Saurat and Gueneau (1976) found that the growth-stresses in beech trees from single-storeyed plantations were almost double those in trees from multi-storeyed; the former group have a much less stable hierarchy of dominant and sub-dominant crowns.

Kubler (1987) concluded his review section on silvicultural control of growth stresses, with the statement that the principle of growth stress control is to "keep those factors constant that influence the stem's position, and avoid stimuli for re-orientation; strive for vertical stems, but let leaning stems lean." Malan (1988) concluded that for Eucalyptus grandis silvicultural practices may not be effective in reducing growth stresses, as variation between trees is large and the primary factors influencing the stresses are not environmental.

2.3.7.4. ROLE OF GROWTH STRESSES IN FORMATION OF SHAKES IN STANDING TREES.

Koehler (1933) proposed three possible causes of shakes, and suggested that the most probable was a greater rate of circumferential than radial growth in the stem, which would result in internal separations of the wood. He advanced the hypothesis that "shakes and rift cracks in timber are due to transverse compressive and tensile stresses resulting from growth and are not due primarily to bending, although bending stress may supplement growth stress." Dinwoodie (1966) also cited growth stresses as sole cause of ring and star shakes.

James (1939) noted that winter-felled and axe-felled timber were less prone to shake than summer and saw-felled timber respectively; perhaps this was due to a slower release of growth stresses similar to the effect reported by Kubler (1987) concerning felling of girdled trees.

However, Boyd (1950b) said that growth stresses could only be great enough to cause ring failures if supplemented by external stress or if acting on weakened xylem. Kubler (1987) showed that the highest tensile growth strains recorded in tree boles were only half the magnitude at which wood fails tangentially in tension (star shakes); but he said that the discrepancies might have been explained by the fact that there was a dearth of measurements at the points of greatest strain: i.e. at the tips of the shakes.

Kubler (1987) attributed three groups of defects in standing trees to the consequences of high growth stress in the wood. Two of these groups were shake defects, which Kubler called 'heart checks' and 'ring shakes'. He cited the work of various authors, to define and illustrate the nature of heart checks: longitudinal-radial separations passing through or extending from the pith where tangential tension is greatest, usually developing only in large diameter stems in which the stress reaches a high level, and never reaching the compression area of new wood. Kubler did not include "frost-cracks" in this group, but did include the wound-related star shakes described by Shigo (1972).

Reviewing research into ring shakes and growth stresses, Kubler (1987) found a preponderance of evidence against the role of radial tensile growth stress in ring shake formation. He said that if these stresses were the only cause of ring shake, then most shakes should lie close to the pith, should devel p during cross-cutting, should tear as well as separate cells, and should follow porous earlywood; but these are not characteristic features of ring shake. He said that ring shakes develop at all distances from the pith (though it seemed that he believed ring shake to form close to the pith only rarely). Kubler thus dismissed the possibility of growth stresses being the sole cause of ring shake, but then did not address the possible role of growth stress as a secondary factor. Shigo (1972) and McGinnes et al. (1974) suggested that growth stresses might cause ring shakes to develop in zones weakened by cambial damage or bacterial degradation of wood; Kubler cited such weak zones as evidence of a mechanism other than growth stress being the cause of ring shake.

Wood structural evidence of a link between high growth stresses and shake, is suggested by a report (USDA, 1956) that radial separations in hickory were associated with the gelatinous fibres of tension wood. Chafe (1977) associated gelatinous fibres with high levels of growth stresses, and proposed that the convoluted form of the gelatinous-layer in tension wood was due to growth stress release (tensile forces pulling the wall into the space of the lumen).

CHAPTER 3

SURVEYS.

3.1. INVESTIGATIONS INTO THE NATURE OF SHAKE IN BRITISH OAK.

3.1.1. CHOICE OF DEFINITIONS FOR THIS STUDY.

The term "shake" has been used by other authors for a number of c nditions causing splits in timber. True shakes, although variable in severity and attributed to many different causes, are defined in this study as distinct from splits due to felling damage and seasoning.

The following definitions were compiled during this study from all the information gathered, and from observations in the field. They are used as standards for the rest of the thesis. ther descriptive names qualifying the basic star or ring shake pattern (e.g. 'spider shake' for multiple star shake) are not used here.

SHAKE IN TIMBER.

Shake is a defect which occurs in the wood of a standing tree. It becomes important when the tree is felled and the log converted. It is present in the green timber and is not a seasoning defect, although splits may open further on drying, and thus be more readily apparent.

"Shake" - a longitudinal separation of the woody tissues in a standing tree.

"Star shake" - one or more shakes, radial in direction but not necessarily separations of the wide rays themselves from the rest of the wood (Plate 3.1). The splits rarely cross more than the inner two thirds of the log radius, unless extended by felling shock or frost cracking into the sapwood or even to the bark. The longitudinal extent of star shake is variable - usually up to one to two metres, sometimes more. Seen in long section, the splits run in different planes, with ends overlapping (Plate 3.3). Star shakes may emanate from ring shakes, without having any origin at the pith (Plates 3.2 and 3.6).

"Ring shake" - a shake which occurs within one annual ring, or between annual rings (Plate 3.2). Seen in cross-section, ring shakes may encompass from a few degrees of the circle of the ring, up to a complete ring. The full longitudinal extent of a ring shake remains in the same ring; in later rings of mature trees therefore, this extent can be several metres (Plate 3.4).

OTHER SPLITS AND SHAKE-LIKE DEFECTS IN TIMBER.

"Heart crack" - a single short, radial split which runs through the pith at the base of the butt-log of virtually every mature oak, whether shaken or sound (Plate 3.8). This is not regarded as a defect, and is usually less than 8 cm across the diameter, unless extended by felling shock.

"Frost crack" - radial splits found at the base of the trunk, which may in cross section appear to originate externally (though the outer edge may be healed) and to run towards the pith. The splits are stained (Plates 3.9 and 3.10). Frost cracks seen in this study were always accompanied by shakes, and are treated as an associated phenomenon in discussion of the work (further details in section 2.3.6.) but they were not included in assessments of shake index (i.e. severity: section 3.2.2.3).

"Felling shock" - trees which drop awkwardly when felled, twisting or landing on a heavy branch or across other timber, can suffer rough breaks in the wood. Splits due to felling damage are irregular, do not run within rings, and are not necessarily radial. They often run into the sapwood and even through the bark. The splits are not stained, and usually look splintered but clean edged (Plate 3.8).

"Checks" - are radial splits which can be seen in the ends of old felled logs, or on the faces of boards (more common on the tangential face, less common on the radial face). Checks result from the drying of the surface of the log or boards, and the differential shrinkage of wide rays from adjacent tissues. These splits are usually numerous, short, shallow and tend to curve. In a log-end they can be scattered over all the surface of the heartwood, but do not originate fr m the pith (Plate 3.6). Checks can also occur inside oak boards if seasoned wrongly.

"Cup shake" - a term sometimes used to describe an inc mplete ring shake as seen in the end of a log, but more usually used to describe the manifestation of a ring shake in a board. The pieces of wood on each side of the shake part, and may come away altogether leaving a curved depression in the board.

3.1.2. FIELD OBSERVATIONS OF THE NATURE OF SHAKES IN OAK AND SWEET CHESTNUT.

The following observations were made in the field during the course of visits and surveys.

In oak, although star shake was often seen without ring shake, ring shake without star shake was seldom seen. Ring shakes of more than 120° to 180° were rare.

Ring shakes in oak rarely appeared in rings beyond about two thirds of the radius from the pith; further out, slight separations at the site of a wound might occur but no separation further round that ring was seen. This zone of the cross-section of an oak butt was also the maximum limit of star shakes running from the pith or from ring shakes. Splits which did cross through this zone to the bark were rare: they were the 'frost-cracks' which were associated with healed or healing ribs on the outside of the tree (Plates 3.9 and 3.10) and were seen on a very few sites, within which their incidence was high.

Shake in sweet chestnut (Castanea sativa) by contrast, was characterised by multiple ring shakes, often of complete rings, and very rarely included star shake (Plate 3.5).

ak shakes were frequently accompanied by either a dark stain on the surface of the splits (Plate 3.2), or a milky white exudate (Plates 3.1 and 3.7). The two forms of stain were not exclusive of one another, because cutting the sawn surface of a newly-felled dark-stained log with a chisel could sometimes raise the white exudate from the wood. The white exudate was sometimes just a film on the shake surfaces, and sometimes abundant as shown in Plate 3.1; it was a suspension of granular white material which sometimes dried on shake surfaces as a powdery deposit (Plate 3.7). The wood of oaks containing stained shakes (dark or white) was usually very wet from the shakes. Shakes in oak were not always stained however, and prevalence of staining appeared to be site related. The white exudate was rarely seen in sweet chestnut.

A shaken ring close to the pith in the butt of an oak will have a short longitudinal extent - i.e. at the most, it can be only equivalent to the height of the tree in the year that the ring was formed. However, the development of early ring shakes should not be dismissed as insignificant, because star shakes frequently arise from the outer boundary of a ring shake, and can then extend radially into the later-formed wood.

Individual oaks of notably bad form (twisted, leaning and permanently suppressed) rarely contained shakes, whatever the condition of the rest of the stand.

Star shake, if it was present at the top of a log, was always seen in the base of the log. Ring shake however, was seen very occasionally at the top of a log with no evidence of shake at the bottom.

In oak, shakes were visible immediately on felling; even if the shake splits were closed, a line of moisture or stain indicated their presence. In sweet chestnut, shakes often do not become apparent until one or two weeks after felling.

In a few oaks seen on certain sites, the shake splits had become very wide inside the standing tree, and filled with clear brown fluid. The fluid and the wood had a very strong sour smell, as of organic acids. This same smell, though less str ng, was detectable in most oaks with stained shakes.

Ring shakes were often associated with changes from rings of average growth rate, to one or more rings of extreme size (wide or narrow).

Plate 3.1. Star shake, seen in cross-section of oak butt. Note white stain spreading from shake splits.

Plate 3.2. Ring and star shakes, seen in cross section (stump) of oak. Shakes are dark-stained; some star shakes run from the ring shake, without any origin at the pith.

Plate 3.3. Star shakes (S) and ring shake (R), seen in longitudinal section of oak log.

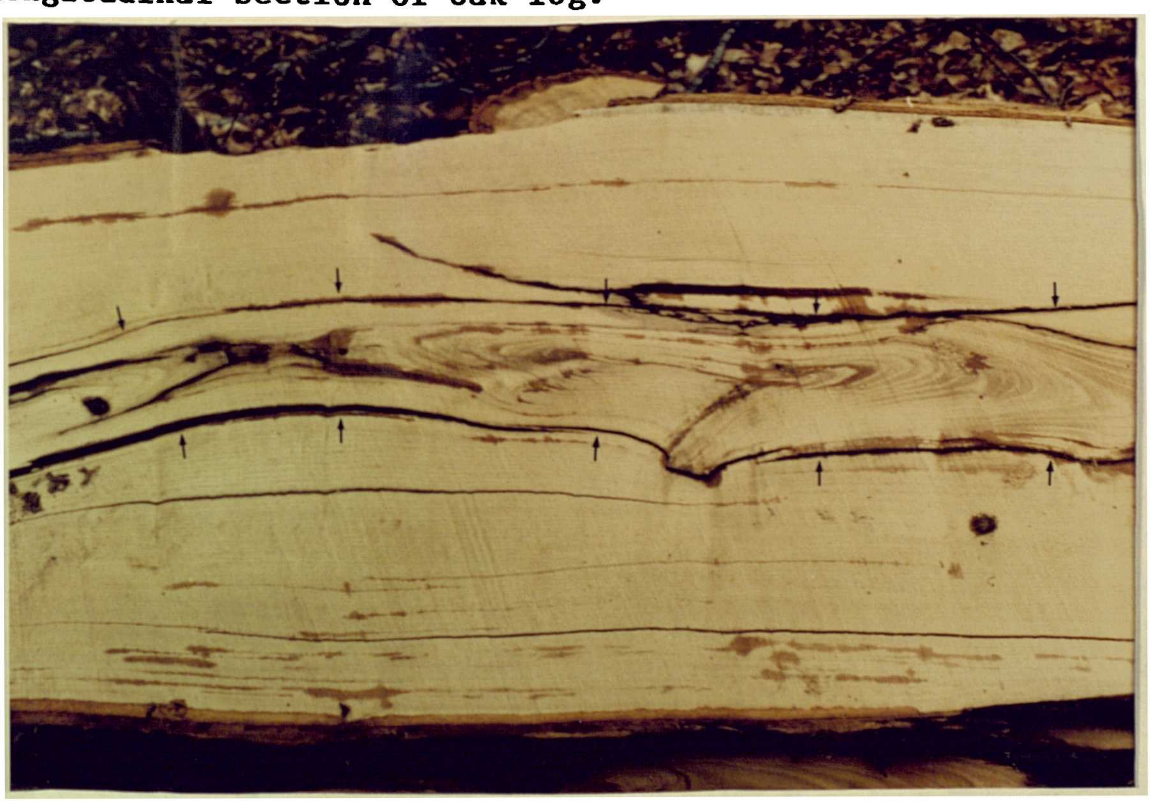


Plate 3.4. Ring shake in sweet chestnut (<u>Castanea sativa</u>), seen in longitudinal section, following a complete annual ring (arrows).

Plate 3.5. Ring shake in sweet chestnut, seen in cross-section. (Pencil for scale = 14 cm long).

Plate 3.6. Cross-section of oak butt showing pith (P) and compartmentalised rot behind barrier zone (BZ). Ring shake has formed at barrier zone, and star shake (S) is developing from ring shake. The causative wound was below level of section. The small splits (DC) are drying checks.

Plate 3.7. Felling hinge on oak stump, showing chalky, white deposit on tangential longitudinal surface.

Plate 3.8. Sound oak butt, showing heart crack (between arrows; extended by felling shock, F).

Plate 3.9. Cross section of oak butt showing frost-cracks (FC) and associated ribs; star shake (S), ring shake (R) and a felling crack (F) are also present.

Plate 3.10. Cross section of oak butt with white-stained ring and star shakes, and frost cracks which have healed without re-opening to form a rib. Patches of decay (D) have formed at the point where the split once opened to the bark.

Plate 3.11. Mineral stain (dark banding) in shaken oak.

Plate 3.12. Mineral stain in sound oak.

Plate 3.13. Groove in oak bole which may indicate a shaken interior.

Plate 3.14. Seam in oak bole which may indicate a shaken interior.

Plate 3.15. Open crack on oak bole which may indicate a shaken interior.

Plate 3.16. Healed cracks on oak bole which may indicate a shaken interior.

3.1.3. QUESTIONNAIRE - "THE PROBLEM OF SHAKE IN OAK".

Answers to preliminary enquiries had suggested that shake in British oak is very variable in appearance, incidence and severity. The defect was found to be of great concern to timber growers and merchants, and the subject of much speculation - and yet it was little documented. Therefore a questionnaire was devised to record the experience of foresters and timber merchants in England and Wales, and gain a clearer impression of the extent and economic importance of the problem.

The questionnaire asked for information on the prevalence of shake in Britain, its association with site and tree characteristics, and the end-uses and values of shaken and sound l gs. A prototype of the questionnaire was shown to a number of timber merchants and foresters who were invited to comment on its design before the final version was circulated. Appendix 3.1 is a copy of the questionnaire.

Two hundred copies of the questionnaire were distributed in the early summer of 1984. The majority were circulated with the help of the British Timber Merchants' Association, the rest being sent to regional offices in the Forestry Commission and the Tilhill company, and to oak growers with whom contacts had been made at the National Hardwoods Programme and other meetings.

Thirty-two completed questionnaires were returned from twenty counties in England and Wales. Many other respondents had much interest in, but no first-hand experience of shake in oak. Replies referred to experience of oak in thirty-five counties of England and Wales, plus the Scottish Borders. Respondents generally recognised the pre-1974 county boundaries.

3.1.3.1. QUESTIONNAIRE RESULTS.

The questionnaire asked for information from the respondents' own experience, and in each case separate replies for ring and star shake were required. The wide variety of replies to each question made any sophisticated analysis of results inappropriate. Results are therefore expressed as frequencies of the different replies to each question. Questions and replies are summarised in turn.

Part 1: the association of shake with growing-conditions.

Q1: Is the occurrence of shake related to soil type?
Replies to this question were more consistent than to any other. Replies reported high incidence of both forms of shake on sandy, stony and gravelly soils, and low incidence of shake on clay soils (Figure 3.1)

Q2: List counties or localities within the U.K., associated with the incidence of shake.
Replies to this question are biassed by the past and present working locations of the respondents. Ring and star shake can be treated together in the results because they were nearly always reported together in replies; exceptions show up in Figure 3.2.

Cornwall, Cumbria, Dorset, Gloucestershire (particularly the Forest of Dean) and Gwynedd, were frequently associated with high incidence of ring and star shake. Devon was equally associated with low and high incidence - regional differences within the county being marked. Herefordshire, Oxfordshire, East and West Sussex, Warwickshire and Worcestershire were most often reported to have low incidence of shake; Lincolnshire and Shropshire were also cited. Counties cited in equal numbers as having high or low shake incidence were: Bedfordshire, Berkshire, Hampshire, Kent, Northamptonshire, the Scottish Borders, Surrey and Wiltshire. Single reports were received of shaky oak in Cheshire, Clwyd, Nottinghamshire, Powys, Somerset, Staffordshire and West Yorkshire. Single reports of sound oak quoted Gwent, Leicestershire, Norfolk, Suffolk and East Yorkshire. Figure 3.2 displays the results for regions cited by three or more respondents.

Q3: List any environmental factors associated with incidence of shake.

Wind exposure was the factor most commonly associated with shaky crops (9 replies), after soil type. Shallow soil (eight replies), steep slope (six replies), high altitude (six replies), disturbed or unstable ground (five replies) and water stress (three replies) were also associated with high incidence of shake. Reports from the Forest of Dean and Nottinghamshire blamed shake on mine-drainage lowering the water-table. Frost was also cited as a causative factor (four replies). Both good and bad soil drainage were linked to high incidence of shake.

Q4: List any ground vegetation types associated with incidence of shake.

Few respondents answered this question. Sites with a dominant ground flora of bracken (*Pteridium aquilinum*) (eight replies), or heather (*Calluna vulgaris*) (seven replies), were reported to be associated with occurrence of shake in oaks; sites with *Rhododendron* sp. and bilberry (*Vaccinium myrtilis*) were also implicated. Bramble (*Rubus* spp.) was associated with both low and high incidence of shake (four and two replies respectively). Four respondents stated that no association had been observed.

Q5: asked about other biotic factors associated with incidence of shake.

Few replies were received. Most stated "no effect". Damage to the trees by deer or rabbits was associated with development of shake, as was fungal attack.

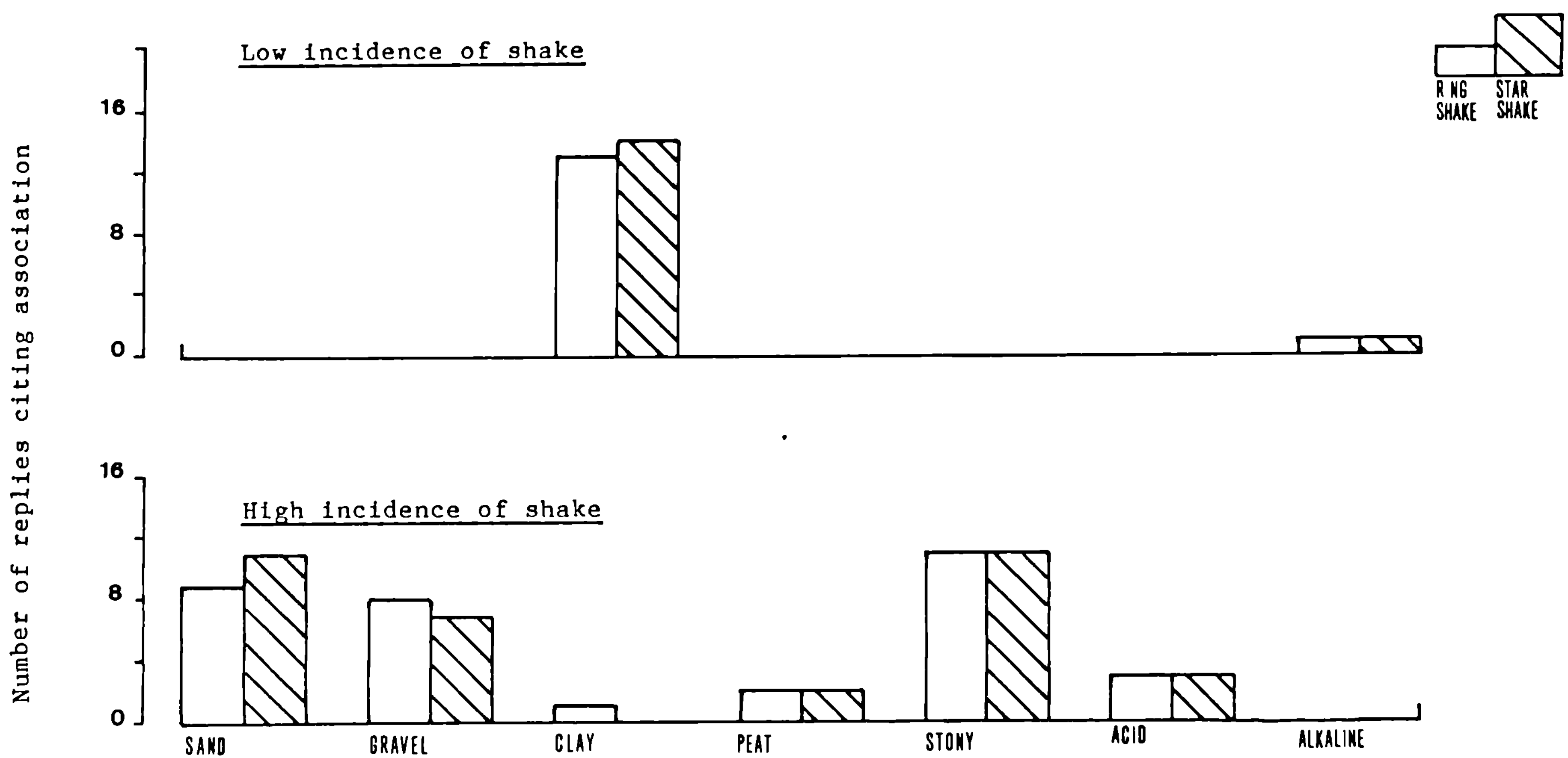


Figure 3.1. Questionnaire replies concerning associations of soil type and incidence of shake in oak.

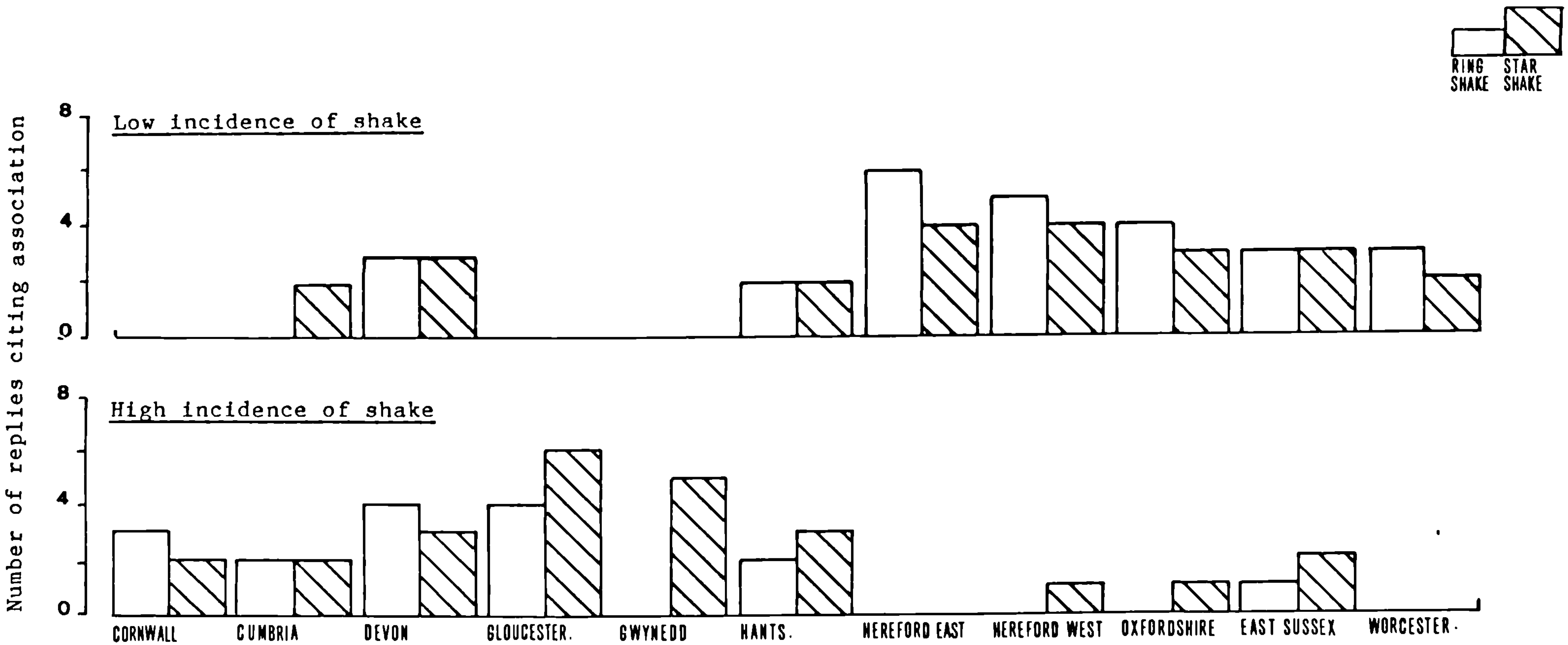


Figure 3.2. Questionnaire replies associating regions of England and Wales with incidence of shake in oak.

Q6: List any silvicultural techniques associated with shake incidence.
Oaks of coppice origin were the most frequently associated with high incidence of shake (eight replies). Nearly twice as many replies associated coppicing with star shake as with ring shake. Replies of individual respondents reported low incidence of shake in naturally regenerated crops, planted crops and "well cut" coppice; also in open grown trees and those "of good seed". Development of shake was attributed to sudden release of growth, spiral grain in the wood, trees with small and imbalanced crowns, and to lightning-strike. High incidence of shake was reported equally in oaks of slow and fast growth.

Part 2: the association of shake with outward characteristics of the tree.

Q7: List any aspects of tree form linked with the incidence of shake.
Four respondents said that trees with poor or stag-headed crowns were more likely to be shaken. Five said that no association had been observed.

Q8: asked about identification of shakes in the cut end of a log.
A characteristic feature of shakes, which was frequently reported, was white exudate or dark staining along the splits. Drying cracks were described as shorter and shallower than shakes, and very numerous; felling cracks, as longer and irregular. Drying and felling cracks were distinguished by lack of staining.

Q9: List, in order of importance, any reliable indications visible before felling, that a tree is shaken.
Twenty-five replies described vertical cracks, ribs and seams in the bole as indicative of star shake; eight of these also cited them as linked to ring shake. One respondent said there

were no reliable signs of star shake, and four that there were none for ring shake. Some respondents mentioned as indicators: basal swelling of bole (ring and/or star shake), root-sprawl and 'feet' (ring shake), spiral grain in bark or fluting (ring and/or star), and dark bark (ring shake).

Q10: List tree diameters with relatively high and low incidence of shake.
The majority of replies reported high incidence of ring shake at 45 cm dbh or above; and high incidence of star shake at 30 cm dbh or above. Eight respondents found no association between shake incidence and tree diameter.

Part 3: is there a genetic influence on susceptibility of oak to shake?

Q11: asked whether variations in the severity of shake within a wood are greater or less than those between woods.
Replies were inconclusive. Respondents described within-site variation as greater than (five replies), equal to (three replies), or less than (six replies) between site variation.

Q12: in the context of shake incidence, are there any major differences between species of oak (sessile, pedunculate, Turkey, etc)?
Four replies noted pedunculate oak as more shake-prone, one said that sessile oak was the worst. An almost equal number of replies suggested that Turkey oak was more shake-prone (five) or less prone (four), than the British oak species.

Part 4: utilisation of shaken timber.

Q13: asked what products could be converted from logs in various conditions of ring and star shake.
Fencing was the most usual market for timber with slight ring and star shake. Beams and mining timber (requiring large,

boxed sections) could also use slightly shaken timber. Severely shaken logs also entered the fencing and mining timber markets, but a greater proportion of these logs were used for fire wood, and the cost of extraction often could not be recouped from the low value market.

Q14: what factors do you take into account when valuing a log containing shake?

There are no set grading rules in the UK for amounts of shake. Most respondents to this question first took into account the cross-sectional extent of the shake, then considered log size and form.

Q15: asked for an illustration of the economic importance of shake, by indication of the approximate roadside value of various grades of log, and the value if the same log was severely shaken.

The average figures (rounded to the nearest £5) are given below (Table 3.1).

GRADE	**VALUE - DEPENDING ON CONDITION (£/m³)**		
	Sound	**Ring shaken**	**Star shaken**
Veneer	200	70	60
Saw logs	100	50	40
Beams	70	35	35
Fencing	40	25	20
Mining	20	20	15

Table 3.1: Depreciation in value of logs of various form-qualities, if found to be shaken. (Figures quoted in questionnaire replies from England and Wales in 1984).

Replies from the North of England, the Midlands and the West Country gave a lower price per cubic metre for sound timber of the higher grades, than those from the South and South East. By contrast, poorer grades and shaken timber (mining and fencing grades) fetched better prices in the West Country and North than in the South and South East.

3.1.3.2. DISCUSSION OF THE QUESTIONNAIRE.

Respondents consistently associated incidence of ring and star shake with soil type. Sandy, gravelly and stony soils were said to produce shaken crops, while sound oaks were more often found on clays. Thus the reputations of regions in England and Wales for sound or shaken timber, generally could be explained by their predominant soil types.

The common factor in the soils reputed to produce shaken oak, seemed to be a variable water-table with a tendency for periods of high water-deficit. This is a characteristic quality f many areas in the West of Britain, where there is high seasonal rainfall over poor and free-draining soils.

Reports of disturbed soils being associated with shake came from mining areas, and it was suggested that mine drainage affected the water-table and caused shake. However - mine drainage might be expected to affect only the crop growing at the time - whereas two or more generations of oak from these same sites have been found to be shaken.

The nutrient, pH and water statuses of soils are reflected by the ground flora. The species which were most often reported to be associated with shaken oaks were bracken and heather. These thrive on acid, free-draining soils, and heather can acidify lime-rich soils locally, by calcium uptake. Bramble, for which conflicting observations were reported, is a genus of very many similar species with different site 'preferences'; it is therefore not an easily used indicator in a study of this type.

Wind exposure was very often cited as a cause of shake, while some noted that exceptions challenge this view. The splits were said to be due to mechanical damage from bending and twisting. It has to be assumed that the questionnaire replies cite this from observations, but the view seems also to be a traditional one.

The contradictory replies to the question designed to investigate any genetic influence on susceptibility of oak to shake, may suggest that site effect is the dominant influence, but that genotype differences show up where similar site-types are being compared. They may equally have been due to unclear wording of the question, which in retrospect seems a difficult one to answer.

The contradictory opinions about shake in Turkey oak (*Q. cerris*) may well be because this species is notoriously fissile and prone to checking during seasoning.

Open or healed cracks in the standing tree were frequently said to be indicators of shake (Plates 3.13 - 3.16 are examples). Some respondents made the additional comment that the signs were not reliable: the absence of such marks did not guarantee a sound tree. The question in the questionnaire did not allow for this negative association, and so seems to have missed a point of view which is otherwise commonly held.

The economic importance of shake in oak timber was clear from questionnaire replies. The down-grade of shaken logs is very great - the reduction in value could be to as little as one fifth of their potential if sound. Timber merchants reported that they have to reduce prices offered for oaks suspected of being shaken, to cover the risk inherent in the custom of buying standing timber. Growers faced with trying to win a good price for large parcels of oak in woodlands suspected of being shaky, will sometimes arrange a sample-felling before offering a parcel for sale by tender; otherwise, if able, they will sell at stump or roadside.

The economic importance of shake in woodlands throughout Britain could not be judged accurately, because provenance of replies to the questionnaire was patchy. However, the site conditions reported as being associated with high incidence of shake are characteristic of much of the land used currently for tree-growing in Britain.

FURTHER INFORMATION ON SHAKE, COLLATED FROM CORRESPONDENCE AND INTERVIEWS.

Further reports, gathered independently of the questionnaire, are given in Appendix 3.2. Associations of site type, silviculture, tree condition and timber characteristics are noted.

3.2. FIELD SURVEYS.

PURPOSE OF FIELD SURVEYS. The initial aim of field visits was to gain first-hand experience of the nature of ring and star shake in the British oak species _Quercus robur_ and _Q. petraea_. More information was needed about the appearance, within-tree extent and prevalence of the defect.

Site type was frequently implicated as a cause of shake (section 3.1), therefore the field visits were extended in order to carry out surveys of incidence and severity of shake on a variety of site types.

3.2.1. SITES

Site choice had to be opportunistic. Initially, study sites were volunteered by owners or managers in response to requests in journals or at meetings; these sites almost always carried badly shaken crops.

The storm winds of October 1987 caused the clear-fall of numerous mature oak woods in the South-East of England. This provided an excellent opportunity to study shake in large numbers of oaks grown on a wide range of site and soil types. Owners of storm-damaged oak woodlands listed in a register compiled by the Forest Windblow Action Committee, were contacted. Sites were chosen from the list, to sample a variety of soils and geology along a line from Lowestoft at the North-East extreme, to the New Forest at the South-West; the majority of sites were in Kent and West Sussex, as the largest number of woods affected were in these counties. A major advantage of these surveys was that the trees had been felled without the bias of selection for age, size or quality - n r even bias towards non-windfirm trees, as oaks were frequently left standing by the hurricane, but then felled because of severe crown damage.

The sites surveyed, their soil types, underlying geology and species of oak are listed in Table 3.2 below; approximate locations are illustrated in Figure 3.3. Full descriptive details of each site and the nature of its crop (other than the quantified data presented in this thesis) are given in project notes lodged with Forestry Commission archives. All sites visited were of mature oak, so written records of the history of the site or crop were rarely available.

Brief tallies of shake incidence, with notes on site type and tree condition were made at seven further sites during interview visits. Information from these visits is incorporated into section 3.1 and Appendix 3.2, and soil samples were taken from site 46 (Section 3.2.2.4).

Site Code	County	Grid Ref.	Soil Texture	Geology	Oak sp.
1	Hampshire	SU 370 184	SL	Oligocene and Eocene BBB beds (sands/clays)	-
2	Kent	TQ 554 535	SCL	Lower Greensand	S
3	Suffolk	TM 510 825	S	Pleistocene/Pliocene	P
4	Suffolk	TM 105 715	SC	Chalk	P
5	Suffolk	TL 803 623	CL	Chalk	P
6	Suffolk	TL 813 632	SL	Chalk	-
7	Kent	TQ 641 362	SSiL	Wealdon (sandstone/ clay alternations)	P
8	Kent	TQ 478 526	SL	Lower Greensand	H
9	West Sussex	TQ 248 308	SSiL	Wealdon	P
10	West Sussex	TQ 251 298	SSiL	Wealdon	S?
11	West Sussex	TQ 249 296	SSiL	Wealdon	-
12	West Sussex	TQ 311 358	SSiL	Wealdon	H
13	West Sussex	TQ 328 342	CL	Wealdon	-
14	West Sussex	TQ 388 338	SL	Wealdon	P
15	Kent	TQ 536 543	SL	Lower Greensand	P
16	Kent	TQ 548 533	SiL	Lower Greensand	S/H
17	Surrey	TQ 183 514	C	Chalk	-
18	Surrey	SU 851 264	SL	Wealdon	P/H
19	West Sussex	SU 954 080	SiL	Chalk	H
20	Surrey	TQ 131 427	SL	Lower Greensand	H
21	Hampshire	SU 382 186	S	Oligocene/Eocene BBB beds(sands/pebbles)	H

Table 3.2. Sites surveyed for incidence of shake in oak. Keys to abbreviations are on third page of table.

Site Code	County	Grid Ref.	Soil Texture	Geology	Oak sp.
22	Hampshire	SU 293 054	SL	Oligocene/Eocene BBB beds	-
23	Hampshire	SU 268 052	SL	"	S
24	Hampshire	SU 284 034	SL	"	P
25	Hampshire	SU 328 038	CL	"	S
26	Hampshire	SU 680 306	C	Chalk	P
27	West Sussex	TQ 248 307	SL	Wealdon	P
28	Surrey	TQ 426 524	SSiL	Lower Greensand	-
29	Powys	SO 088 975	SSiL	Silurian shale, & sandstone	P
30	Gwynedd	SH 455 762	SaL	Pre-Cambrian schists	S
31	Hereford	SO 522 332	SSiL	Devonian marl and sandstone	H
32	Powys	SJ 15 20	SSL	Boulder clay over Ordovician	H
33	Cumbria	NY 464 370	SaL	Boulder clay over Permian Sst	-
34	Cumbria	NY 460 345	SSL	Boulder clay on Culm Measures	-
35	Cumbria	NY 470 354	SaL	Boulder clay over Permian Sst.	S
	(All Cumbrian sites with overlying sandy, loamy drift (Pleistocene) of varying depth.)				
36	Gloucester	SO 537 136	SaL	Devonian Sstone	S
37	Gloucester	SO 627 135	CL	Carbonif.sstone Coal measures	H
38	Hampshire	SU 551 620	SSL	Eocene: London Clay & BBB Beds	P

Table 3.2. (continued). Sites surveyed for incidence of shake in oak.
Keys to abbreviations are on third page of table, overleaf.

Site Code	County	Grid Ref.	Soil Texture	Geology	Oak sp.
39	Devon	SX 760 800	-	Border of Granite and Carboniferous	S
40	Devon	SX 780 870	-	Carboniferous	-
41	Devon	SS 695 490	-	Devonian (Old Red Sandstone)	-
42	Devon	SX 730 730	-	Carboniferous (Culm Measures)	P

Table 3.2 continued. Sites surveyed for incidence of shake in oak.

Key to soil textures: C - clay; CL - clay loam; S - sand; SC - sandy clay; SL - sandy loam; SiL - silt loam; SSiL - sandy silt loam; SCL - sandy clay loam.

Key to species: S - sessile oak (*Q. petraea*); P - pedunculate oak *Q. robur*); H - hybrid characters of sessile and pedunculate oak.

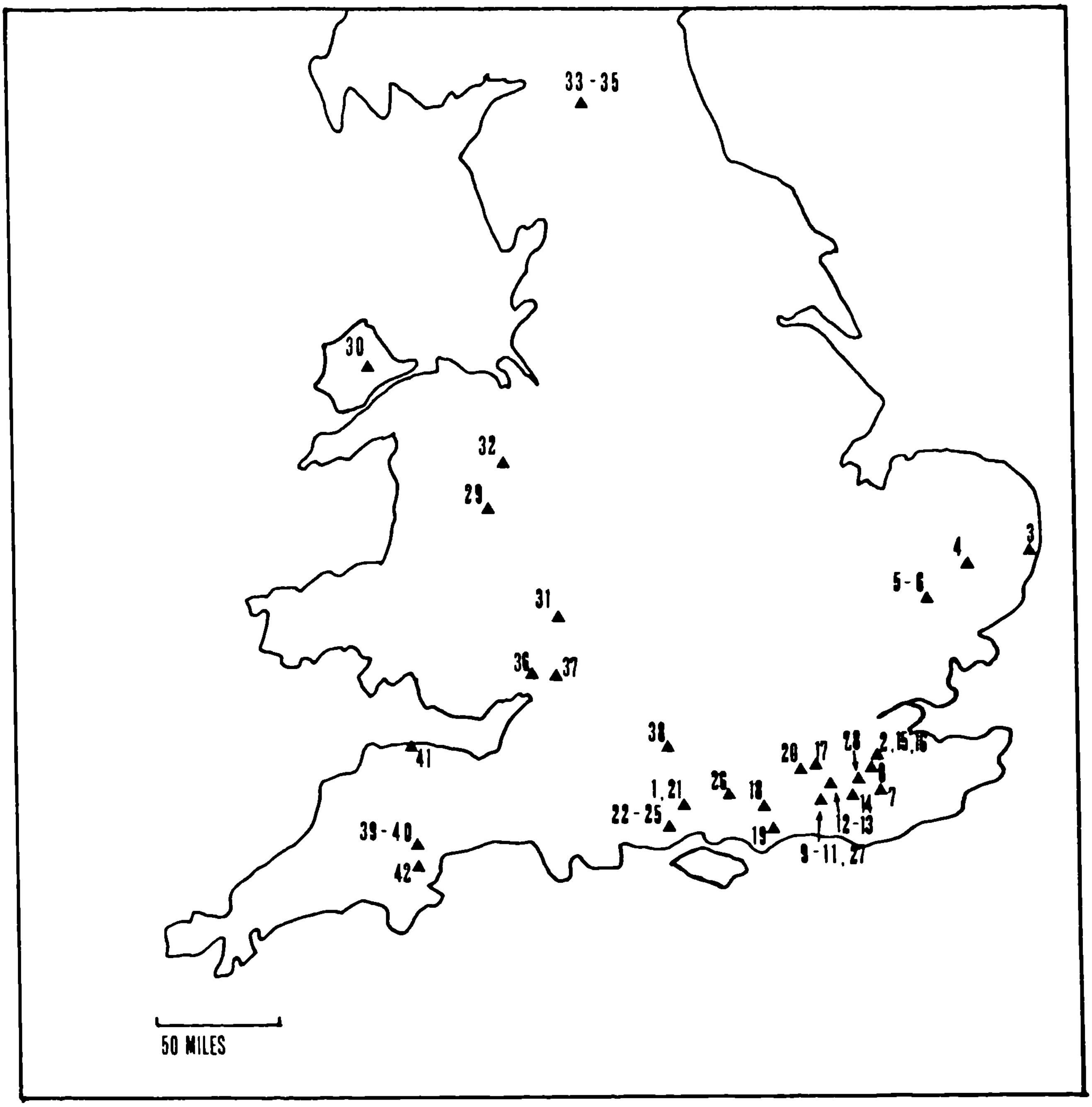


Figure 3.3. Locations of woodlands in England and Wales surveyed for incidence and severity of shake in oak.

3.2.2. SURVEY METHODS

3.2.2.1. FIELD WORK

TIMING OF SURVEYS. Sites 1 - 28, surveyed following the 1987 hurricane, were visited in April 1988 because few wind-damaged trees were crosscut or felled until the spring of that year. Sites 30 and 38 were surveyed in July and May respectively, and the remainder were surveyed during autumn/winter (late September to March). Most sites were visited within two weeks after felling (usually one week), so that shakes and associated staining were not obscured by weathering. The colour of the fresh wood was noted only on trees seen within one or two days of felling.

SAMPLE SIZES. Woodland or compartment sizes and types varied greatly, making any standardisation of sampling difficult. Therefore, all trees of each clear-fall were included in the assessments, in order to avoid bias. Consequently, the number of trees assessed was very variable. Between 20 and 60 trees were seen on half the sites; more than 60 were seen on six sites, and 10 to 20 were seen on eleven sites. On five sites (numbers 4, 9, 24, 27 and 28) fewer than ten trees were seen; these were included in the analyses because their condition was representative of previous crops reported from the site. Random sub-samples from larger surveys suggested that fifteen trees gave a satisfactory estimate of the amount of shake in a crop.

THE OAK SPECIES SURVEYED. Pedunculate and sessile oak (*Q. robur* and *Q. petraea*) were studied. Turkey oak (*Q. cerris*) was encountered frequently in the South of England, but was not included in the surveys. Red oak (*Q. rubra*), and occasional oaks with wood and bark markedly uncharacteristic of the two British oaks (*Q. cerris* x *robur* hybrids perhaps?) were also omitted.

EXAMINATION OF BUTTS AND STUMPS. Two early surveys allowed the comparison of butts with the particular stumps from which they had been felled. They generally exhibited a very similar shake pattern, although shake in the butts was sometimes extended by felling shock. This exercise was useful for future recognition of differences between felling-shock and true shake, and showed that examination of stumps or butts would give results comparable between sites. At the majority of sites, shakes were studied in the stumps.

At three sites where boles had been cross-cut and stacked, it was possible to note the longitudinal extent of the shakes; observations are included in the shake descriptions of section 3.1.2.

3.2.2.2. DATA COLLECTED.

SITE DATA. The soil profile at each site was recorded together with aspect, altitude and a rough assessment of slope. The ground vegetation was noted, but information was limited at sites visited in winter. The presence of honey fungus Armillaria mellea) in oak or other trees on the site was noted.

TREE CROP DATA. The species of oak was identified where possible, by leaf type and tree form, using characteristics described by Jones (1959) and Cousens (1965) (Section 2.1.1.2). The type and proportion of other woody species was noted in mixed woodlands, and any evidence of nurse crops recorded.

TREE SIZE, AGE AND VIGOUR. It was not possible to measure tree diameter at breast height at the majority of sites, because trees were rarely left at stump. Therefore tree diameter was recorded as diameter of stump or butt. This was a less suitable measurement than dbh, but care was taken to avoid buttresses, and a mean of two perpendicular diameters was taken for each tree. Even if dbh was recorded before falling, stump/butt diameter was used in comparisons between trees from all sites.

Ring counts were made on a few trees at each site. Annual rings which were exceptionally wide or narrow relative to the norm for that tree, were recorded.

A rough calculation of the overall growth rate of the oaks was made. Mean ring widths were calculated for individual trees on which ring counts had been made. In even-aged stands, the mean butt radius was divided by the crop age, to give the mean ring width achieved during the life of the trees. In uneven-aged stands (a minority) mean ring width data from individual trees were averaged to give a figure for the whole crop. This parameter gave an indication of the vigour of the trees, although no information on height was collected.

SHAKE. For each tree, a sketch was drawn of any ring and star shakes, as seen in the cross-section of the stump or butt. An index of the shake severity was calculated in the field. The first three surveys were an exception: for these, the index was calculated in retrospect from drawings and descriptions. No index was calculated for site numbers 1 and 13. Section 3.2.2.3 describes the method of calculating the index.

The annual rings containing ring-shakes were recorded in shaken trees for which ring-counts had been made. Ring shake separations were frequently on a ring boundary between the latewood and earlywood. The year of the ring shake in such cases was counted as that of the adjacent earlywood (i.e. the year of the following ring).

STAIN. The presence of milky or dark staining associated with shakes was noted.

ROT. The presence of any rot in the butt was recorded.

WOOD COLOUR. Colour of freshly cut wood was recorded, because in the first site surveyed there was a strong association between 'pink' wood and presence of shake. There were three distinct categories of heart wood colour: 1) a pale, honey colour, 2) a range of light-brown to dark bracken colours, 3) a dark pink-brown.

MINERAL STAIN. Bands of grey colour were observed in the cross-sections of oaks on some sites; these ran within, or undulated between, the annual rings (Appendix 3.2 and Plates 3.11 and 3.12). Timber merchants referred to such bands as "mineral stain". Mineral stain in individual trees was recorded when abundant over most of the diameter.

ECCENTRICITY. Where the pattern of annual rings in the stump suggested very eccentric growth throughout the life of the tree, this was recorded.

SAPWOOD THICKNESS. Sapwood and bark thicknesses were measured because interviews had suggested associations of these parameters with presence of shake in oaks (section 3.1). Sapwood thickness was measured to the nearest 0.5 cm, in two places on opposing sides of the stump diameter. Buttress wood, which generally had extremely wide sapwood, was avoided.

BARK THICKNESS AND TYPE. Bark thickness was measured to the nearest 0.1 cm, in two places on opposing sides of the stump diameter. Where bark was deeply creviced, the thickest part of the bark was measured. Bark type was recorded as: smooth, platy, rough, or knobbly.

FREQUENCY OF WIDE RAYS. Wide rays were easily visible and the number crossing a 2 cm tangent as seen in the cross-section of the stump was counted. The count was made at the heart/sap wood boundary as a standard position, and expressed as number of rays per centimetre tangent.

3.2.2.3. INDEX OF SHAKE SEVERITY

DEVELOPMENT OF THE METHOD. A means of quantifying shakes as seen in the stump/butt cross section was needed, in order to ensure consistency in recording, and an accurate record of severity of the shake. An index was devised, and the range of scores divided between five categories from "sound" to "severe shake".

The index was designed as though recording the loss of yield of saw timber, because the shake defect is a problem for the timber merchant rather than for the health of the tree. The methods of valuing oak logs with shake, described by questionnaire respondents (section 3.1.3), were borne in mind.

The method had to make the assumption that the pattern of shake was the same throughout the trunk. This was not strictly correct (Sections 3.1.1 and 3.1.2) but was tenable in that the worse the shakes at the base of the tree, the greater the longitudinal extent of the defect is likely to be. Moreover, the most valuable part of the tree is generally the butt log.

Numbers of shakes were represented by additive factors in the index. The number of quarters affected by shake in the cross section of a tree, was made a multiplicative factor. This was so that the importance of ring shakes (even single ring shakes in the absence of radial splits) would be adequately represented. Small ring shakes near the pith are important because they give rise to star shake at some level (Section 2.3.5); ring shakes far from the pith, even if only partial rings, are important because their longitudinal extent is often large.

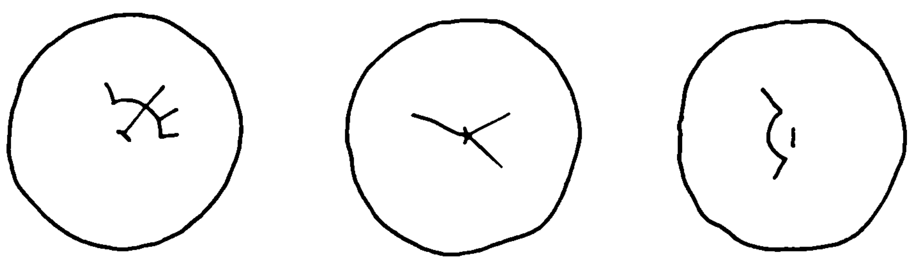
Sawing through-and-through is more economical than quarter-sawing, so presence of shake in two opposing quarters was regarded as worse than shake in two adjacent quarters. That the quarters will be of equal cross-sectional area (thus volume) assumes a central pith; this was accepted, as very eccentric trees were rarely shaken (Section 3.1.2.), although they would have other problems of quality.

TESTING THE INDEX. A base was needed on which to test the prototype and final methods of calculating an index. A set of thirty-nine drawings taken from field sheets was made, showing a complete range of typical shakes with various combinations of ring and radial splits. Each drawing was numbered and listed in one of five categories: sound, slight-, moderate-, bad- or severe-shake. The calculations were applied and modified, and the range of scores allocated to each category of shake were modified until a consistent index could be obtained for each case, and each case could be consistently allocated to the correct category on the basis of the index. The method of calculating the index was finally tested by asking a number of people to use it on fifteen of the drawings; results were very close, and large inconsistencies occurred only in the highest scores, all of which would have fallen into the category "severe" shake). The method described below was adopted.

CALCULATION OF THE SHAKE SEVERITY INDEX:

Examine the cross-section of the stump or butt:

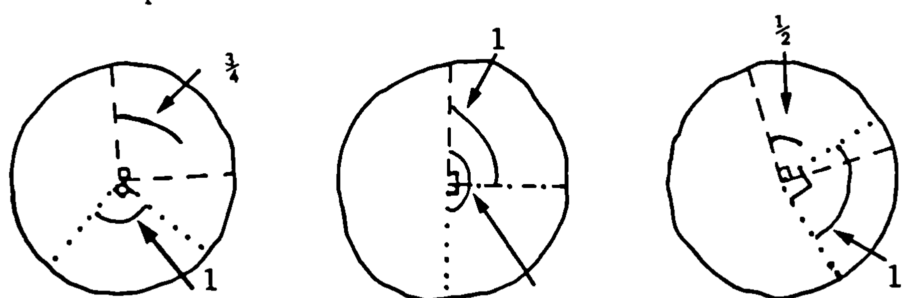
1. Calculate A: A = the total number of radial splits, originating from the pith or (separately) from a ring shake. For example:



A = 4 A = 3 A = 2

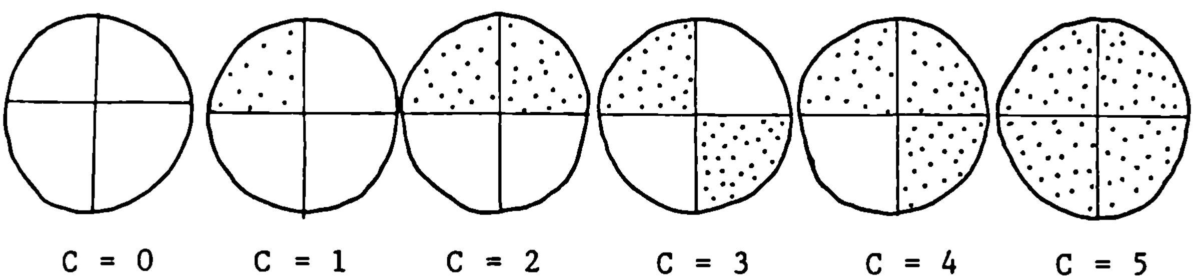
Do not include heart crack, or splits due to felling damage or drying (described in section 3.1.1).

2. Calculate B: B = the sum of quadrants traversed by each ring shake. Quadrants may overlap, but are still treated separately. Scores of ¼, ½ and ¾ can be used for incomplete quadrants. For example:



B = 1¾ B = 3 B = 1½

3. Calculate C: C = a score for quarters of the log affected by shake, as seen in cross section. Draw a pair of perpendicular lines on the cross-sectional face, such that the maximum number of shake-free quarters falls between the lines. Scores are then calculated as in the diagrams below, where unshaded quarters are free of shake.



4. Calculate the index of severity of shake for each tree:

$$\text{Index} = (A + B)C$$

5. The categories of shake in individual trees correspond to the following ranges of indices:

Category	Index
Sound	0
Slight shake	1 - 6
Moderate shake	7 - 18
Bad shake	19 - 30
Severe shake	31 or more.

3.2.2.4. SAMPLE COLLECTION.

SOILS. One to two soil samples were collected from all main survey sites. Samples were collected from the middle of the A-horizon of the soil profile, because the fine-rooting of the oaks was usually concentrated in the A-horizon.

Soil samples were transported in polythene bags. Tests requiring soils in the fresh state were carried out as soon as possible - usually within two days, though after a maximum of 19 days for soils collected during the first of the 1988 surveys.

Pairs of samples, consisting of one from beneath a sound oak, and one from beneath a shaken oak, were collected from eight sites to investigate any local differences associated with shaken individual oaks (site numbers 8, 11, 14, 16, 20, 21, 23 and 46). Site 46 had a low incidence of shake; the remainder had a high percentage of shaken oaks.

WOOD. Samples of wood were collected from some sites. The analysis of the wood samples is described in Chapter 4.

3.2.2.5. SOIL ANALYSIS

THE SOIL COMPONENTS ANALYSED. The following soil characteristics were analysed: pH, moisture content, stone content, organic matter content, and soil texture (proportions of clay, sand and silt). Levels of the following exchangeable cations were analysed: calcium, magnesium, potassium, sodium and manganese. Levels of potassium pyrophosphate extractable iron (fresh, amorphous iron oxides) and aluminium were determined.

Soil moisture is partly dependent on season and current weather conditions, but also reflects the moisture-holding capacity of the soil and drainage characteristics of the subsoil. No samples were collected during the usual months of water-deficit in soils, and the majority (75 %) were collected during a three-week spell of fair weather in April, so this soil characteristic was considered to be suitable for investigation. Relative levels of soil moisture, rather than actual, will be of importance in the results.

The exchangeable cations analysed, were chosen (from the range which could be analysed using the spectrophotometry methods described below) for the following reasons. Calcium is important in the soil in relation to pH balance; it is important in the tree as a constituent of the middle-lamella between cell walls. Calcium deficiency in trees reduces the ability of terminal buds and root tips to develop (Tisdale & Nelson, 1975). A link between the calcium:iron ratio of soils and the incidence of shake was suggested by Lachaussée (1953). Magnesium is the central component of the chlorophyll molecule, and also important in enzyme systems and osmosis (Courtney and Trudgill, 1976). Potassium is an important nutrient for plant growth, health and vigour; high potassium levels in the tree have been shown to improve drought resistance in some hardwoods, by reducing transpiration rates (Driessche, 1984). Manganese is an important micronutrient for plants, being involved in various enzyme reactions. Sodium may have similar roles to potassium (Courtney and Trudgill, 1976). Deficiency of any of the above elements would lead to loss of vigour or health of a tree. The levels of these elements in the A-horizon soils will give an indication of the relative growing conditions at the sites surveyed; they have been expressed as milli-equivalents per 100 g of soil. This is a measure of the cation exchange capacity of the soil for each of these elements, i.e. the ability of the clays and humus in the soil to yield cations for plant use (Courtney and Trudgill, 1976).

Iron is an essential element for plant growth, but can become toxic in high concentrations. Iron toxicity is most likely at soil pH of less than 3.2 (Khanna and Ulrich, 1984), and when other essential elements with which iron competes for uptake are relatively scarce.

Aluminium can affect root health of plants; in soils of pH less than 4.2, aluminium toxicity becomes important; low calcium:aluminium ratios in the soil solution inhibit the growth of fine roots of trees (Khanna and Ulrich, 1984).

METHOD. Analyses of pH, moisture content and organic matter content were carried out as soon as samples were returned to the laboratory. The rest of each sample was then air-dried and kept until large batches accumulated, before the remaining analyses were carried out.

The standard analysis methods used, were those described in an Institute of Terrestrial Ecology typescript of 1966: "Meth ds of soil analysis used at Bangor Research Station.".

pH was measured in water and in 0.01 M $CaCl_2$. The latter meth d is described by Black (1965); the results gained are representative of the soil under field conditions, and are comparable between samples taken at different times of year. pH values used in analysis of results were those measured in $CaCl_2$ solution; pH values measured in water are included in Appendix 3.3.

Moisture content of fresh soil was expressed as a percentage by weight, following oven-drying at 105° C. Stone content was expressed as a percentage by weight, of air-dried soil. Loss on ignition (estimate of organic matter content) was determined by roasting in a muffle furnace at 375° C for 16 hours, and expressed as a percentage of oven-dried (105° C) weight.

Mechanical analysis of soil samples used a Bouyoucos hydrometer to measure sedimentation rates of soil suspensions in cylinders. Soil texture classes used were the Avery classes (particle sizes: clay <2 um, silt 2 - 60 um, sand 60 -

2000 um); percentages of sand, clay and silt are calculated after removal of gravel and stone larger than 2 mm diameter.

Exchangeable cations were extracted in N Ammonium Acetate solution, adjusted to pH 7.0; extracts were analysed by atomic absorption spectrophotometry and results are expressed as milli-equivalents per 100 g of soil (me/100 g).

Iron and aluminium were extracted from soil samples in 0.1 M Potassium Pyrophosphate (pH 9.8); extracts were analysed by atomic absorption spectrophotometry and results are expressed as parts per million (ppm).

Ratios of calcium to iron and aluminium, are calculated from ppm for all three elements.

Results of soil analyses were averaged for the A-horizon of each site.

3.2.2.6. ANALYSIS OF RESULTS FROM FIELD SURVEYS

The amount and severity of shake in sites numbers 1 to 42 was analysed in relation to means of quantified crop parameters and site conditions.

The percentage of trees with any type or degree of shake was calculated for each site; also the percentage of trees with ring shake (with or without star shake), and the mean index of shake severity. Sound trees (index = 0) were not included in the mean index.

Means of tree growth characteristics were calculated for the oaks on each site (Section 3.2.2.7 is a summary of factors measured) and percentages of trees with rot and with mineral stain were calculated for each site.

The differences between the means of sessile and pedunculate sites for tree and site characteristics, were tested using t-tests (calculated using the MINITAB package). This was done in order to identify any influence of species on tree characteristics or any association of species with site characteristics.

Records of ground flora and presence of honey fungus were not sufficiently thorough to be analysed separately, but notes are included in the site summary forms in project notes for Forestry Commission archives.

REGRESSION ANALYSES. Simple single and multiple linear regressions were calculated, in order to examine the mean data from site numbers 1 - 42. The form of the regression equations for single independent variables is that of the equation for a straight line: $Y = a + bX$; for equations with two r n re independent variables, the form of the equation is $Y = a + b_1X_1 + b_2X_2 + \ldots + b_kX_k$.

Regression equations were calculated using the MINITAB statistical package on the UCNW mainframe computer (VAX). The computational methods used by MINITAB were Givens transf rmations using "Linpack" routines. Any sites which contained one or more missing values for any given regression (either the dependent, or one or more of the independent variables) were not included in the calculation of that regression.

Analyses of variance were calculated to test how well each regression equation described the relationship of the dependent and independent variables - i.e. whether the part of the variation in Y that is explained by the fitted line is significantly greater than the part that is left unexplained; the P value quoted in the results is the level of significance of F in the ANOVA calculation. A good fit does not imply that a linear relationship is the best description of the data; plots of single regressions are also shown in the results.

The r^2 values quoted in the results illustrate how well the regression line fits the sample data, and are adjusted for the number of degrees of freedom.

Associations between site conditions, soil conditions and tree parameters (other than shake) were tested. Linked characteristics were not used together in multiple regressions of shake incidence or severity on tree and site characteristics.

The percentage of shaken trees in a crop was regressed on a) site conditions, b) soil conditions, c) tree parameters. Similarly, the percentage of trees with ring shake, and the mean shake index were regressed on factors in these three groups.

STUDY OF ANNUAL RINGS WITH RING SHAKES.

Records of exceptionally wide and narrow annual rings, and those c ntaining ring shakes were used to plot frequency charts f r individual sites. These charts have been summarised in a single diagram (Figure 3.20.). This illustrates which annual rings most often contained ring shakes, and any associations of these shakes with common growth patterns.

SEPARATE EXAMINATION OF SHAKE INCIDENCE IN SESSILE AND PEDUNCULATE OAK SITES.

Regressions of shake incidence on tree and site characteristics were also calculated separately for the eight sessile oak sites and the thirteen pedunculate oak sites. This was done in order to find any species differences in response to site factors. Results are given in Appendix 3.7.

3.2.2.7. SUMMARY OF INFORMATION RECORDED IN FIELD SURVEYS.

* = measurement used in regression analyses.

INCIDENCE OF SHAKE: IN OAK	*PERCENTAGE OF TREES WITH ANY FORM OF SHAKE
	*PERCENTAGE OF TREES CONTAINING RING SHAKE
SEVERITY OF SHAKE:	*MEAN INDEX OF SEVERITY IN INDIVIDUAL SHAKEN OAK TREES
NATURE F CROP: AND TREES	OAK SPECIES
	AGE OF OAKS
	SILVICULTURAL METHOD
	*MEAN DIAMETER OF OAKS
	*MEAN RING WIDTH OF OAKS
SITE CONDITIONS:	*ALTITUDE
	SOIL DEPTH
	ASPECT

(continued...)

SUMMARY OF INFORMATION RECORDED IN FIELD SURVEYS (continued).

* = measurement used in regression analyses.

GROSS WOOD STRUCTURE AND PROPERTIES OF OAKS:	*MEAN SAPWOOD THICKNESS
	*MEAN BARK THICKNESS
	*MEAN FREQUENCY OF WIDE RAYS
	*PERCENTAGE OF TREES WITH MINERAL STAIN
	*PERCENTAGE OF TREES WITH ROT IN THE BUTT
	ANNUAL RINGS OF EXTREME WIDTH OR NARROWNESS
	ANNUAL RINGS CONTAINING RING SHAKES
	C LOUR AND STAINING OF FRESH-CUT WOOD
	ECCENTRIC GROWTH PATTERN IN BUTT
SOIL C NDITIONS IN A-H RIZON:	*SOIL TEXTURE (PERCENTAGES OF CLAY, SAND AND SILT)
	*SOIL pH
	*PERCENTAGE STONE
	*PERCENTAGE MOISTURE
	*PERCENTAGE ORGANIC MATTER
	*EXCHANGEABLE CATIONS (Mg, Ca, K, Na, Mn)
	*IRON AND ALUMINIUM

3.2.3 RESULTS OF FIELD SURVEYS.

Appendix 3.3 contains the site-means of tree and site characters from surveys of sites 1 - 42. Appendix 3.4 summarises the co-efficients of determination (r^2) and their level of significance for all significant ($P < 0.050$) single and multiple regressions calculated. Tables 3.6 and 3.7 (at the end of Section 3.2.3.3) give the regression equations of the most significant of these regressions. Appendix 3.5. shows the analyses of variance of the regressions from Tables 3.6. and 3.7.

3.2.3.1. DIFFERENCES IN SITE AND TREE CHARACTERISTICS BETWEEN SESSILE AND PEDUNCULATE OAK SITES.

The means of data from the eight sessile oak sites and from the thirteen pedunculate oak sites were compared.

There was no significant difference between the means of the sessile and pedunculate oak sites, for site factors, tree characteristics or incidence and severity of shake. The results of t-tests of species-means for all tree characteristics and site factors, are summarised in Appendix 3.6.

The lack of significant differences between the means of sessile and pedunculate oak sites for both tree characteristics and site factors, suggested that this potential source of variation was not important in the analysis of between-site data using all 42 sites.

3.2.3.2. ASSOCIATIONS BETWEEN SITE FACTORS AND TREE CHARACTERISTICS OTHER THAN SHAKE.

Suspected links between various tree and site characteristics, were tested by regression analysis. This was done in order that characters identified as being linked would not be used together in a multiple regression. Factors associated with mineral stain, which was found to have no association with the incidence and severity of shake (sections 3.2.3-3/5/& 7), were also investigated.

ASSOCIATIONS BETWEEN SITE FACTORS. The expected positive association of pH and calcium in the soil appeared to be strong (r^2 = 90.0% with $P < 0.001$; Figure 3.4), and soils of higher pH also tended to have a higher level of magnesium (r^2 = 23. % $P = 0.004$); see note in section 3.2.3.3 concerning pH measurements. Soils with high levels of magnesium also had higher levels of potassium (r^2 = 39.3%; $P < 0.001$); and levels of calcium and potassium may have been positively associated (r^2 = 9.0%; $P = 0.038$). For the linear association between calcium and magnesium levels, r^2 = 13.2% ($P = 0.14$), but for values of calcium below 7.5 me/100 g, the r^2 value was high (r^2 = 65.4%; $P < 0.001$); see Figure 3.5. There was no association between soil moisture or exchangeable cation levels and the proportion of clay in the soil, but soils with higher levels of organic matter tended to have a higher moisture content (r^2 = 45.8; $P < 0.001$; Figure 3.6).

FACTORS ASSOCIATED WITH THE OCCURRENCE OF MINERAL STAIN. Significant negative associations were found between the percentage of oaks with mineral stain, and the levels of potassium and magnesium in the soil. Figure 3.7 is a plot of the data for potassium and mineral stain, with the regression line superimposed. The regression equations are given in Table 3.6., together with the values of r^2 and the significance of each regression. Low potassium levels in the soil gave the best explanation of the occurrence of mineral stain in oaks. There was little or no association (linear or otherwise) between the occurrence of mineral stain and any of the other site factors or tree characteristics measured.

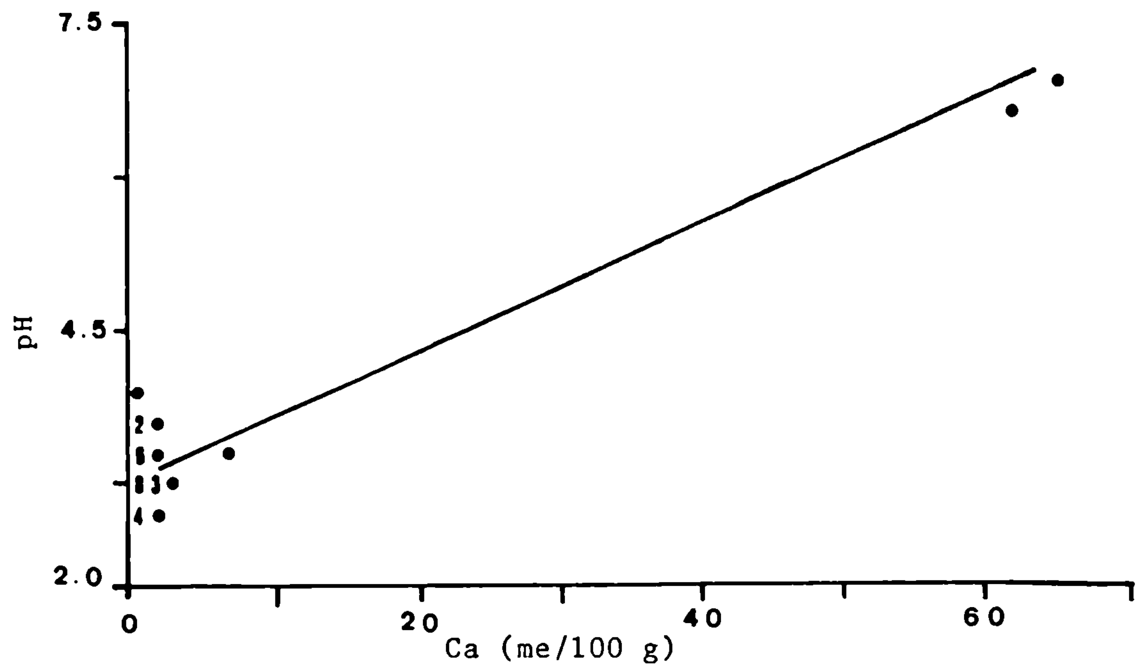


Figure 3.4. Relationship between pH and calcium levels in soils from survey sites.

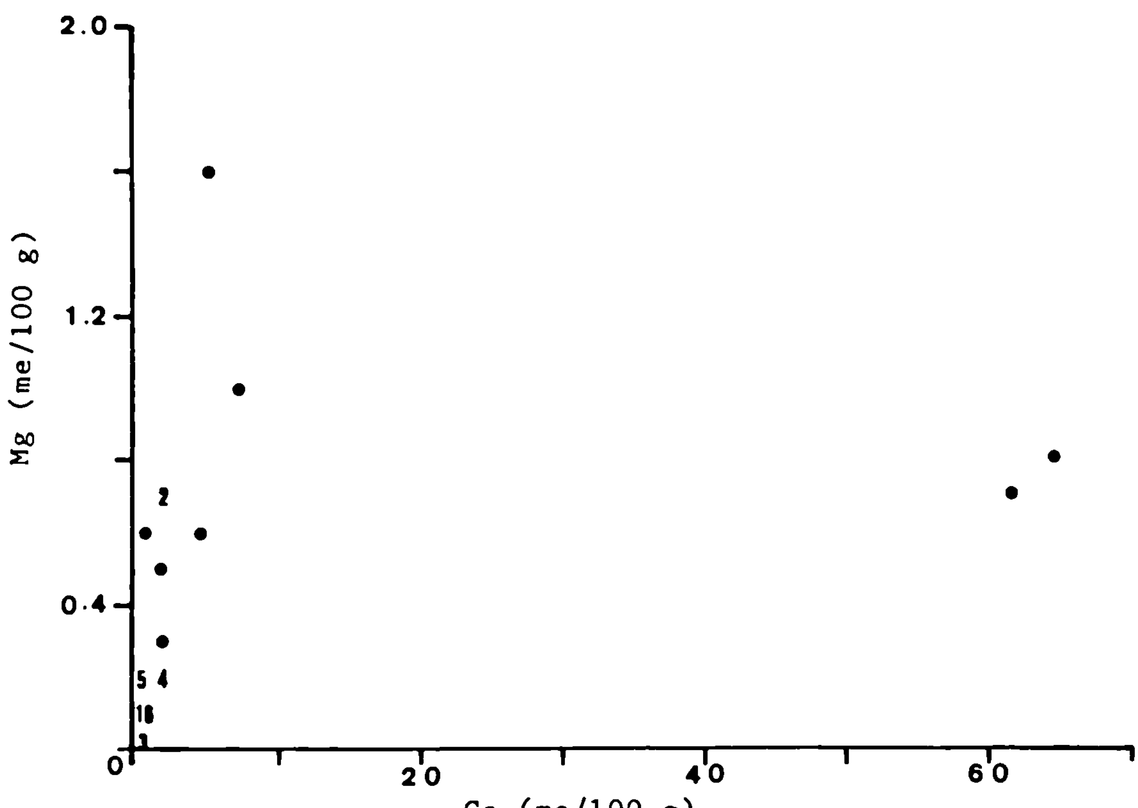


Figure 3.5. Relationship between magnesium and calcium availabilities in soils from survey sites.

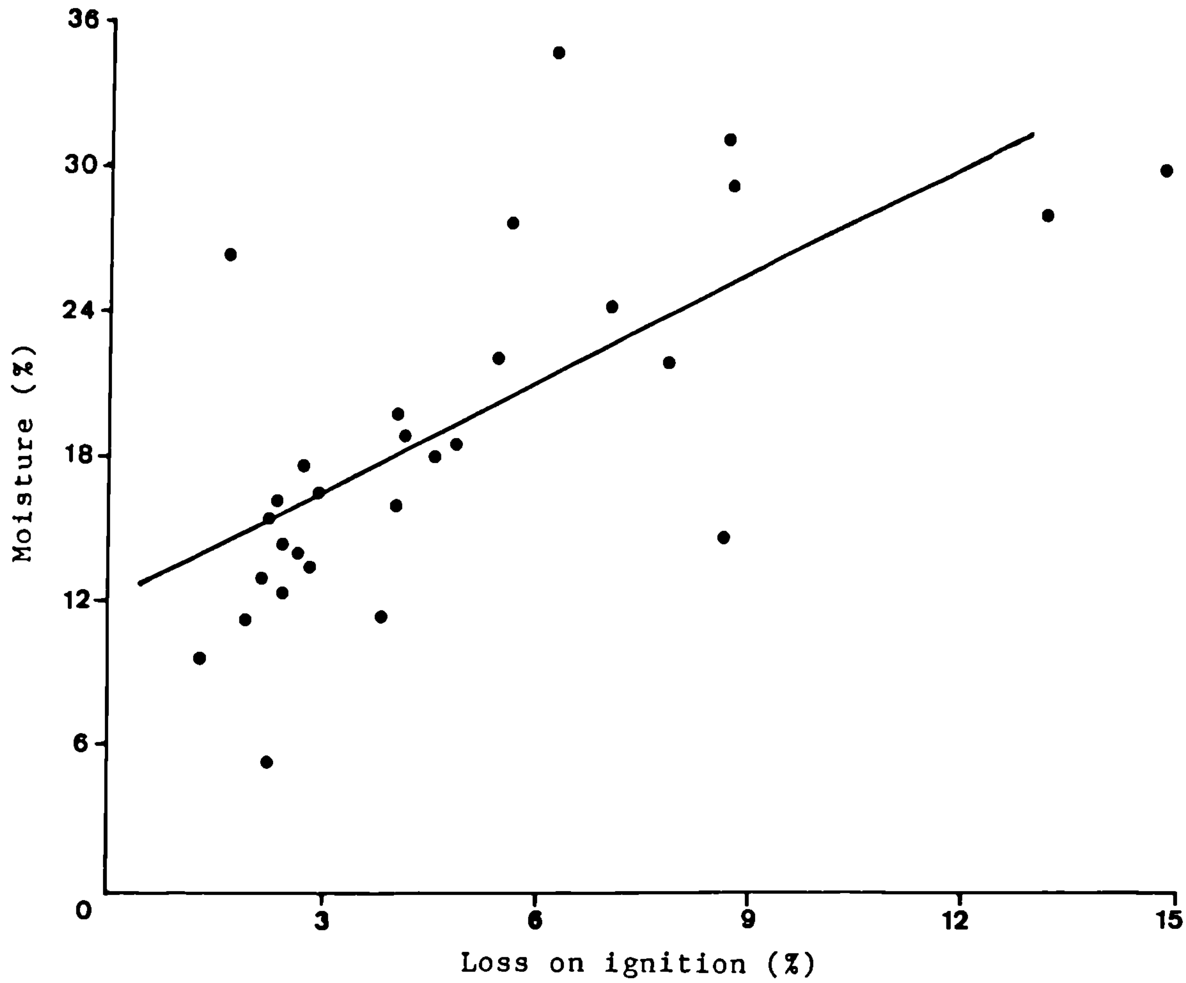


Figure 3.6. Relationship between soil moisture content and amount of organic matter in soils from survey sites.

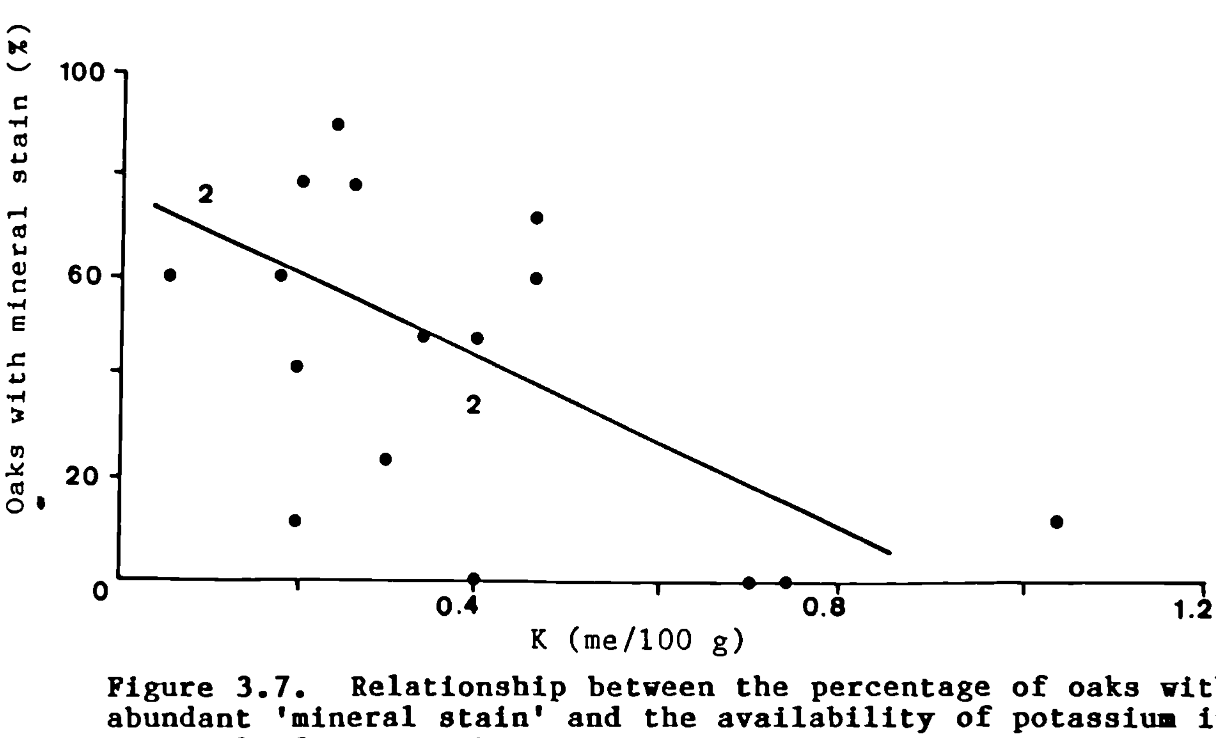


Figure 3.7. Relationship between the percentage of oaks with abundant 'mineral stain' and the availability of potassium in the soil of survey sites.

3.2.3.3. FACTORS RELATED TO THE INCIDENCE OF ALL SHAKE.

TREE CHARACTERISTICS, SOIL FACTORS AND SITE ALTITUDE. When the percentage of shaken trees in a site was regressed separately on tree and site characteristics, the highest r^2 values obtained were with the independent variables of calcium in soil, mean ring width, soil moisture content, ratios of calcium to iron and aluminium, and levels of magnesium in the soil. These were all negatively associated with incidence of shake. The regression equations are given in Table 3.6., together with the values of r^2 and the significance of each regression. Regressions of percentages of shaken oaks on four main site factors are illustrated by the plots in Figures 3.8 - 3.11.

Anomalous sites where growth rate was slow but shake incidence was low, were sandy soils with high calcium levels; in these cases growth rate was probably limited by water availability, but tree health was good due to good nutrition.

P sitive associations between shake incidence and a) the percentage of trees containing rot in a site, and b) aluminium levels in the soil were apparent; and sites with a high clay content tended to have a lower incidence of shake, but r^2 values were very low in all these cases (see Appendix 3.4).

The range of pH values in the soils was very unevenly represented, with a concentration of data in the lower end of the range and two extreme high values (Figure 3.4.). Consequently, although regressions on shake incidence which included pH as an independent variable produced relatively high r^2 values, the regressions were not significant. The association between pH and calcium in the soil may have been the influence which caused the apparent association of pH and shake. The sites which had the highest values of soil pH and calcium also had exceptionally sound oak crops, but if the two sites with pH greater than 7.0 are omitted from regression calculations, then no clear relationship exists between pH and the incidence or severity of shake; this suggests that the level of calcium in the soil may be a more important factor than pH, in association with shake. The multiple regressions on shake incidence which were calculated using pH, gave high r^2 and probability results, but are omitted because of the nature of the pH data.

There was little or no association (linear or otherwise) between the percentage of shaken oaks in a site, and the following crop and site characteristics: mean tree diameter, sapwood thickness, bark thickness, wide ray frequency, percentage of trees with mineral stain, altitude of site, soil proportions of silt, sand, or stone, and amount of organic matter, potassium, iron, manganese or sodium in the soil.

UNDERLYING GEOLOGY. Table 3.3. below shows the mean incidence of shake in sites on the six most frequently represented geological substrates of the site surveys.

Geological system	Mean incidence of shaken oaks	number of sites	standard deviation
Wealdon	38%	9	22
BBB beds	34%	7	26
Lower Greensand	52%	6	10
Chalk	13%	6	13
Devonian sandstone	71%	3	18

TABLE 3.3. INCIDENCE OF SHAKE IN OAK, ON SITES OF DIFFERENT UNDERLYING GEOLOGIES.

The low incidence of shake on Chalk reflected the results of the regression analyses which suggested that sites with higher clay and nutrient levels in the soil are more likely to be shake free. Likewise, the consistently high incidence of shake on the Lower Greensand was as expected from soils, the parent rock of which is sandy, poor in many plant nutrients, and high in iron content. The Wealdon strata and the Barton, Bracklesham, and Bagshot (BBB) beds of Pliocene/Pleistocene strata are variable in nature, being alternating layers of sands and gravels, and (in Wealdon strata) clays. This variability is reflected by the high standard deviations of shake incidence means on sites with such geology, and by the soil textures which ranged from sand to clay loam.

SOIL TEXTURE. Soil texture classes are based on the relative proportions of sand, silt and clay in the soil after stone (greater than 2 mm diameter) has been removed; they are normally represented on the triangular diagram which is the basis of Figure 3.12 (end of Section 3.2.3.3). Symbols representing classes of shake incidence at the different sites are plotted on this texture diagram, to illustrate the variation in shake incidence which was found on soils of different textures.

Incidence of shake was low on clay and clay loam soils (those with a clay fraction of greater than 18%). Sites with a high incidence of shake were all on sandy soils, though some of these soils also carried oak crops with a low incidence of shake. These latter differed from the shaky sites in that the sands either had higher calcium levels (greater than 1.0 me/100 g), or, if calcium was low then levels of aluminium were low also (less than 5 ppm).

There were a few remaining anomalous sites where soils were sandy but calcium levels were high (a combination which was usually associated with lower shake incidence), and yet shake incidence was high. In these, other factors existed which produced poor rooting conditions for the oaks: a high water table, giving an anoxic B-horizon; a very high iron content of soil; a high stone content; or an extremely low clay content (2 - 3%).

The mean percentage of sound and of ring-shaken oaks on sites with different soil textures is given in Table 3.4 below:

Soil texture:	**Sand/sandy loam**	**Sandy silt loam**	**Clay/clay loam**
% shaken:	45	48	18
% ring shaken:	26	26	6

Table 3.4. INCIDENCE OF SHAKE ON SOILS OF DIFFERENT TEXTURES.

Data are means of percentages of shaken oaks within sites. Clay clay loam includes sandy clay. Sandy silt loam includes silt loam.

TOPOGRAPHY OF SITE AND SOIL DEPTH. Eleven of the sites recorded were on a steep slope, and thirty-three were on flat or slightly sloping ground. The condition of oak crops in these two broad categories is shown below in Table 3.5:

Percentage of shaken oaks on site	Percentage of sites in shake class.	
	Sites with flat or slight slope	Sites with steep slope
51 - 100	30%	73%
31 - 50	30%	9%
0 - 30	40%	18%
	100%	100%

Table 3.5. INCIDENCE OF SHAKE IN RELATION TO TOPOGRAPHY. Data are percentages of a) 11 steep sites and b) 33 flat or slightly sloping sites.

Table 3.5 above, shows that the majority of sites on steep slopes had a high incidence of shake, whereas those on flat to gentle slopes were evenly divided between the shake classes. The drainage or exposure of slopes may be implicated, but it must be noted also that none of the steep sites had the clay soils which have been shown to be associated with sound oak.

A comparison of the slope under individual trees on site 29 (159 oaks on an overall steep site), showed no difference between percentages of sound trees on four arbitrary grades of slope from level to steep. However, there were differences in shake severity in those trees which were shaken: the majority on level microsites were only slightly shaken, whereas the majority on medium to steep slopes were moderately to severely shaken.

On sites with soils of less than 50 cm depth, the mean percentage of sound oaks was 40 % (n = 14; s.d. = 16). Deeper soils produced crops with a mean of 74 % sound trees (n = 20; s.d. = 22).

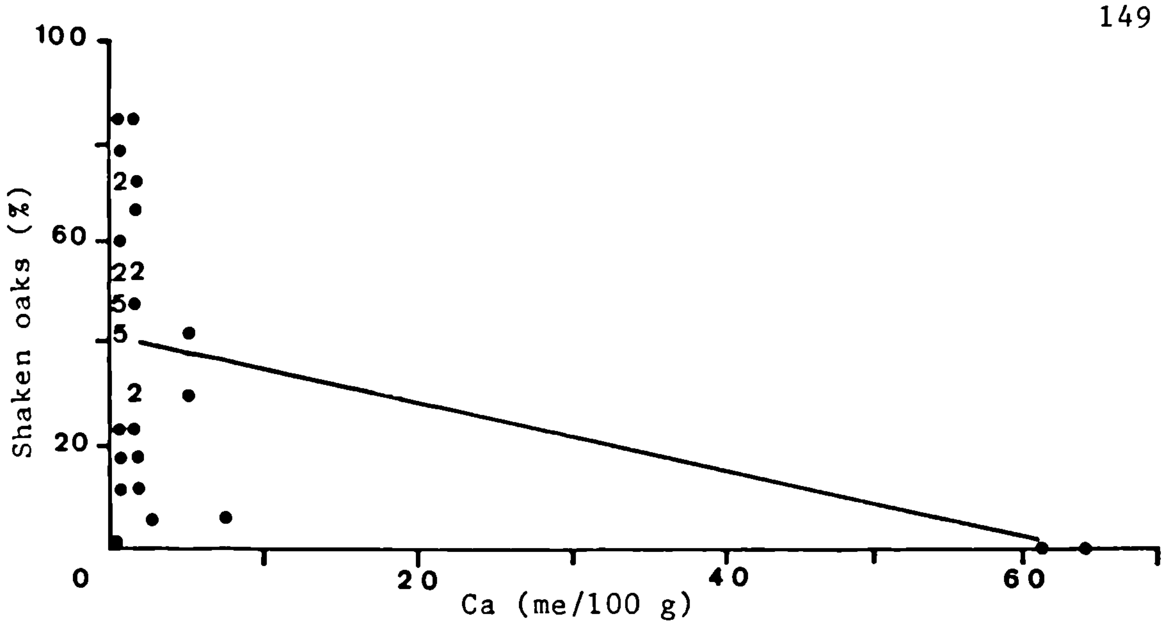


Figure 3.8. Relationship between the percentage of oaks containing shakes and the availability of calcium in soils of survey sites.

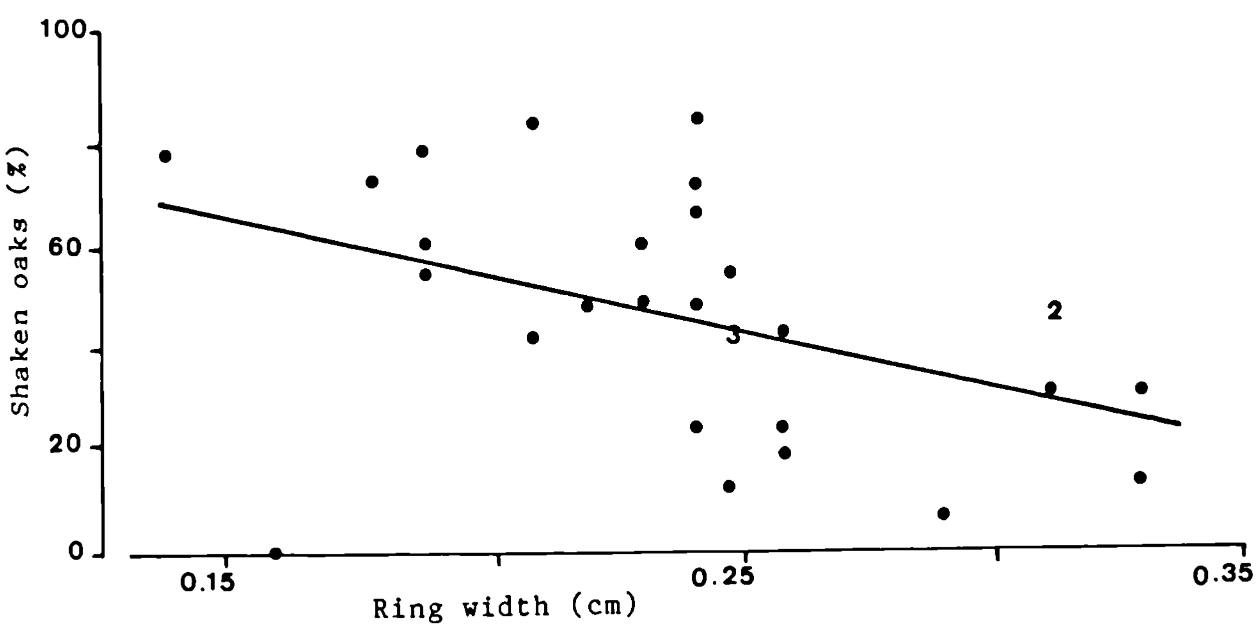


Figure 3.9. Relationship between the percentage of oaks containing shakes and the mean growth rate of oaks on each survey site.

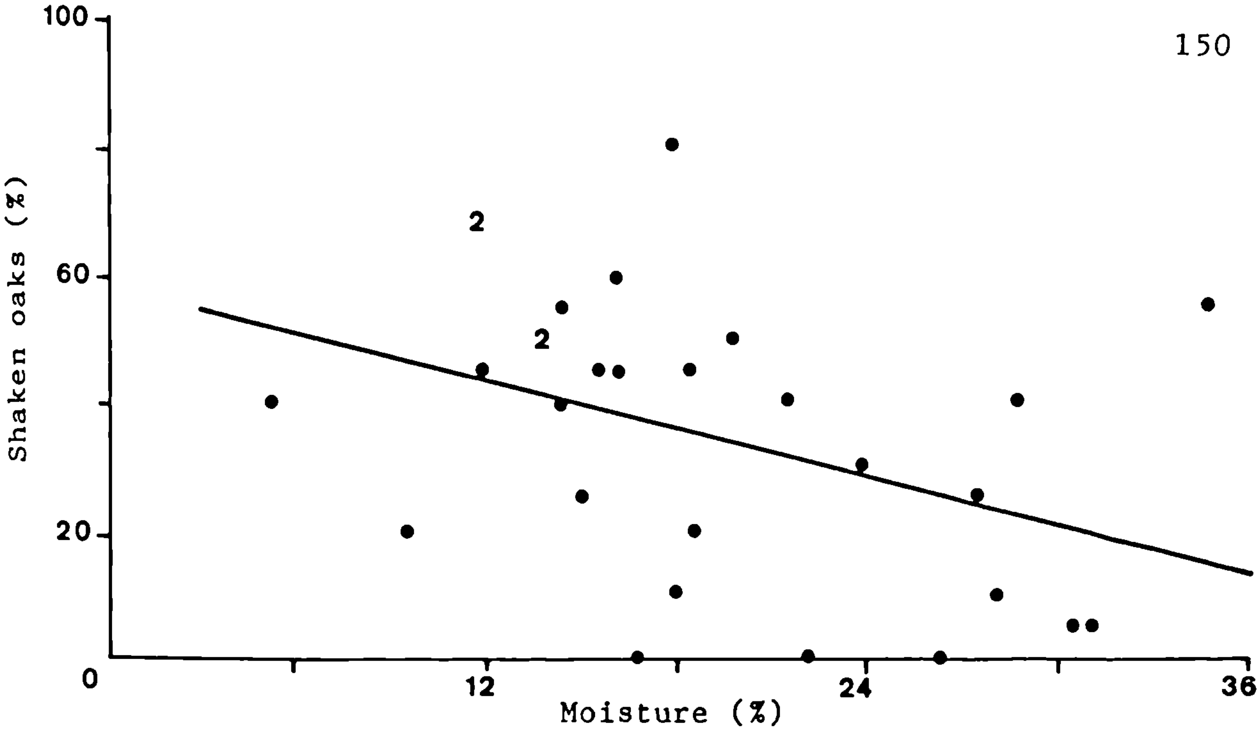


Figure 3.10. Relationship between the percentage of oaks containing shakes and soil moisture content at survey sites.

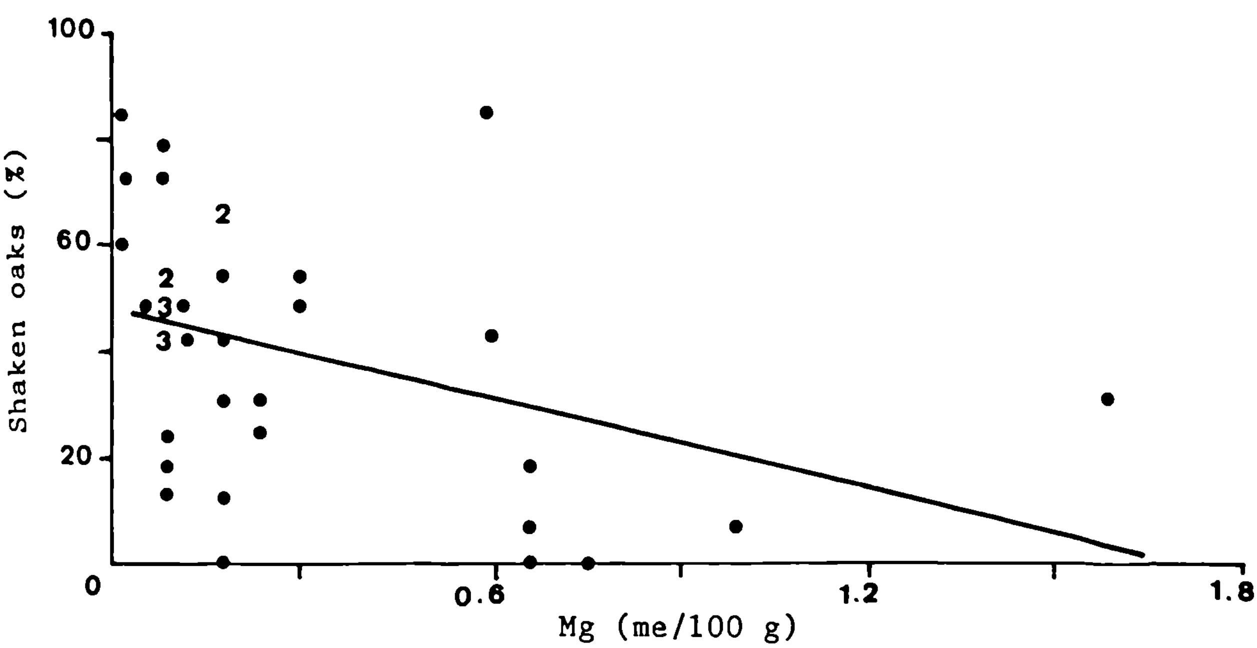


Figure 3.11. Relationship between the percentage of oaks containing shakes and the availability of magnesium in soils of survey sites.

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P	TOTAL DF
pH of soil	= 3.1 + 0.06 (Calcium in soil (me/100 g))	90.0	<0.001	30
Magnesium in soil	= 0.2 + 0.01 (Calcium in soil (me/100 g))	13.2	0.014	37
Potassium in soil	= 0.3 + 0.05 (Calcium in soil (me/100 g))	9.0	0.038	37
Potassium in soil	= 0.2 + 0.4 (Magnesium in soil (me/100 g))	39.3	<0.001	37
Moisture in soil	= 12.0 + 1.5 (Organic matter (%LOI))	45.8	<0.001	28
Percentage of shaken oaks on site	= 43.3 - 0.7 (Calcium in soil (me/100 g))	17.1	0.006	37
"	= 96.3 - 213.0 (Mean ring width (mm))	16.2	0.016	29
"	= 60.1 - 1.3 (Percentage moisture in soil)	14.4	0.024	28
"	= 42.6 - 0.6 (Calcium:Iron (ppm))	14.4	0.011	37
"	= 42.5 - 0.2 (Calcium:Aluminium (ppm))	14.2	0.011	37
"	= 48.0 - 28.8 (Magnesium in soil (me/100 g))	14.1	0.012	37

Table 3.6. SUMMARISED RESULTS OF SINGLE REGRESSIONS ON DATA FROM SITE SURVEYS. (Continued on next page)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P	TOTAL DF
Percentage of oaks with ring shake	= 15.6 + 0.7 (Percentage of oaks with rot in butt)	26.9	0.001	34
"	= 66.6 - 169.0 (Mean ring width (mm))	17.3	0.013	29
"	= 27.7 - 21.5 (Magnesium in soil (me/100 g))	13.0	0.017	35
"	= 15.4 + 0.8 (Aluminium in soil (ppm))	10.3	0.031	35
"	= 23.9 - 0.4 (Calcium in soil (me/100 g))	8.2	0.050	35
Mean index of shake severity	= 31.0 - 1.5 (Organic matter in soil (% LOI))	11.7	0.031	31
"	= 27.9 - 42.1 (Manganese in soil (me/100 g))	10.9	0.034	32
"	= 15.3 + 0.07 (Altitude of site)	9.4	0.041	33
("	= 38.0 - 0.6 (Percentage moisture in soil)	10.7	0.066	23)
Percentage of oaks with mineral stain	= 72.7 - 76.7 (Potassium in soil (me/100 g))	36.3	0.003	19
"	= 59.5 - 43.7 (Magnesium in soil (me/100 g))	30.8	0.007	19

Table 3.6. continued. SUMMARISED RESULTS OF SINGLE REGRESSIONS ON DATA FROM SITE SURVEYS.

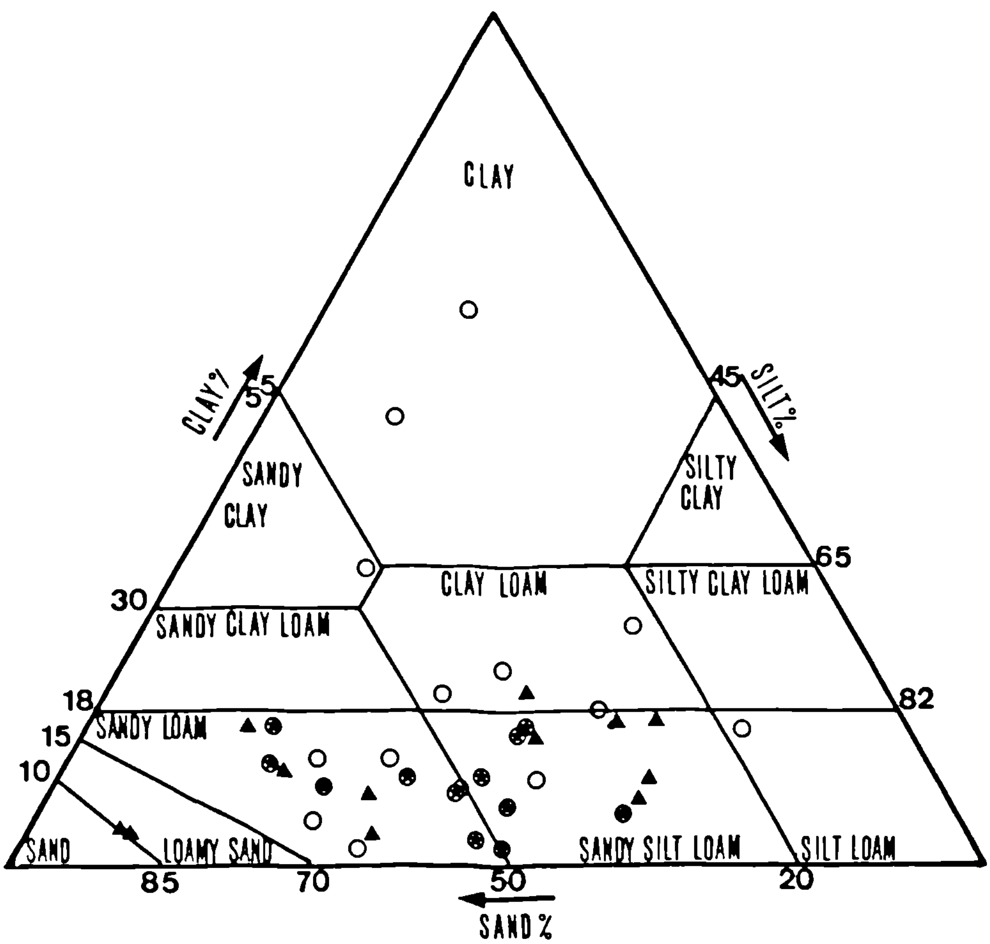


Figure 3.12. Incidence of shake in oak woodlands on soils of different textures (Avery soil texture classes).

Percentage of shaken oaks per site:
⊛ 51 - 100%; ▲ 31 - 50%; ○ 0 - 30%.

3.2.3.4. MULTIPLE REGRESSIONS OF FACTORS ASSOCIATED WITH INCIDENCE OF ALL SHAKE.

The best multiple regressions obtained when percentage of shaken trees was regressed on tree and site characteristics (i.e. those regressions with the highest r^2 values, which were also significant at between $P < 0.001$ and $P = 0.004$), are given in Table 3.7 overleaf. The full analysis of variance for the first three listed, is given in Appendix 3.5. Other combinations of independent variables which gave fair to good regression results, are listed in Appendix 3.4.

High percentages of shaken oaks in a site were best explained by a combination of low soil moisture and calcium, high aluminium in the soil and a slow growth rate of the crop. The balance of these factors is not necessarily a direct cause of the shake, but is associated with its presence.

Inclusion of the percentage of trees with rot in the multiple regression increased the value of r^2, but the significance of the regression was slightly lower. Multiple regressions of magnesium with moisture, aluminium and rot also gave highly significant regressions, but the co-efficients of determination (r^2 values) were lower than the same regressions with calcium in place of magnesium as an independent variable. Inclusion of ring width in the regressions with magnesium gave slightly less significant regressions.

DEPENDENT VARIABLE		INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P	DF
Percentage of shaken oaks	=	106.0 - 0.9 moisture - 0.9 Ca + 1.1 Al - 214.0 r.width	60.9	<0.001	21
"	=	104.0 - 0.9 moisture - 0.9 Ca + 1.2 Al - 214.0 r.width + 0.1 rot	66.7	0.001	19
"	=	122.0 - 0.8 moisture - 260.0 r.width - 1.0 Ca + 0.2 rot	61.4	0.001	19
"	=	91.3 - 0.6 moisture - 169.0 r.width + 1.2 Al - 13.7 Mg + 0.05 rot - 7.3 Ca:Fe	65.6	0.002	19
"	=	46.8 - 0.7 moisture + 1.4 Al - 42.9 Mg + 0.2 rot	54.8	<0.001	24
"	=	122.0 - 303.0 r.width - 1.2 Ca	42.3	<0.001	27
Percentage oaks with ring shake	=	80.7 + 0.3 rot - 248.0 ring width - 0.7 Ca + 0.5 Al	59.1	<0.001	25
"	=	76.6 - 0.6 Ca - 0.7 moisture + 0.9 Al - 185.0 r.width + 0.3 rot	61.8	0.002	19
"	=	90.7 + 0.3 rot - 276.0 ring width - 0.8 Ca:Fe	55.1	<0.001	25
"	=	125.0 + 0.3 rot - 234.0 r.width - 0.7 moisture - 10.2 pH	60.1	0.001	19
"	=	115.0 + 0.4 rot - 248.0 ring width - 10.3 pH	50.8	0.001	21

Table 3.7. SUMMARISED RESULTS OF MULTIPLE REGRESSIONS ON DATA FROM SITE SURVEYS.(Continued on next page)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P	DF
Mean index of shake severity	= 11.8 + 0.1 altitude - 0.5 moisture + 0.2 sand	40.4	0.004	23
"	= 27.5 - 0.7 moisture + 0.1 altitude	33.7	0.005	23
"	= 8.9 + 0.1 altitude - 1.0 organic matter + 0.2 sand	24.9	0.013	30
Percentage of oaks with mineral stain	= 70.4 - 53.1 K - 18.9 Mg	35.5	0.009	19

Table 3.7. continued. SUMMARISED RESULTS OF MULTIPLE REGRESSIONS ON DATA FROM SITE SURVEYS.

3.2.3.5. FACTORS RELATED TO THE INCIDENCE OF RING SHAKE.

When the percentage of oaks with ring shake in each site was regressed on tree and site characteristics, the most significant single regression obtained was for percentage of oaks with rot. There was a less strong association of incidence of ring shake with mean ring width of oaks, and weak associations with levels of magnesium and aluminium in the soil. There was no link with soil moisture, unlike the result for the percentage of oaks which also contained star shake.

Figures 3.13 - 3.15 are plots of the data, with the regression line superimposed. The regression equations are given in Table 3.6 (end of Section 3.2.3.3), together with the values of r^2 and the significance of each regression.

There was a positive association between the percentage of oaks with ring shake in a site, and a) percentage of trees with rot (Fig. 3.13), and b) levels of aluminium in the soil.

There was a negative association between the percentage of oaks with ring shake and a) mean ring width of the oaks (Fig. 3.14) and b) levels of magnesium in the soil (Fig. 3.15).

There was little or no association (linear or otherwise) between the percentage of oaks with ring shake, and the remainder of the tree characteristics and site factors measured (Section 3.2.2.7 lists all variables measured in site surveys).

3.2.3.6. MULTIPLE REGRESSIONS OF FACTORS ASSOCIATED WITH INCIDENCE OF RING SHAKE.

The best multiple regressions obtained for the percentage of oaks with ring shake regressed on tree and site characteristics (i.e. those regressions with the highest r^2

values, which were also significant at between $P < 0.001$ and $P = 0.004$), are given in Table 3.7 (at the end of Section 3.2.3.4). The full analysis of variance for the first three listed, is given in Appendix 3.5. Other combinations of independent variables which gave significant regression results, are listed in Appendix 3.4.

The combination of factors which best explained high percentages of ring shaken oaks in a site, was: high percentage of trees with rot, low levels of calcium and high aluminium in the soil, and slow growth rate of the crop. The balance of these factors is not necessarily a direct cause of the shake, but was associated with its presence.

The highest r^2 value was obtained when soil moisture was included in the regression, but the significance of the regression was slightly reduced; soil moisture was negatively associated with incidence of ring shake. The inclusion of magnesium in place of calcium as an independent variable resulted in lower r^2 values and significances of regressions, despite the fact that a better single regression was obtained for magnesium than for calcium. Inclusion of pH with rot, ring width and moisture in the multiple regression gave similar results as inclusion of calcium (see note about pH in section 3.2.3.3).

3.2.3.7. FACTORS RELATED TO THE SEVERITY OF SHAKE IN OAKS FROM DIFFERENT SITES.

TREE CHARACTERISTICS, SOIL FACTORS AND SITE ALTITUDE. When severity of shake in shaken oaks at each site (mean index) was regressed on tree characteristics and site factors, the most significant single regressions obtained were for organic matter and manganese contents of soil, and altitude of site. However, all these associations were weak. The regression equations are given in Table 3.6, together with the values of

r^2 and the significance of each regression. Figures 3.16 - 3.18 are plots of the data.

There was a negative association between the severity of shake and a) organic matter (Fig. 3.16) and b) manganese in soil (Fig. 3.17). A positive association between the severity of shake and altitude of site was found (Fig. 3.18). There appeared to be no association (linear or otherwise) between the severity of shake and the remainder of the factors measured (Section 3.2.2.7 lists all variables measured in site surveys).

SOIL TEXTURE. Symbols representing classes of mean shake severity at the different sites are plotted on a soil texture diagram (Figure 3.19). There was no consistent association of shake severity and soil texture as was found for incidence of shake (compare with Fig. 3.12, Section 3.2.3.3). It should be noted that on sites with low shake incidence, those individual trees which **were** affected often had severe shake.

3.2.3.8. MULTIPLE REGRESSIONS OF FACTORS ASSOCIATED WITH SEVERITY OF SHAKE.

Severity of shake in individual oaks was not clearly explained by any single factors. When multiple regressions were calculated, the best explanation of severity was: greater site altitude and amount of sand in the soil, together with low soil moisture (Table 3.7). The full analysis of variance for the equation is given in Appendix 3.5.

The associations of sandy soil and of low organic matter content with severity of shake would seem to be due to their effect on moisture retention of the soil rather than to provision of nutrients; soil moisture was weakly related to shake severity (Appendix 3.4), but levels of major nutrients which had been associated with shake incidence did not appear to be so.

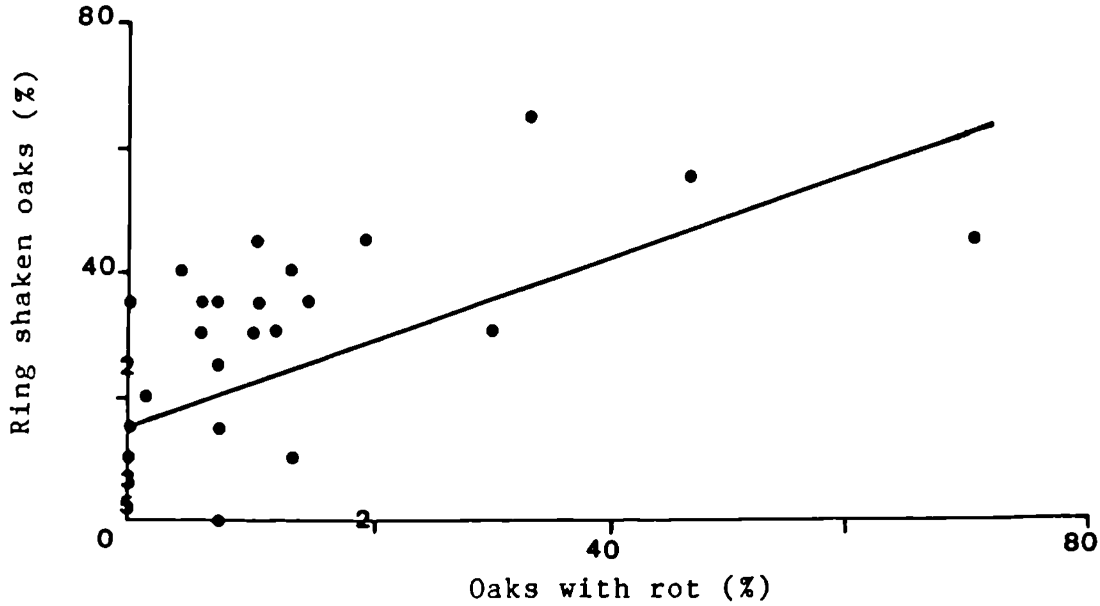


Figure 3.13. Relationship between the percentage of oaks containing ring shake and the percentage of oaks with rot in the butt; data from survey sites.

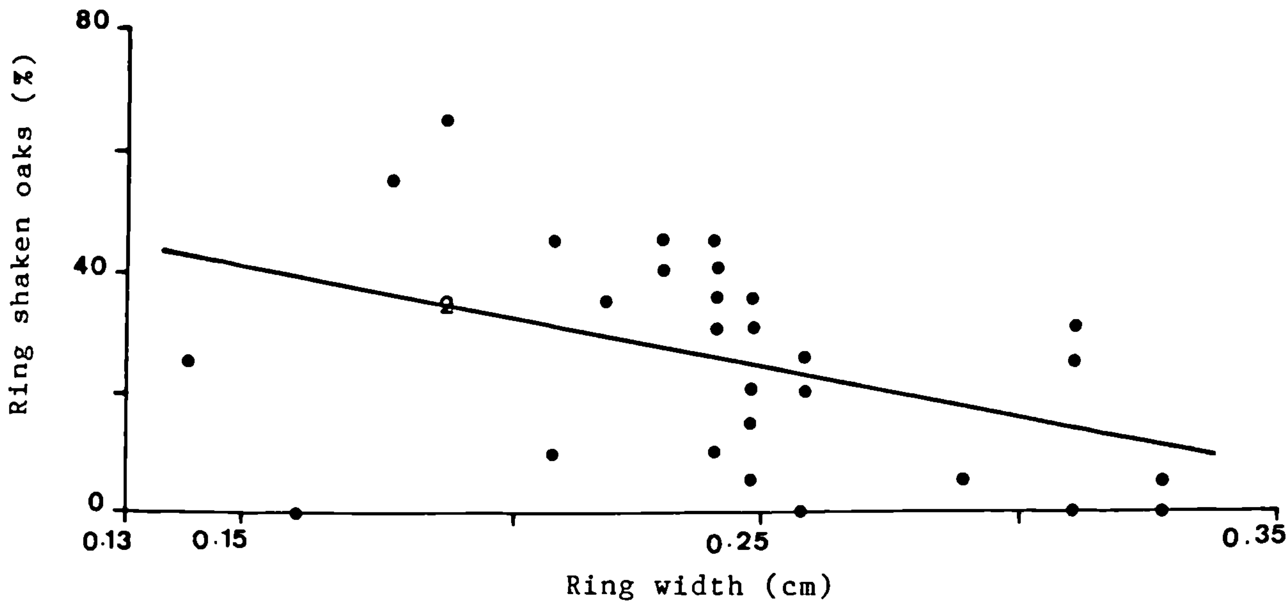


Figure 3.14. Relationship between the percentage of oaks containing ring shake and the mean growth rate of oaks on each survey site.

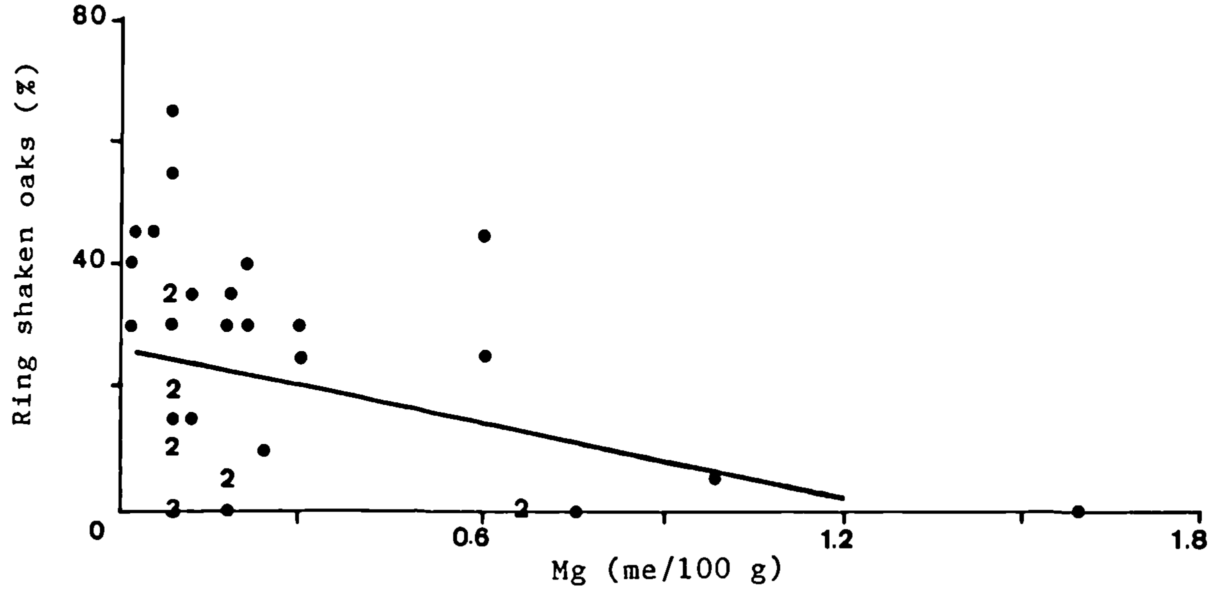


Figure 3.15. Relationship between the percentage of oaks containing ring shake and the availability of magnesium in soils of survey sites.

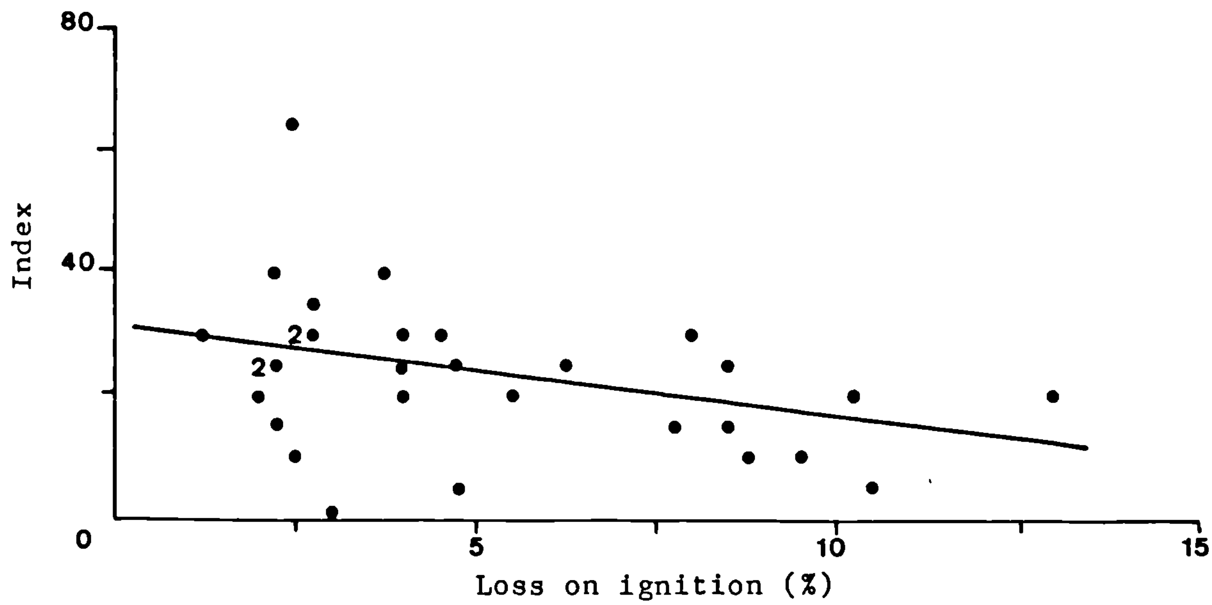


Figure 3.16. Relationship between shake severity (mean index of shaken trees) and amount of organic matter in soils at survey sites.

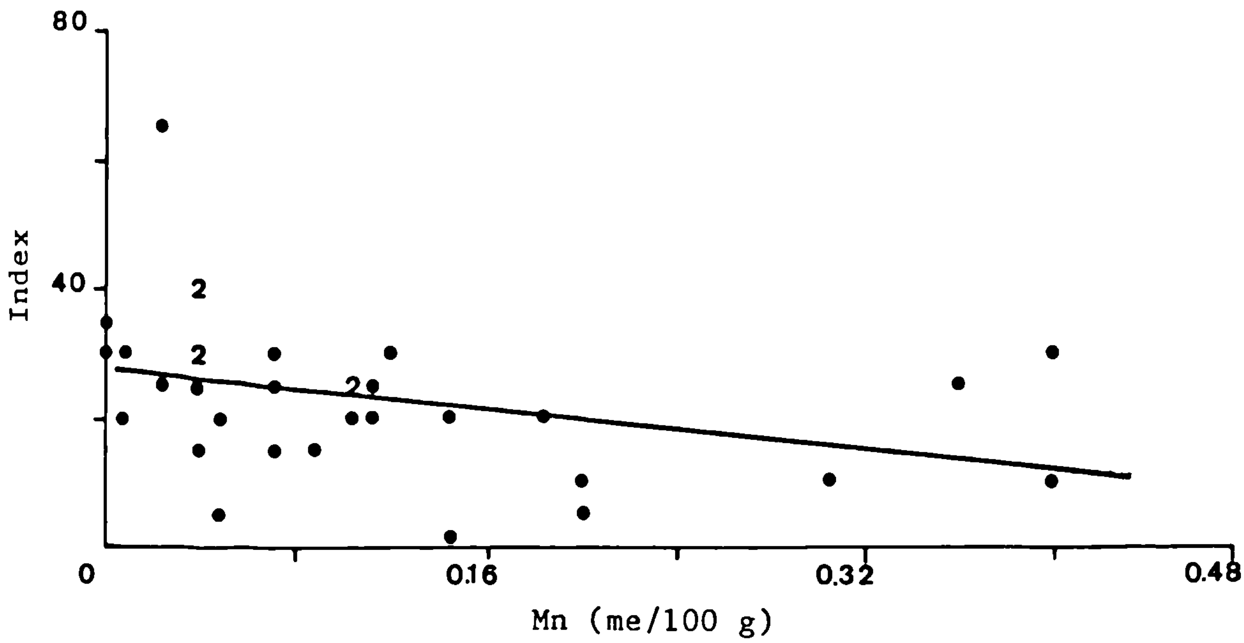


Figure 3.17. Relationship between shake severity (mean index of shaken trees) and availability of manganese in soil at survey sites.

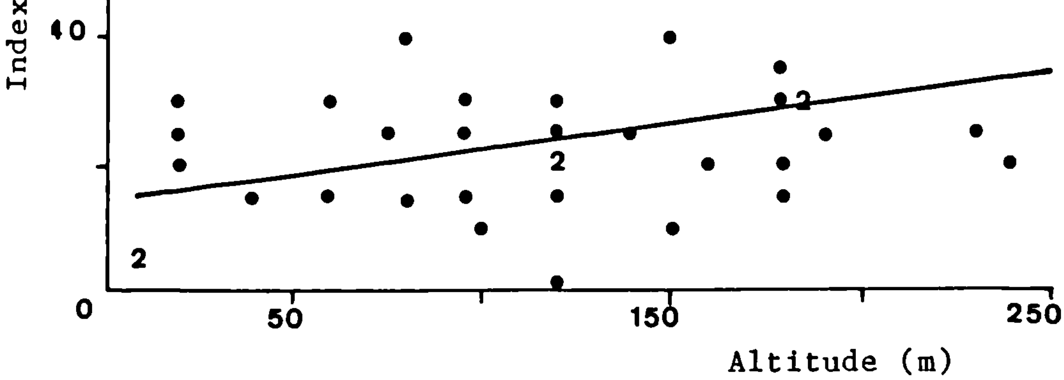


Figure 3.18. Relationship between shake severity (mean index of shaken trees) and altitude of site; data from survey sites.

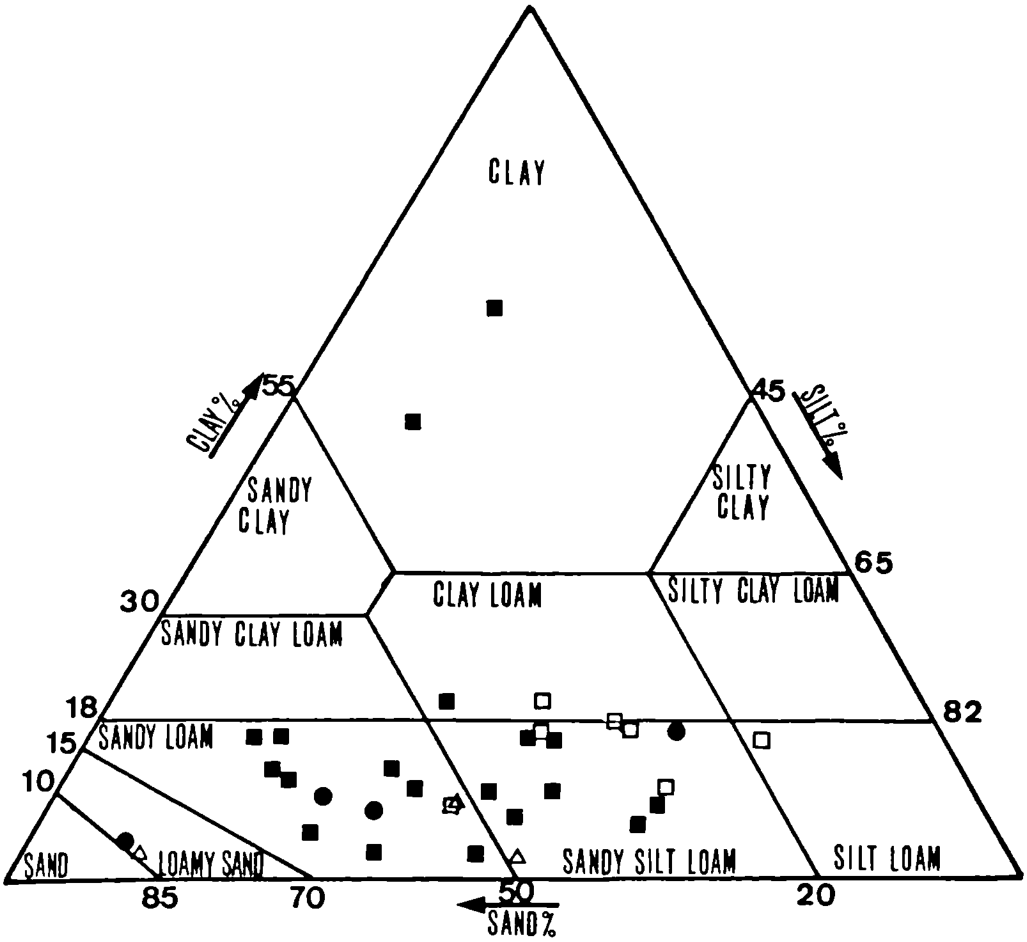


Figure 3.19. Severity of shake in shaken oaks on soils of different textures (Avery soil texture classes).

Mean severity of shake in shaken oaks:
△ slight; □ moderate; ■ bad; ● severe.

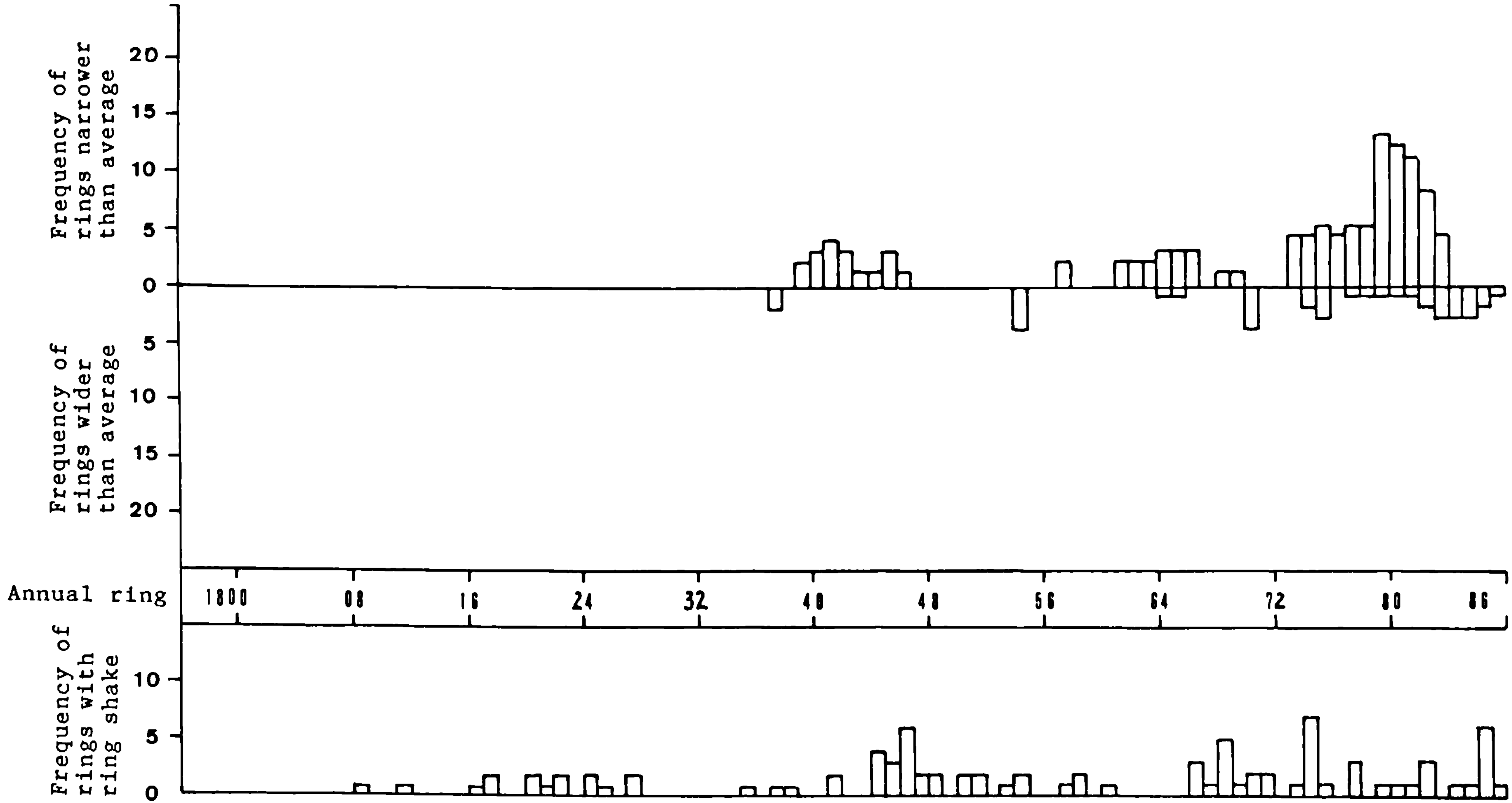


Figure 3.20.a. Relative frequencies of abnormally wide or narrow annual rings, and rings with ring-shake.
Continued ...

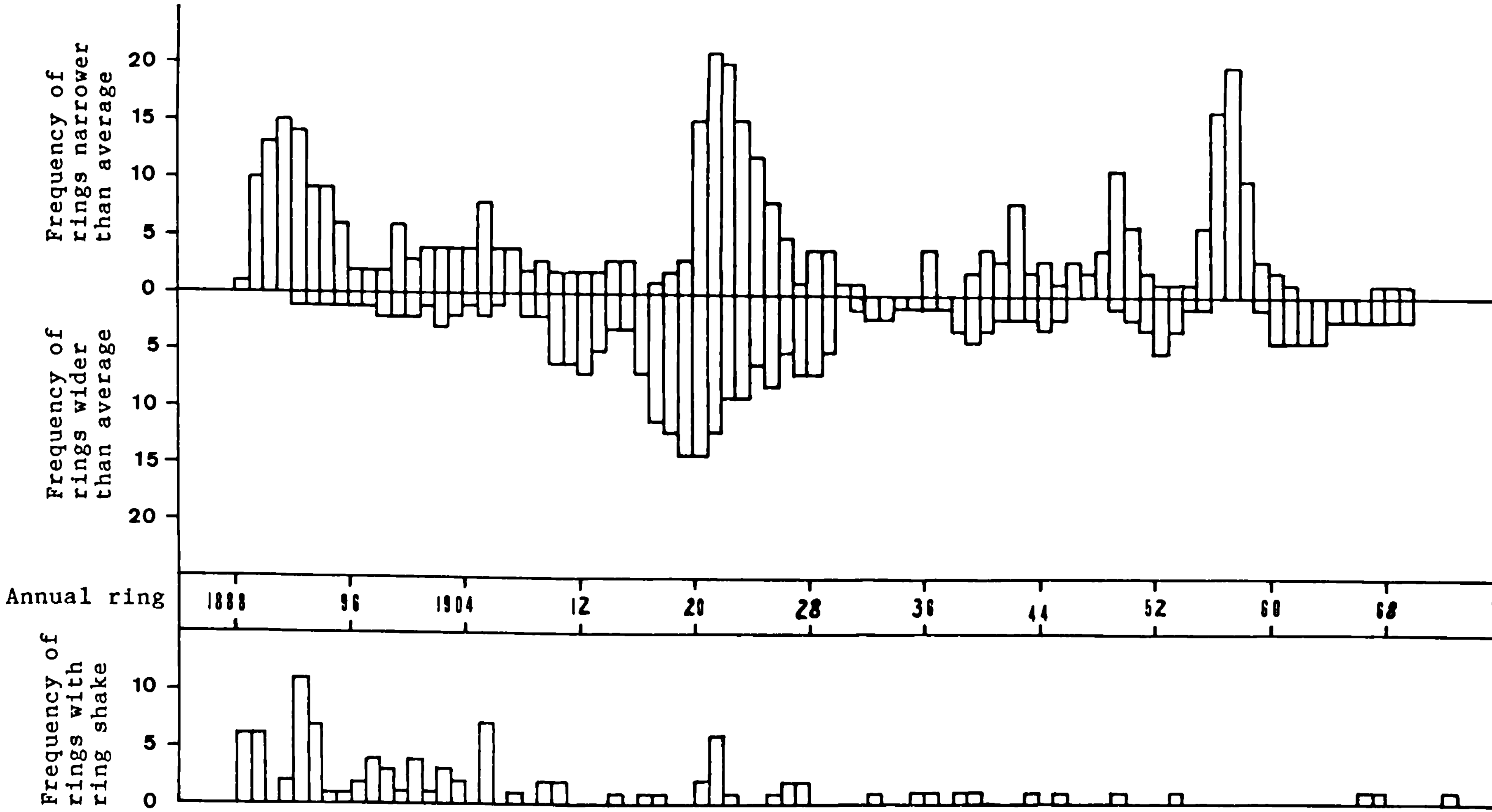


Figure 3.20.b. Relative frequencies of abnormally wide or narrow annual rings and rings with ring-shakes.

3.2.3.9. COMPARISONS OF SOILS UNDER PAIRS OF SHAKEN AND SOUND OAKS.

Means of soil factors under individual sound trees were compared with means of soil factors beneath individual shaken trees, and difference between the means was tested. The results of the t-tests are summarised in Appendix 3.9.

There was no statistically significant difference between the means of any soil factors from under individual shaken and sound oaks. In some cases this was because the lowest value for a factor on one site, exceeded the highest value on another. There was virtually no difference in pH or exchangeable cation contents of the soils under the sound and shaken individuals. The largest differences found were the tendency for lower stone content, higher moisture, clay and organic matter content of the soil under the sound oaks. Higher moisture retention would be expected in soils with less stone and more clay and organic matter; therefore it seemed that moisture deficit, rather than nutrient deficiency, made the difference between presence or absence of shake in pairs of trees within sites. Also, aluminium levels in the soil tended to be higher under shaken individual oaks.

3.2.3.10. ASSOCIATIONS BETWEEN YEARS OF RING SHAKE AND EXTREME ANNUAL RING WIDTHS.

Many of the ring shakes seen during site surveys had developed in zones where an abrupt change in width of annual rings occurred. Ring counts made in a few trees per site were collated and are illustrated in Figure 3.20. It should be noted that as most ring shakes were at a latewood/earlywood boundary and were counted as belonging to the adjacent earlywood, they will appear in the diagram as associated with the later year although their cause may be linked to wood development in the earlier year.

Years with a high frequency of ring shake often appeared to be associated with a change in ring width, such as a reduction in growth rate, or a return to normal following a series of unusually wide rings (e.g. shakes in 1886, Figure 3.20a), or during a series of unusually narrow rings (e.g. 1889 - 1899, Figure 3.20b). Some shake years appeared to be associated with a single year of poor growth (e.g. 1905 in Figure 3.20b).

3.2.3.11. FURTHER OBSERVATIONS MADE DURING SITE SURVEYS.

RELIABILITY OF EXTERNAL INDICATORS OF SHAKE. The author, timber merchants and foresters working at sites 32 and 43 before felling, attempted to predict from external features of the trees, the amount of shake expected in the individual oaks on these sites. After felling, the accuracy of the predictions was found to be a maximum of 33% correct. This supported the questionnaire findings concerning the unreliability of external indicators of shake in individual oaks.

GROUPING OF SHAKEN TREES. On several sites, the shaken trees tended to occur in groups rather than scattered throughout the crop; the groups were not isolated from sound trees, and there were no apparent reasons for this pattern (site numbers 3, 11, 12, 14, 20, 22, 35, 37 and 38).

PINK HEARTWOOD. Many oaks on sites 11, 29 and 35 had heartwood of a markedly pink-brown colour, compared to the light brown (sites 29 and 35) or pale straw colour (site 11) of the remaining trees. Within these sites, the proportion of the pink heartwood oaks which were shaken was high; the proportion of the pale heartwood oaks which were shaken was low. However, when all sites were compared, there was no association between shake incidence and the proportion of the crop which had pink heartwood; this was because shake could be prevalent on sites where there was no pink coloured timber.

WOUNDED TREES AND SHAKE. Ring shakes were often observed to be associated with wounds or with the inrolled ring structure associated with wood adjacent to healed wounds. On sites where shake incidence was high, wounds nearly always had associated ring shakes; and on shake-free sites, wounds were always well-healed and compartmentalised and showed no signs of ring shake development along the barrier zone.

3.2.4. DISCUSSION OF SURVEY RESULTS.

3.2.4.1. ENVIRONMENTAL CONDITIONS ASSOCIATED WITH INCIDENCE OF SHAKE IN OAK.

ROOTING CONDITIONS.

SOIL TEXTURE: The surveys confirmed that low incidences of shake are found on clay soils (all soils with more than 20% clay had a low incidence of shake). Although the traditional view that sandy soils are associated with high incidence of shake was supported by the summary of data from war-fellings (Brown, 1945), the site surveys described here found no association of shake incidence with percentage of sand in the soil. This was because not all sandy soils carried shaken oak crops; however, all crops with high incidence of shake did occur on sandy soils. The survey results thus qualified the traditional view, suggesting that other aspects of site condition can modify the potential of sandy soils to increase susceptibility of oak to shake.

SOIL MOISTURE: The idea that conditions leading to water stress are also associated with high shake incidence was given some support by the present evidence that the more freely draining site types and those with shallow soils were more likely to carry shaken oak crops, and that shake severity tended to be worse on sites with poor moisture retention.

Sandy soils are free-draining unless an impermeable layer exits beneath (clay or iron pan), but since many dry sites carried sound crops (and in some French forests the sites are drained to keep growth rate slow and even for veneer timber) it seemed that constancy of water table was more important than actual level, as long as the soil was not permanently droughted or waterlogged. Adamczyk and Fajto (1987) showed that Q. robur in a Polish forest was sensitive to large variations in oxygen and water status of sandy soils. Despite the high capacity of this species to modify root distribution to suit a site type, the fluctuations in these conditions within a site caused root dieback; stabilisation of the water table was recommended to combat the deteriorating health of the stands.

PLANT NUTRIENTS: Another characteristic of sandy soils is that they can be poor in plant nutrients because they leach easily and many are derived from parent rocks which are poor in the essential elements for plant growth. The survey results suggested that the anomalous crops showing low shake incidence on sandy soils could be explained by variations in levels of nutrients and toxic elements (for example, the Drybrook sandstone geology of parts of the Forest of Dean produces very poor soils for oak growing, yet the Old Red Sandstone of Herefordshire forms quite fertile soils which support good quality oaks in the main). It seemed that the unfavourable influence of a sandy soil texture could be less if calcium:aluminium ratios were high or else aluminium levels were very low. The few shaky crops found on calcareous sands could be explained by other causes of unfavourable rooting conditions, such as iron-pan formation and water-logging.

The association of high calcium content of the soil and low incidence of shake was one of the most important results of the site surveys; a negative association of magnesium and shake incidence was also indicated, although this may have been due in part to the association of magnesium and calcium levels in soils. The calcium results supported the findings of less wide-ranging studies by Lachaussée (1953) and Galoux (1978). Lachaussée studied three sites in the Saone valley in France (altitude and silvicultural regimes were equal for all three) and found that the site with a high incidence of shake had a leached soil, poor in calcium and rich in iron; the site with a little shake and no staining of the shaken timber had a slightly leached soil, rich in calcium but poor in iron content; and the shake-free site had a good brown earth, rich in calcium and with moderately high levels of iron. Galoux studied logs of indigenous sessile and pedunculate oak from Brabant forests on Loess drift over light calcareous schists; the soils were silts and pebbly silts, and presumably drought-prone; on the less calcareous versions of these soils, 52% of the oaks were shaken, but on more calcareous versions, only 31% of oaks were affected.

Questionnaire and interview results suggested that incidence of shake in oak was high on stony soils and gravels. The survey results did not support this fully; however, a) stone-free sites were nearly always shake-free, b) all oak woods seen on gravels had a high shake incidence, and c) very high stone-content of soil under individual oaks in a site was often associated with shake in those trees. As with sands, very stony soils are likely to be free-draining, thus being prone to leaching and drought; moreover, it is more difficult for roots to take up available nutrients from stony soils. However, if the stone is of a friable sedimentary type which contains and releases minerals of use to the oaks, the growing conditions may be less difficult for the tree. Such variability may explain the lack of clear association between shake and stoniness of soil.

Thus, various aspects of the root environment were associated with the incidence of shake. Overall, the nutrient availability to the oaks seemed to be more strongly associated than the moisture availability. Miller (1984) stated that most broadleaved species are 'site demanding': this does not mean necessarily that they are nutrient demanding, rather that their nutritional efficiency is affected by "their relative inability to obtain nutrients from intractable soil sources". If incidence of shake is somehow related to root health and tree vigour, this may in part explain the variability in association of shake with soil type. The role of mycorrhizal associations in this context may also be an area worth investigation.

The geological systems most frequently cited as likely to carry shaken oaks were Lower Greensand and the Granite of the West Country. The surveys assessed sites on the former of these and confirmed its associations with high shake incidence.

One of the most notorious regions in Britain for shaken oak is the Forest of Dean, the cause being attributed frequently to drainage and disturbance from mining activities. However, the areas of mining activity do not always correspond to the areas of shaken oak and it is more likely that the shallowness of the soils which Day and Peace (1947) cited as the cause of low vigour, poor growth, and susceptibility to pathogens in the Dean oak, is a contributory factor. Day and Peace did not consider soil fertility to be important in relation to the lack of vigour and poor disease-resistance which they found, and in the two stands of oak from the Forest of Dean studied in the present shake surveys there was no difference in the calcium contents of the soils; however, the site with the high incidence of shake had a shallow, sandy, stony soil, also lacking magnesium, whereas the site with low incidence of shake had a soil type (less frequently represented in the Dean) which was deep, moist, of high clay content and with a higher magnesium content.

TOPOGRAPHY AND EXPOSURE.

Surveys confirmed the contention of several questionnaire respondents that steeply sloping sites were more likely to have a high incidence of shake. Wind exposure was not assessed in surveys, but would generally be expected to be greater at higher altitudes and on aspects exposed to prevailing winds. The universal belief that wind sway is an important factor in shake development, together with the (slight) tendencies found in surveys for lower incidence of shake in aspects sheltered from prevailing winds and at lower altitudes, suggest that this factor should not be discounted altogether, although its importance cannot be assessed from these results.

3.2.4.2. TREE GROWTH PATTERNS RELATED TO SHAKE IN OAK.

TREE SIZE AND GROWTH RATE.

Most oak crops studied in the site surveys consisted of mature trees of 40 cm diameter and over. Individual trees below this size were rarely shaken, a fact which supported the majority of reports collated from other people. The singled coppice of site 41 was an exception in that shake was frequent in these oaks, even in the individuals of diameter less than 35 cm.

Survey results suggested a higher incidence of shake in sites where the overall growth rate of the oaks was slow (although this may have hidden relevant growth patterns, e.g. fast early growth followed by later decline). The primary factor limiting ring width is water supply to the tree (Section 2.2.2.2), yet survey results discussed in Section 3.2.4.2. above suggest that where slow growth is due to constantly dry but fertile soils, low shake incidence might be expected. The observed association of low growth-rate with high shake-incidence might be expected where slow growth is due to poor rooting conditions and tree nutrition, because these conditions are shown to be associated with shake. Perhaps the less vigorous, less healthy tree is less able to combat invasion of pathogens and heal wounds which can lead to shake (Section 3.2.4.3).

GROWTH PATTERNS ASSOCIATED WITH SILVICULTURE AND ENVIRONMENTAL CHANGE.

Associations between shaken rings and growth patterns which were observed during surveys supported previous reports that ring shake frequently occurs in association with an abrupt change in growth rate. Sudden increase of growth was the most often reported pattern, but abrupt decrease was observed to be associated with shake more often during the surveys. Reported information associated sudden acceleration of growth with silvicultural operations: the release of suppressed trees, removal of competing coppice or understorey, or heavy crown-thinning of thriving trees. The lack of detailed site histories of survey sites prevented confirmation of such causes. Sudden reduction in growth rate was probably associated with traumatic events, since stand aging or crown interaction effects would develop more gradually. One, or successive, years of drought or defoliation, or a heavy mast year, can all cause marked reduction in ring width of oaks (Section 2.2.2).

Questionnaire and interview replies did not make any association between natural events and changes in ring width leading to ring shake. However, evidence of such associations was found during the site surveys. Ring shakes in narrow growth rings were occasionally associated with known drought years. For example the drought of the early 1920s had caused reduced increments in oaks on drier sites, and may have been associated with the observed higher incidence of ring shakes in these years; on wetter sites the water supply cannot have become limiting and the high temperatures appeared to have enhanced growth rates. Robinson (1927) reported that the early 1920s were years of severe defoliation of oaks by Tortrix caterpillars (last severe attack in 1923), but separation of this effect from drought effect in oaks from the site-surveys was not possible. At site 29 it was found that in shaken trees the very narrow 1888 and 1889 rings almost always contained a ring shake. The poor growth of these and following years did not seem to be due to drought because remnants of the larch nurse crop in the same stand (growing vigorously at the same rooting depth) showed no check in growth for the same period. The cause of growth reduction in the oaks may therefore have been due to defoliation or to a heavy mast year. The former seems the more likely as Elwes and Henry (1906) reported 1888 to have been a year of almost total defoliation of oaks in Britain by caterpillars.

3.2.4.3. WOUNDS AND PATHOGENS ASSOCIATED WITH SHAKE IN OAK.

DAMAGE TO THE BOLE.

This was rarely associated with shake in replies to the questionnaire and interviews, but observations made during surveys fitted the descriptions of wound-related shakes reported in the thorough studies made by Butin and Shigo (1981) (e.g. Plate 3.6). The association of high incidence of rot on sites with a high incidence of ring shake, also suggested a wound association with shake.

In contrast it was observed that on soils which typically produced sound oak, similar wounds compartmentalised well and did not lead to shake development.

HONEY FUNGUS.

An apparent association between presence of honey fungus in a site and abundance of frost-cracks in oak was seen during site surveys. No reports of a direct association have been found, although two questionnaire respondents noted a link between "fungal attack" and shake. However, Shigo (1964) described a 'collar-crack' in birch (which could extend from several inches to several feet up the bole), induced by the influence of honey fungus on growth substances and subsequent abnormal growth in the root-collar region of the tree. Given that defence reactions to wounding and pathogen attack can lead to changes in wood structure associated with ring shake (Section 2.3.4.2) and that frost-crack appears to be associated with shake, this might be an area worth further study. A few replies to the questionnaire had cited basal swelling of oaks as an external sign that the tree might be shaken. Plate 3.18 (end of this section 3.2.4) shows swelling and cracking of the lower bole of an oak from survey site 38 which was characteristic of many oaks on the site. Shake incidence was high on this site, and honey fungus apparent at the base of many trees. Similar symptoms were seen on a few other sites, although multiple cracking which looked superficially similar to the collar-crack of birch reported by Shigo was more usual than swelling (Plate 3.19). In most of these cases, the soil had a low clay content in the upper horizons, but was prone to water-logging. Such poor rooting conditions would make oaks more susceptible to attack by honey fungus, and the more physiologically stressed the tree and its root system, the more probable the invasion success of the pathogen (Section 2.1.1.5). The acid sands on which oaks were more prone to shake have also been reported to show a higher incidence of honey fungus attack (Redfern, 1978).

COLOURED HEARTWOOD AND STAINING OF SHAKES.

The presence of staining, wetness, rancid smells and pink coloured heartwood in oaks on many of the sites which had a high incidence and severity of shake, seemed to parallel the observations made in American studies of bacterially-caused wetwood in oak (Section 2.3.3.4). Also, the associations of site and shake incidence found in the present surveys paralleled the associations of site and wetwood incidence reported in America, where oaks and other hardwoods were found to be more susceptible to bacterial attack when grown in lowland areas prone to water-logging or upland areas with shallow or rocky soils (Ward, 1982). Ward (1983) stated that loss in vigour due to drainage of wet sites can lead to bacterial infections in trees which are accustomed to a higher water table; and Ward et al. (1969) stated that infected trees were commonly mature or over-mature.

In Britain, Rishbeth has studied bacterial wetwood in elm (Ulnus species) and in horse chestnut (Aesculus hippocastanum), trees in which it is common (Rishbeth, 1980) and which are also prone to shake (though less often affected than oak and sweet chestnut). Rishbeth described the condition as widespread in Britain, and known in Western Europe for at least 150 years. Rishbeth's summary of the pattern of wetwood formation within a tree suggests confinement by wall-4 of the 'barrier-zone' (formed in compartmentalisation of wounds: Section 2.2.2.3). Its boundary is similar to the course of a severe ring shake: "characteristically, bacterial wetwood forms a continuous column which tapers upwards and is circular or wavy in cross-section ... [it] may extend into quite small branches." Severe ring shake in yew and in oak (Appendix 3.2.3.) was reported to extend into branches in this way.

Rishbeth (1980) reported that colourless or brown/black watery fluxes often characterise infected trees (being released on cracking of boles or breaking of branches). The fluxes are foul-smelling, and would seem to be the same as those described by timber-fellers in association with shake. Plate 3.17 (end of this Section 3.2.4) shows such a flux in an oak at site 35; it was typical of a group of shaken trees at one end of the site. When dried up, the fluxes often leave a chalky deposit on the bark below the point of emergence (Rishbeth, 1980); this is a symptom also seen on the surface of many shakes (Plate 3.7, Section 3.1.2).

The composition of this chalky deposit (or milky stain in wood which was very wet) was not analysed, but Janin and Clément (1972) reported other authors' observations of calcium carbonate or calcium oxalate on shake surfaces. McGinnes et al. (1971) reported large concentrations of calcium at the shake face in oak and walnut, along with unusually high levels of magnesium and potassium (typical of inorganic build-up in regions of damaged tissue). Wetwood is usually alkaline in hardwoods (Ward and Pong, 1980) and this has been attributed by some authors to bacterial production of ammonia and precipitation of calcium carbonate (reported in Ward and Zeikus, 1980). However, Janin and Clément (1972) demonstrated that in poplar wood, calcium carbonate was not necessarily associated with trauma but was naturally present in all except one of the species and their hybrids examined; its presence was not affected by soil type. Perhaps genetic variations in such internal conditions of trees may in part influence susceptibility of genotypes or individuals to colonisation by bacteria. It is interesting that central European literature reviewed by Ward and Pong (1980) shows poplar species to be particularly prone to wetwood and frost-crack.

Spread of any pathogens after attack will also be limited by the strength of the tree's defence response, and possibly by competition between pathogens. There is evidence that anaerobic bacteria, having invaded, maintain conditions suitable for colonisation by maintenance of high moisture content in the wood. This accords with the high moisture content of shaken timber reported by some interviewees (Appendix 3.2.4.). Wood colonised by anaerobic bacteria is less likely to be colonised by fungi because the anaerobic conditions are successfully maintained (Ward et al., 1969).

Rishbeth reported that trees can contain much bacterial wetwood without showing external symptoms, but that the fluid in wetwood is toxic and if it enters the sapwood and the transpiration stream it may cause dieback in the crown. Similarly, if bacterial wetwood extends to the cambium, this is killed (Rishbeth, 1980). This perhaps explains the presence of channels in the bark said to be associated with some shaken trees (Plate 3.13 in Section 3.1.2, and Section 3.2.4.4 below). Blocks of wetwood in contact with the cambium would probably run vertically for some distance, as the untylosed vessels and the unaspirated pits in walls of living cells in the adjacent sapwood could allow rapid vertical spread of the causative bacteria in the transpiration stream. If wetwood is the cause of such marks, then presumably the tree is able to compartmentalise the infected wood and restore the circle of cambium by gradual renewal from the edges of the affected strip, but a longitudinal depression is left in in the wood.

It is interesting that symptoms of die-back in oak in France described by Macaire (1984), match those of bacterial infection described by Rishbeth (1980): branches dying and breaking off, longitudinal cracks in the bark, a dark discharge from these cracks, and brown marks on the bark. Macaire noted that this was sometimes associated with honey-fungus under the bark; honey-fungus has been implicated as a cause of the root lesions which can allow infection by the bacteria which cause wetwood.

3.2.4.4. EXTERNAL SIGNS OF SHAKE.

Splits, seams and shallow grooves in the bark of oaks, and swellings under the bark were described by questionnaire respondents as external indicators of oaks with shake. In the site surveys, such marks were found often to be associated with shake in individual trees on shaky sites, but absence of such indicators was no guarantee of a sound oak. Moreover, on sites with a low incidence of shake, individuals might carry such marks externally, yet be free of shake.

Large disruptions of the bark can be indicative of underlying major or slowly healed wounds, and ribs or seams in the bark can be explained as derived from successive inrolls of new wood over frost-cracks which have re-opened over a number of years. Lightning strike was the explanation sometimes given by interviewees, of grooves or channels in the bark where the wood production beneath the bark was apparently retarded (such as Plate 3.13, Section 3.1.2); no other type of wound seemed likely to produce such a long, narrow lesion. The incidence of such marks however, is more frequent than this explanation alone can allow. The cause may be localised killing of the cambium by toxins resulting from bacterial infection as described above (Section 3.2.4.3.).

Another external sign of shake cited in some replies to the questionnaire was the presence of 'feet' or low buttressing of main roots at the base of the bole. During the site surveys, no association of such form with the presence of shake in individual trees was found, nor was there any consistent link with the incidence of shake on a site. For example, site 37 (on wet ground) had numerous trees with particularly extreme flange buttresses, yet a very low incidence of shake. Such form was generally seen in oaks growing on certain particularly steep, shallow or waterlogged soils, so may be circumstantially linked to high shake incidence in some sites.

3.2.4.5. SHAKE STUDIED SEPARATELY IN SESSILE AND PEDUNCULATE OAK.

There was no evidence that either of the two British oak species were more prone to shake than the other. Reports of differences in the relative susceptibility of sessile and pedunculate oak to shake, were conflicting. When survey results from stands of sessile and pedunculate oak were studied separately, the trends of shake association with site conditions and growth rate were similar. These results must be interpreted with care, being based on very few sites, however Galoux (1978) also found no difference in susceptibility to shake between sessile and pedunculate oak indigenous to the Brabant forests of Belgium.

Plate 3.17. Watery flux from shaken oak on site 35.

Plate 3.18. Swelling and cracking of lower bole of oak on site 38.

Plate 3.19. Vertical cracking in an oak from site 35.

Shake incidence and external cracking were high on both sites; many trees of site 38 were heavily infected with Armillaria mellea (honey fungus); many trees of site 35 contained a white rot.

3.3. A MODEL OF SHAKE DEVELOPMENT, AND THE ROLE OF SITE FACTORS.

The evidence of the site surveys suggested that poor rooting conditions, leading to reduced root health and tree vigour, were associated with high incidence of shake in oak crops. However, not every oak on a shake-prone site would develop shake; microsite conditions under individual oaks may in part explain the presence of the anomalous trees, but study of microsites demonstrated that this cannot be the sole explanation.

In individual oaks, damage to the bole was often related to shake development, but shakes cannot be caused by wounds alone since anomalous sound trees on shake-prone sites did not always lack stem wounds; moreover, wounded trees on sound sites were rarely shaken.

Many other factors seemed to have a role in shake formation (defoliation in some cases, for example). A model of shake development is proposed below. Factors associated with shake may play combined or alternative roles in the model.

3.3.1. A MODEL OF SHAKE DEVELOPMENT.

It is proposed that shake development is a complex process which can be represented in two stages, although it may be continuous over a number of years:

Firstly, some predisposition to shake develops in the wood - this is a structurally weak zone which may be further weakened within the tree before shake develops.

Secondly, some force acting on, or in, the tree triggers the weak zones in the wood to part, and the shake develops within the wood.

If the predispositions develop, but the triggers are absent throughout the life of the tree, then shakes will not form. Likewise, if the triggers to shake are present, but no predisposing weak zones exist within the tree, then the tree will remain sound.

It is also proposed that the severity of shake within each tree reflects both the strength of the triggers acting on that tree, and the action of any factors which aggravate the weakness of the predisposition.

3.3.2. PREDISPOSITIONS TO SHAKE IN OAK.

There seem to be a number of ways in which predisposing weaknesses can develop within individual trees:

1/ Resulting directly from cambial damage by wounding, fire-scorch or freezing: the structurally weak tissue of the barrier zone is formed in response to wounding (Pearce, 1982; Shigo, 1984); the wood structure of the edges of consecutive rings in-rolling and merging over large wounds can also be a line of weakness, from which radial splits can develop.

2/ Following invasion of anaerobic and facultative anaerobic bacteria, via root lesions or wounds: these may weaken adhesion between cells by degradation of the middle lamella (McGinnes, et al., 1974; Schink et al., 1981). Where the infection is compartmentalised behind the barrier zone, the interface of the infected tissue and the barrier zone may become the site of a ring shake. If initial colonisation is at the edges of a wound inroll, it is possible that shake separations begun in these zones could be aggravated and continue to 'unzip' as bacteria degrade the middle lamellas at the advancing edges of the splits.

3/ At boundaries of change in ring width: these may be accompanied by weaker wood structure, and/or by bacterial infection and middle lamella degradation (changes consequent upon physiological stress or wounding associated with the growing conditions which altered growth rate).

Where ring width change is due to factors which reduce growth (defoliation, drought, mast years), it is possible that cell wall adhesion or strength is lowered in the plane of the ring compared to the surrounding wood, because materials needed for growth are in poor supply or diverted elsewhere at the time the wood is formed. In addition, the physiological stress such events impose on the tree may allow attack by root pathogens and infection by bacteria, in turn leading to shake formation as described in point 2/ above.

Where ring width change is due to accelerated growth, the supply of water and most nutrients must be adequate, and increased light or reduced competition encourages growth. Perhaps one element in short supply leads to weaker wood formation or reduced ability to combat pathogens, without limiting growth rate. For example, shortage of calcium could lead to a weaker middle lamella, of which calcium pectate is an important component (most shake separations have been observed to occur between cell walls, rather than across them (Section 2.3.3.3).

Predispositions to shake in oak could be reduced by:

1/ Reducing incidence of wounding or other cambial upset.

2/ Planting oaks on sites where conditions are suitable for healthy, vigorous growth, with minimised physiological stress; thus a) roots are less susceptible to attack by fungal pathogens (allowing entry of bacteria), b) wound healing is rapid and efficient, c) spread of pathogens is combatted more successfully through efficient compartmentalisation, and d) resources for normal growth are not largely diverted to compensate for extra demands made on the tree due to defoliation or mast production.

also, if future research indicates suitable genetic types, by:

3/ Selection of genotypes which compartmentalise rot successfully enough to prevent serious decay, but do not produce over-extensive barrier zones which may become sites of ring shakes (Section 2.2.2).

4/ Selection of genotypes which possess structural or chemical characteristics which discourage the spread of bacteria.

3.3.3. TRIGGERS OF SHAKE IN OAK.

Triggers of shake could be a number of external or internal forces acting on the tree:

1/ There is a strong probability that natural growth stresses in the stems of oaks could act as triggers to shake. The strain (combination of stress magnitude and wood strength) alone in oak is not large enough to split the wood, but the stresses are high compared to many other tree species (Section 2.3.7). If the strain is increased in parts of the tree by the presence of weak or weakened zones of wood, then this may lead to shake. There has been little study of growth stress in oak, and apparently none relating growth stress to shake in oak, but there is circumstantial evidence of the role of growth stress as a trigger. Shakes in oak rarely extend into the outer layers of wood (Section 3.1.1 and 3.1.2): it is in this outer zone that the strong tangential growth stresses in trees are compressive, so radial crack propagation would be unlikely. In the centre of the tree, where the radial splits of star shake are seen, the tangential growth stresses are tension forces, which could be expected to trigger weak zones to shake. Ring shakes are less likely to be triggered by radial growth stresses, even though these are tensions across the whole diameter, because these stresses are weak; it is more probable that separations of ring shakes result from re-direction of tangential stresses released through the parting of perpendicular weak zones (Section 2.3.7); ring shakes in oak are usually in the inner two thirds of the bole cross-section also, i.e. where these tension stresses are greatest.

2/ Wind exposure may have a slight role (by bending or torsion of stems in strong winds) but must act as an additional force to some other form of trigger, otherwise a much greater incidence of shake in oaks would be expected. Wind may be important on more exposed sites, but is unlikely to trigger separations in apparently vulnerable stems at the time of thinning, because ring shakes associated with thinning develop later.

3/ Although the two factors above may be triggers of shake (which develops as an internal defect), they seem unlikely to be involved in the formation of frost cracks (which pass through the bark of the tree, yet may not reach the inner wood). Frost cracks may develop under the influence of other mechanical stresses: perhaps from the freezing and expansion of the watery fluxes produced in wetwood, perhaps from variations in cold shrinkage around a structurally weak stem. If frost cracks are regarded simply as another form of shake, then the action of frost could be classed as another type of trigger, developing stresses which cause the cracks to run out to the bark. In parts of America and continental Europe, much lower winter temperatures occur than in Britain, and frost cracks are more frequently reported; Ward and Pong (1980) review some of these reports and regard frost cracks as another consequence of wetwood formation in a number of species. Cinotti (1987) studied the mechanics of stresses resultant from freezing of oak.

3.3.4. COMPLETING THE MODEL.

Most of the predispositions and triggers to shake are strongly influenced by site factors and silvicultural treatments, either directly (e.g. wind) or indirectly (e.g. modification of growth patterns and therefore ring structure and growth stresses). Anomalous sound trees in a shaken crop can be explained partly by microsite differences, but the British oak species are notably variable in all their characteristics (Section 2.1 and 2.2) and it is probable that genetic differences play an important part too.

As noted above, genetic differences affecting the susceptibility of a tree to shake could include strength of ability to compartmentalise decay, tolerance of poor site conditions without loss of vigour, suitability of internal conditions for colonisation by pathogens, etc. Some differences may be expressed in the wood structure: e.g. growth rate could affect growth stresses, e.g. cell sizes and proportions could be related to wood strength or to routes of pathogen attack. Chapter 4 examines the wood structure of shaken and sound oak samples collected at survey sites. Chapter 5 is a study of genetic differences in wood structure and properties of oaks from a seed origin trial.

3.4. CONCLUSION OF CHAPTER 3.

This chapter has demonstrated that sites with favourable rooting conditions for oak trees generally produce shake-free oak timber. Such sites are level or slightly sloping, with deep soils of a high clay content (over 20%), good nutrient supply (in particular, calcium availability of over 1.0 me/100 g) and fairly constant water table (though not permanently droughty or waterlogged), and will produce a moderate to good growth rate in the crop. Risk of shake will be further reduced in crops which are kept at an even growth rate. Cambial damage is a major factor leading to the development of shake, and although total protection against wounding of forest trees is not feasible, oaks should be protected as far as possible from severe cambial damage (forest operations, fire and animal attack).

The ideal growing conditions described above are not present in a large proportion of the land used currently for woodland in Britain. Sites which do not provide these growing conditions will not necessarily produce shaken oak, but the risk will be higher. Prescriptions for site choice in this less suitable group of soil types can not be so clearly defined because of the complexity of soils and their effect on tree growth. Parent rock type, texture and chemistry of soil will have a primary influence on rooting conditions; climate may modify this (for example by leaching in areas of high rainfall). Fertility and then moisture-retention of A-horizon soils in which the majority of the feeding roots lie are important. High levels of aluminium in the A-horizon may prove toxic if soils are low in calcium and pH; leaching of iron, leading to iron-pan formation, would also be a feature of sites to avoid; both these sets of conditions will inhibit development of healthy roots.

Even if the ideal site conditions for growing sound oaks are not all present, the more factors which ameliorate the root environment for oaks, and the fewer of the debilitating factors that are present, then the better the chances of growing sound oaks on that site.

CHAPTER 4

COMPARISONS OF WOOD STRUCTURE IN SOUND AND SHAKEN OAKS.

The aim of this work was to identify any wood structure characteristics associated with the susceptibility of oaks to shake. Wood structure patterns in the mature wood of sessile and pedunculate oaks were assessed.

Any associated wood structure patterns might either be linked directly to shake formation (for example, causing general structural weakness or growth stress in the tree), or else be secondary to the causes of shake development (being indicative of some other physical or physiological state of the tree which confers a susceptibility to shake). They might be associated always with development of shake (i.e. found in shaken trees but not in sound); or they might be associated with predisposing factors, thus not necessarily resulting in shake formation in every tree. Therefore comparisons were made:

i) between shaken oaks and sound oaks (taken from woodlands with high and low incidences of shake), and

ii) between oaks grown in shake-prone woodlands (i.e. with a high incidence of shake) and those grown in 'sound' woodlands (low incidence of shake), irrespective of the condition of individual trees.

The characteristics chosen for study were:

a) the growth rate (ring widths and proportions of earlywood and latewood in the annual rings)

b) the characteristics of the earlywood vessels

c) the size and proportions of wide rays.

Reasons for choosing these characteristics were as follows:

a) Growth rate: some continental foresters believe that susceptibility to shake in oak is linked to growth rate (subsequently this was suggested by results of site surveys also, in which mature oak crops with a low mean growth rate tended to have a higher incidence of shake).

b) Earlywood vessels: earlywood vessel size (cross-sectional area) and number are important in the conductive capacity of trees (Sutcliffe, 1979; Gasson, 1984); this could affect drought tolerance. High transpiration rates may cause increased physiological stress in root systems of trees growing on occasionally droughty soils (e.g. free-draining soils in areas of high annual rainfall) where they are adapted to a normally high water availability. The size of earlywood vessels depends on radial and tangential diameters: radial diameter can be related to tree vigour and site quality, while tangential diameter is probably under the control of factors other than environmental (Zasada and Zahner, 1970).

c) Wide rays: wide ray size and proportions were of interest because of their influence on wood density and anisotropy of shrinkage (Section 2.2.1.1) and because they are dominant structures during wood formation and cell expansion (Section 2.1.2.1); it was thought that they might be linked to intensity of growth stresses, thus perhaps predisposing or triggering shake formation. Also, since wide ray proportions in oak have been reported by several authors to be associated with site quality and/or growth rate (Section 2.2.2.2), any variations found in ray proportion might indicate parallel associations with factors predisposing oaks to shake.

Data were collected from blocks of rings, therefore any traumatic and transitory patterns would not have been recorded individually. Study of the structure or ultra-structure of shake zones was not attempted; this has been carried out for oaks by McGinnes et al. (1974) and for eucalypts by Wilkes (1986). A limited study of the association of ring shakes with periods of sudden change in growth rate was made during the field surveys (Section 3.3.3.3).

4.1. MATERIAL.

Most of the wood samples used in this investigation were taken from sites visited during the earlier surveys. As a result, the sample numbers from trees grown on sites with low incidence of shake were limited. Samples from these 'sound' woodlands were therefore supplemented with wood from a Staffordshire timber yard (taken from two trees known to have grown in a sound woodland), and with discs of oaks from Bagley Wood, near Oxford, which had been cut for dendrochronological work and were generously handed on together with detailed site notes by Dr J Fletcher and Dr R Plummer.

Samples from twenty four oaks were studied: twelve sound, twelve shaken (with ring and/or star shake), see Table 4.1 below. The trees came from six woodlands, three with shaken crops and three relatively sound. Within each woodland, one or more pairs of trees were chosen, the pairs being adjacent shaken and sound oaks; pair twelve which was from the timber yard was an exception.

Many samples had to be taken from the stump level, but buttress wood was avoided. Samples from one to two metres above ground would be preferable for wood structure analysis at only one level in trees, and patterns more typical of the bole as a whole would be assessed (for example, there is evidence that mean EWV size of oak is lower in the first 0.5 m of the bole than in the rest (Gasson, 1984). However, samples from above stump-height were obtainable for only four out of the twelve pairs (Table 4.1).

One complete radius from pith to bark was available from twenty of the twenty four trees; the remaining four trees lacked the rings nearest the pith.

Site name or number	Wood-land type	Pair nos.	Sample height (cm above ground)	Species	Age approx (years)
Site 29	shake	2,5,9	15 - 20	Pedunculate	140
Site 30	shake	1	25 - 30	Sessile	140
"	"	7	55 - 60	"	"
Site 36	shake	11	5 - 10	Sessile	>110
Bagley Wood	sound	3,6,10	50 - 55	Sessile	72
Site 47	sound	4,8	5 - 10	Sessile	100
Timber mill	sound	12	?	?	>120

Table 4.1. Sources of samples used for study of shaken and sound oak.

Woodland types = shake-prone or sound.

4.2. METHODS

Wood structure patterns were studied firstly in blocks of rings which had been formed in the same range of calendar years. This was done in order to reduce the amount of variation in results due to the strong influence of seasonal rainfall and growing season length. The response of individual trees to transitory environmental conditions may also be involved in shake formation and reflected in the wood structure; this possibility was studied briefly in Chapter 3 (Section 3.2.3.: association of ring width extremes and ring shake zones).

Wood structure patterns were next studied in rings which had been formed at a similar cambial age to one another (mid-block rings formed when 50 - 65 rings from the pith). These comparisons were made in order to avoid any variations between samples due to intrinsic control of wood structure patterns.

Table 4.2 shows the blocks of rings chosen and their cambial age, in trees from each site. Blocks C to A were placed as evenly as possible within the mature wood. Years generally characterised by extremes of ring width were avoided, as the object was to try and assess average, 'normal' patterns for each tree, rather than traumatic zones.

Blocks A+B from all sites were used to compare wood formed in the same calendar years. Block C of trees from shake-prone woodlands provided 10 rings of a similar cambial age to block A in trees from sound woodlands. This difference in blocks was necessary because the sound woodlands happened to have younger crops. The fact that the sound crops were of younger trees was not believed to be associated with the difference in shake incidence between the woodland types, because all were above the age and bole diameter at which shake becomes apparent (Chapter 3), and site reputation as well as current condition of trees upheld the classifications.

Woodland	Annual rings in each block, and approximate cambial age at mid-blocks		
	Block A 1955-64	Block B 1935-44	Block C 1901-10
Site 29	115	95	60
Site 30	119	99	64
Site 36	Cambial ages not known but crop planted pre-1870		
Bagley Wood	50	30	-
Site 47	50	30	-
Timber mill	Cambial ages not known but crop planted c. 1880		

Table 4.2. Cambial ages at mid-blocks of annual rings used in wood structure comparisons between shaken and sound oaks.

4.2.1. SAMPLE PREPARATION.

Wood samples were sawn to give one radial strip approximately 1 cm wide per tree. Samples were stored in FPA, and sectioned transversely for light microscopy as described in section 5.2.2. At first, sections were mounted unstained in glycerine gel. Later samples were mounted with aqueous safranine added to the gel, as suggested in Jane (1970); the wood gradually takes up the safranine without need for lengthy staining processes. This gave better contrast in images projected onto a digitising table for measurement of early wood vessels.

4.2.2. WOOD STRUCTURE ANALYSIS.

Fourteen wood structure characteristics were assessed. These were: ring width, earlywood width, latewood width, percentage of the ring which was earlywood, number of rows of earlywood vessels, tangential frequency of earlywood vessels (number per centimetre in first vessel row of each ring), wide ray proportion in earlywood (percentage of section width as seen in transverse section), wide ray proportion in latewood, wide ray frequency (number per centimetre tangent to ring, as seen in T.S.), wide ray size in latewood (tangential width as seen in T.S.), tangential diameter of earlywood vessels (EWVs), radial diameter of EWVs, cross-sectional area of individual EWVs, and shape of EWVs. Methods of measurement providing these data are given below.

MEASUREMENT OF RING WIDTH, EARLYWOOD:LATEWOOD PROPORTIONS, AND EARLYWOOD VESSEL ROW NUMBERS. These were measured from sectioned samples, using a binocular microscope and transmitted light, at a magnification of x50. The annual rings lay horizontally across the field of view and an eyepiece graticule with a vertically marked scale was used for measurement. Measurements were not made close to section edges, where sawing may have distorted the wood.

Radial widths of earlywood (EW) and latewood (LW) were measured in each ring of each block, at three equidistant points across the section. EW and LW widths were recorded as a mean of the three measurements per ring. Ring width was recorded as the sum of the EW and LW means for each ring.

IDENTIFICATION OF EARLYWOOD/LATEWOOD BOUNDARIES. The earlywood of each ring began at a very clear boundary with the latewood of the previous ring, where the vessels changed abruptly from groups of very small cells, to rows of large solitary cells. Between the vessels, the boundary was marked by an abrupt change from radially compressed fibres with very thick walls, to fibres and tracheids of irregular and larger cross-section, and very thin walls.

The earlywood of a ring ended where an abrupt decrease in vessel size occurred, and the files or groups of small latewood vessels and tracheids which form the latewood 'flames' began. In many rings, there was a tangential band of vessel-free wood after the earlywood vessels and before the latewood flames formed (Plate 4.1). In these cases, an imaginary line drawn across the tops of the majority of the EWVs was used as the boundary; this line was often delineated by a single or double row of axial parenchyma cells, which preceded the post-earlywood tangential band of fibres (often containing large numbers of gelatinous fibres) which was characteristic of all the oaks examined.

MEASUREMENT OF WIDE RAY SIZE AND PROPORTIONS. These were measured using a light microscope, with transmitted light, at a magnification of x 40, and with a horizontal scale eyepiece graticule. Crossed polarising filters were used to enhance the contrast of the rays with the surrounding tissue.

Wide ray proportion was calculated as a percentage of the ring tangent as seen in transverse section. It was found to be very consistent across the ten-ring blocks and so was measured in the first and last ring of each block only. In the earlywood the tangent was positioned just inside the ring-boundary at the mid point of the ray swelling. In the latewood the tangent was placed just after the tangential all-fibre band which seemed to occur at a consistent distance into the ring and was characteristic of all rings; this gave a standard sampling position, regardless of ring width.

Wide ray frequency was counted as the number of rays crossing the mid latewood of the whole sample width in T.S., and was expressed as the number per centimetre tangent.

Mean wide ray size as seen in T.S. was calculated by dividing total ray width across a section by number of rays in the section.

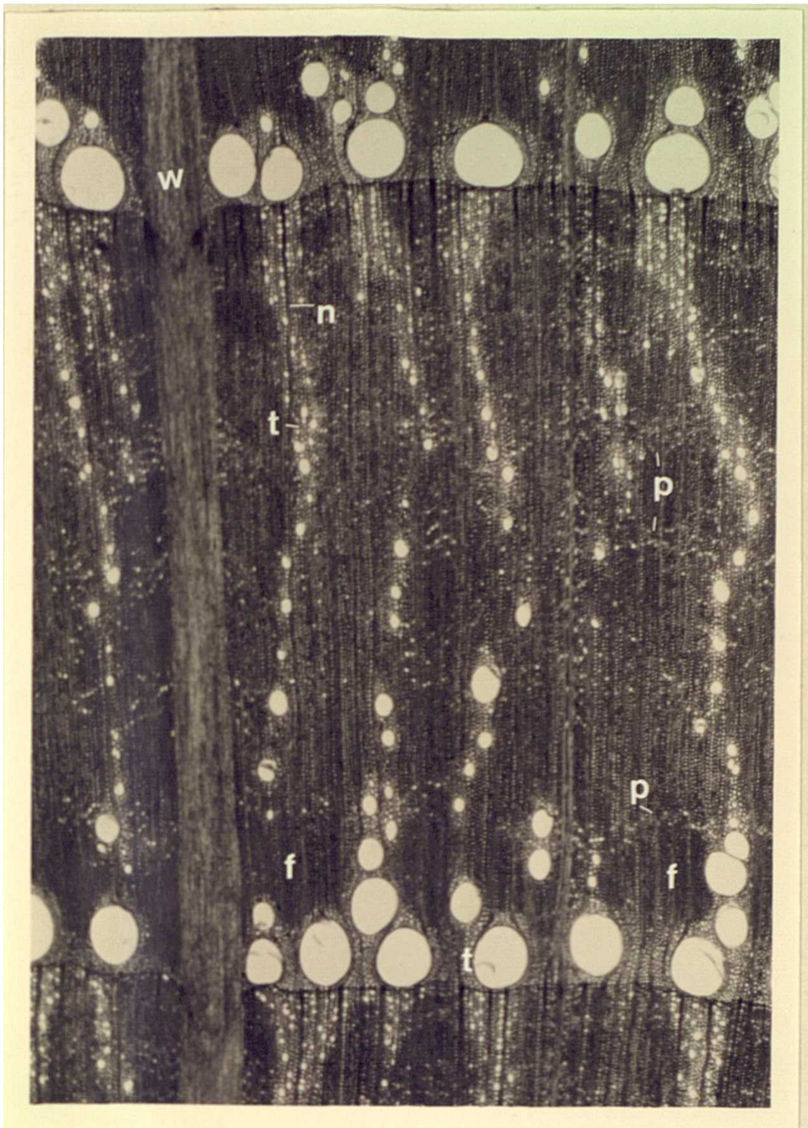


Plate 4.1. Transverse section of Quercus robur stem wood. x20

This plate shows the post-earlywood band consisting of a high proportion of fibres (F), which is described in section 4.2.2 above; also the typical increase in width of wide rays (W) on each side of the ring boundary. N = narrow ray. The tangential bands of axial parenchyma (P) show the most typical pattern encountered in these samples: a discrete band immediately following the post-earlywood fibre band and more diffuse bands of varying frequency and intensity in the later wood of the ring. The groups of tracheids surrounding vessels of earlywood and of latewood flames (T) can also be seen.

This section was stained with safranine, counterstained with fast green, but the analyses of wood structure were carried out on unstained or safranine tinted sections (Section 4.2.1).

MEASUREMENT OF EARLYWOOD VESSEL SIZE AND SHAPE. These were measured by using the digitising technique described in section 5.2.2.5; data were collected from only twelve of the twenty four trees (pair numbers 1 to 6).

Earlywood vessels were measured in all rings of blocks A and B. All vessels in the first row of each ring of a sample, were measured. This gave an average of twenty three vessels measured per ring - approximately 460 per tree for blocks A+B. Vessels were measured if they lay on the ring boundary, or within 0.15 mm of it. The distance of 0.15 mm was approximately half the radial diameter of the larger vessels encountered; vessels occurring further than this distance from the boundary could thus be from a second row.

The radial and tangential diameters of each EWV were digitised, and area and shape for each was calculated as described in section 5.2.2.5.

The calibration of the digitiser was checked at the end of each run, with a programme which accompanied the digitising software (written for this wood structure analysis by Mr D A Davies of UCNW School of Animal Biology). Spot-checks were also made by measuring directly with a ruler the projected image of a calibration slide and particular individual vessels; this tested the accuracy of the digitising (of both system and operator), but not of the image projection; however, the latter would remain constant, and comparative results were more important than true dimensions. There were slight discrepancies between the digitised and direct-measured results, which varied in both size and direction, depending on the run; the average differences of the digitised from the direct measurements were +0.5% (maximum of +6%) for radial diameter, and +1.2% (maximum of +4%) for tangential diameter.

The EWV data, recorded initially onto Nimbus micro-computer, were transferred to the VAX mainframe computer. Data identifying site, woodland type (shake-prone or sound), pair, tree, tree condition (shaken or sound), ring width, calendar year, EWV frequency (number per cm tangent), earlywood percentage of ring, and wide ray percentage in latewood were added for each vessel. The Fortran programme used for adding the data was written by Dr S Kalafatis at UCNW Dept. of Forestry and Wood Science. The statistical package SPSS-X was used to calculate mean data for each ring, for the A + B blocks of each tree, woodland-type and tree condition, and for the other breakdowns of data described below.

4.2.3. ANALYSIS OF DATA

The wood structure data were analysed as follows in order to discover any association between oak wood structure and the susceptibility of individual trees or populations (woodlands) to shake.

1/ Means per tree of wood structure characteristics in each block (A to C), were calculated.

These data are given in Appendix 4.1: Appendix 4.1.1 shows means of characters in the ten rings per tree in block A; 4.1.2 shows means in block B; 4.1.3 shows means in block C. Block C is not represented in trees from sound woodlands (section 4.2). Means per tree of wood structure characteristics in the combined blocks A+B (n = 20) were calculated. These data are shown in Appendix 4.2.

These tree-mean data were used in subsequent comparisons of shaken and sound trees and of trees from shaken and sound woodlands.

2/ Means and standard deviations of characteristics of mature wood formed in the same calendar years (blocks A+B) were calculated for shaken trees and sound trees across both woodland types.

Differences between the means of shaken trees and sound trees irrespective of woodland type were tested using t-tests of paired samples. Paired samples were used in order to try and eliminate the effect of individual sites when testing wood structure associations with tree condition; the pairs were adjacent shaken and sound trees within each site.

Table 4.3 summarises the data for each wood characteristic in shaken trees and sound trees. Appendix 4.4. lists the values of the t-ratios obtained.

3/ Means and standard deviations of structure characteristics in mature wood blocks of equivalent cambial age were calculated for shaken trees and sound trees across both woodland types.

Comparisons were made between rings of equivalent cambial age because of the age difference which happened to exist between trees from shake-prone woodlands and trees from sound woodlands in this study (section 4.2). The data used were from block C of trees from shake-prone woodlands and from block A of trees from sound woodlands: i.e. rings of cambial ages between 45 and 70 years. Subsequently, these analyses also provided data which could be compared with that of Savill (1986) and Cinotti (1987) who both studied oak wood structure in rings of cambial age approximately 30 years to 60 years, but did not specify calendar years of ring formation.

Differences between the means were tested using t-tests of paired samples. Table 4.4 summarises these data for most wood characteristics in shaken and sound trees for rings of equivalent cambial age. Differences between the means of earlywood vessel parameters were not tested because data were missing from the sound woodlands and sample numbers were too small. Appendix 4.5 lists the values of the t-ratios obtained.

4/ Means and standard deviations of characteristics of mature wood formed in the same calendar years (blocks A+B) were calculated for trees from shake-prone woodlands and sound woodlands, irrespective of tree condition.

Differences between the means were tested with t-tests of the independent samples using their pooled mean variance. Table 4.5 summarises these data. Appendix 4.6 lists the t-ratios calculated for each wood structure characteristic, and the significance of the differences between means.

5/ Means and standard deviations of structure characteristics in mature wood blocks of equivalent cambial age were calculated for trees from shake-prone and sound woodlands, irrespective of tree condition. Differences between means were tested with t-tests of the independent samples using their pooled mean variance. Table 4.6 summarises these data. Appendix 4.7 lists the t-ratios calculated for each wood structure characteristic.

6/ Means and standard deviations of structure characteristics in mature wood formed during the same calendar years (the twenty rings of blocks A and B) were calculated for shaken trees and sound trees separately within shake-prone woodlands and sound woodlands. Results are summarised in Appendix 4.3.

4.3. RESULTS.

4.3.1. STRUCTURAL DIFFERENCES IN MATURE WOOD OF SHAKEN AND SOUND OAKS.

4.3.1.1. COMPARISONS OF RINGS OF THE SAME YEAR OF FORMATION.

There was no significant difference between the means of shaken and sound oaks for any of the fourteen characteristics studied in rings formed during the same calendar years. Table 4.3 overleaf summarises these comparisons.

The characteristics with the largest differences between the means (even though not significantly different) were:

a) EWV shape, which was more oval in sound than in shaken trees (t-ratio = 1.98; Student's t for 5 degrees of freedom = 2.02 at $P < 0.10$).

b) EWV area, which was greater in sound trees.

c) EWV radial diameter, which was greater in sound trees. It was this which influenced the area and shape differences between shaken and sound trees, as mean tangential diameters were almost identical.

In Tables 4.3 - 4.6, the quantified wood structure characteristics are means of values from a number of trees per sample. Variation between trees was often high (earlywood percentage of ring (EW%) ranged from 23 - 73% in one case); consequently, the mean EW% figures given in these tables may not equal the earlywood percentages which can be calculated from the mean ring widths and earlywood widths in the tables.

units	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray% in EW	Wide ray% in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
MEANS OF SHAKEN TREES														
$\bar{x}$	1.90	0.57	1.33	35.2	1	17.0	10.3	9.4	4.4	0.19	243	274	54519	1.14
s.d.	0.87	0.26	0.64	7.4	1	2.8	5.5	5.1	2.3	0.04	33	46	14618	0.16
MEANS OF SOUND TREES														
$\bar{x}$	1.94	0.58	1.37	39.2	2	17.2	8.9	8.2	4.4	0.18	250	306	61770	1.24
s.d.	1.63	0.38	1.31	12.4	1	2.2	3.4	3.4	1.2	0.08	22	37	9617	0.18
n of trees	12	12	12	12	12	6	12	12	12	12	6	6	6	6

TABLE 4.3. MEANS AND STANDARD DEVIATIONS OF WOOD STRUCTURE CHARACTERISTICS OF SHAKEN AND SOUND OAKS FROM BOTH WOODLAND TYPES: RINGS FORMED DURING THE SAME CALENDAR YEARS (1955 - 1964, AND 1935 - 1944).

Differences between the means were tested with t-tests of paired samples (pairs are adjacent shaken and sound trees in each site). There was no significant difference between the means for any of the above characteristics.

† See page 201

units	Ring width mm	Early wood width mm	Late wood width mm	Early wood % †	EWV row no.	EWV freq	Wide ray% in EW	Wide ray% in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um^2	EWV shape
MEANS OF SHAKEN TREES														
$\bar{x}$	1.75	0.51	1.24	33.2	2	17.3	10.1	8.8	4.8	0.19	229	238	44196	1.07
s.d.	1.28	0.35	0.96	11.3	1	1.2	5.2	4.8	2.3	0.06	45	32	13682	0.06
MEANS OF SOUND TREES														
$\bar{x}$	1.50	0.49	1.01	42.8	2	15.3	7.7	6.9	4.1	0.19	261	286	60098	1.11
s.d.	0.94	0.24	0.71	21.5	0	3.5	2.8	2.5	1.4	0.08	30	36	12330	0.13
n of trees	10	10	10	10	10	3	10	10	10	10	3	3	3	3

TABLE 4.4. MEANS AND STANDARD DEVIATIONS OF WOOD STRUCTURE CHARACTERISTICS OF SHAKEN AND SOUND OAKS FROM BOTH WOODLAND TYPES: RINGS OF EQUIVALENT CAMBIAL AGE (BETWEEN 45 AND 70 YEARS FROM PITH).

t-tests of paired samples were used to test the differences between the means for all characteristics except earlywood vessel parameters (for which the number of samples was too small). Pairs were adjacent shaken and sound trees from each site. Ten pairs were analysed (not twelve as for blocks A+B) because some data were missing for wood of this cambial age from shake-prone woodlands). No significant differences were found between the means of shaken and sound trees.

† See page 201

4.3.1.2. COMPARISONS OF RINGS OF SIMILAR CAMBIAL AGE.

There was no significant difference between the means of shaken and sound trees for any of the wood structure characteristics measured in rings formed at equivalent cambial ages to one another. Table 4.4 above summarises these comparisons.

The pattern of differences between the means of most characteristics was the same as that found when rings formed in the same calendar year were compared (Section 4.3.2.1), though none were significant differences in either set of samples. Shaken oaks tended to have a smaller earlywood percentage of the rings, larger wide ray percentage, and greater earlywood vessel size (both diameters and therefore area) than sound oaks (N.B. vessel dimensions for samples of equivalent cambial age were available from sound woodlands only).

4.3.2. STRUCTURAL DIFFERENCES IN MATURE WOOD OF OAKS FROM SHAKE-PRONE AND SOUND WOODLANDS.

4.3.2.1. COMPARISONS OF RINGS OF THE SAME YEAR OF FORMATION.

The means and standard deviations are presented in Table 4.5.

There were significant differences between the means of oaks from shake-prone and sound woodlands (irrespective of tree condition) for the following characteristics: ring width, earlywood width, wide ray size and the radial diameter of earlywood vessels. All were greater in trees from shake-prone woodlands, than in those from sound woodlands.

	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray% in EW	Wide ray% in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
MEANS OF TREES FROM SHAKE-PRONE WOODLANDS														
$\bar{x}$	2.40 +	0.71 *	1.72	36.2	2	16.2	10.8	10.0	4.4	0.21 +	252	311 +	63671	1.25
s.d.	1.61	0.38	1.29	7.5	1	2.8	3.0	3.1	1.6	0.07	23	43	11213	0.20
MEANS OF TREES FROM SOUND WOODLANDS														
$\bar{x}$	1.43 +	0.45 *	0.98	38.3	1	18.0	8.4	7.5	4.4	0.17 +	242	269 +	52618	1.13
s.d.	0.56	0.17	0.41	12.7	1	1.8	5.6	5.0	2.1	0.04	32	33	11776	0.12
n of trees	12	12	12	12	12	6	12	12	12	12	6	6	6	6

TABLE 4.5. MEANS AND STANDARD DEVIATIONS OF WOOD STRUCTURE CHARACTERISTICS OF OAKS FROM SHAKE-PRONE AND SOUND WOODLANDS: RINGS FORMED DURING THE SAME CALENDAR YEARS (1955 - 1964, AND 1935 - 1944).

Asterisks denote the results of t-tests. Mean values for each characteristic are marked if trees from shake-prone woodlands and those from sound woodlands differ significantly from each other. The probability level at which the difference is significant is coded by: + = $P \leqslant 0.10$, * = $P \leqslant 0.05$.

† See page 201

units	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray% in EW	Wide ray% in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um^2	EWV shape
MEANS OF TREES FROM SHAKE-PRONE WOODLANDS														
$\bar{x}$	2.74 ***	0.74 ***	2.00 ***	29.4 *	2 *	-	11.2 +	9.3	5.2	0.21	-	-	-	-
s.d.	1.12	0.31	0.85	5.4	1	-	2.7	2.1	1.4	0.08	-	-	-	-
n	10	10	10	10	10	-	10	10	10	10	-	-	-	-
MEANS OF TREES FROM SOUND WOODLANDS														
$\bar{x}$	1.03 ***	0.36 ***	0.67 ***	43.5 *	1 *	- -	7.8 +	7.1	4.1	0.17	246	262	52147	1.09
s.d.	0.54	0.13	0.44	20.4	0	-	4.8	4.6	2.0	0.05	39	40	14544	0.10
n	12	12	12	12	12	-	12	12	12	12	6	6	6	6

TABLE 4.6. MEANS AND STANDARD DEVIATIONS OF WOOD STRUCTURE CHARACTERISTICS OF OAKS FROM SHAKE-PRONE AND SOUND WOODLANDS: RINGS OF EQUIVALENT CAMBIAL AGE (BETWEEN 45 AND 70 YEARS FROM PITH)

Asterisks denote the results of t-tests. Mean values for each characteristic are marked if trees from shake-prone woodlands and those from sound woodlands differ significantly from each other. The probability level at which the difference is significant is coded by: + = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.

† See page 201.

4.3.2.2. COMPARISONS OF RINGS OF SIMILAR CAMBIAL AGE.

The means and standard deviations of wood structure characteristics in oaks from shake-prone and from sound woodlands are presented in Table 4.6.

There were significant differences between the means for the following characteristics: ring width, earlywood width, latewood width, earlywood percentage of the ring, earlywood vessel row number and proportion of wide ray in the earlywood. All were greater in trees from shake-prone woodlands, than in those from sound woodlands.

These results confirmed those for ring width and earlywood width seen in rings formed during the same years as one another. Wide ray size was larger in both sets of samples of oaks from shake-prone woodlands, though the difference was only (and weakly) significant in the rings of equal year of formation. Wide ray proportions were greater in oaks from shake-prone woodlands, though the difference was only significant in width of rays in the earlywood and when rings of equivalent cambial age were compared. Missing data prevented the comparison of earlywood dimensions.

4.4. DISCUSSION.

4.4.1. SUMMARY OF FINDINGS OF CHAPTER 4.

Significant differences in wood structure characteristics were found between the means of oaks from shake-prone woodlands and those from sound woodlands (regardless of individual tree condition). No significant differences were found between shaken and sound trees across the woodland types.

The significant differences between the means of oaks from the two woodland types are summarised in Table 4.7 below.

Wood structure characteristic.	Rings formed in the same calendar years.	Rings of similar cambial age.
Ring width	+	+
Earlywood width	+	+
Latewood width		+
Earlywood percentage		-
Earlywood vessel row number		+
Wide ray %age in earlywood		+
Wide ray size in latewood	+	
Earlywood vessel radial diameter	+	

Table 4.7. Wood structure characteristics and samples for which oaks from shake-prone woodlands differed significantly from oaks from sound woodlands.

Symbol shows direction of difference; oaks from shake-prone woodlands had significantly greater values for most characteristics.

No significant differences were found between shaken trees and sound trees, despite comparison of paired samples to try and eliminate site effects.

The wider rings and greater earlywood and latewood widths found in oaks from shake-prone woodlands compared to those from sound woodlands, contradicted the results of the site surveys. Site survey data had suggested that a narrower mean ring width was associated with high incidence of shake in oak. The discrepancy may be due to the differences in sample types. During site-surveys a very approximate assessment of growth rate (mean ring width) over the whole of the tree's life was made, whereas in the wood structure analyses described in this chapter, only rings in the mature wood were assessed and neither the first fifty or more years of the trees' growth, nor the last twenty were analysed. The discrepancies seen might have arisen if, for example, the trees in shake-prone woodlands made slow growth in the early years, more rapid growth to maturity, and a rapid decline in growth rate over the last twenty years. Cinotti (1987) found a change across the radius in relative ring widths of frost-cracked and sound trees (this is described in section 4.4.4).

The wood structure analyses made in the laboratory were accurately measured and the sample replications better balanced than the data from the field-surveys; the results were also proven as significantly different between woodlands and therefore will be discussed further, but it must be borne in mind that they do not represent the growth pattern throughout the life of the tree. A study taking more account of this might be worthwhile.

The lower earlywood percentage of the rings in oaks from shake-prone woodlands is a function of the proportionately wider latewood in these trees (even though earlywood was also wider in shake-prone compared to sound woodlands). The larger radial diameter of earlywood vessels in the oaks from shake-prone woodlands would be expected given the wider rings (Zasada and Zahner, 1970; this study, Ch. 5).

4.4.2. THE CONTRIBUTION OF WOOD STRUCTURE ANALYSES OF SOUND AND SHAKEN OAKS, TO THE MODEL OF SHAKE DEVELOPMENT.

1. In general, the oaks in shake-prone woodlands had significantly different wood structure patterns from those in sound woodlands (the characteristics which differed are summarised in Table 4.7 above).

2. In general, the differences between shaken and sound oaks within those woodlands were not significant.

3. Fitting this information to the model of shake formation proposed in Chapter 3, it is suggested that either the growing conditions or the genetic make-up (perhaps both) of the oaks in the shake-prone woodlands predisposed those trees to shake. The common growing conditions or genetics were reflected in the wood structure characteristics recorded in this study, and may have been direct predispositions to shake, or else parallel effects of a common cause.

4. Anomalous sound oaks in shake-prone woodlands may have escaped the influence of the trigger to shake. Alternative explanations for anomalous sound oaks on shake-prone sites could be genetic or microsite variations. Microsite cannot always be the explanation however, as a) the oaks were selected as adjacent pairs to reduce microsite effects as far as possible, and b) survey results showed no consistent microsite differences under individual shaken and sound oaks.

5. Reasons for anomalous shaken trees in sound woodlands are not evident until the differences between shaken and sound trees within woodland types are examined. Then it can be seen that for some ring width and earlywood vessel characteristics there were greater differences between shaken and sound trees in sound than in shake-prone woodlands (Appendix 4.3). These differences may be genetic differences or due to microsite variation which pairing failed to eliminate; whatever the cause, the apparent differences were obscured when data for the two woodland types were combined.

Within sound woodlands, significant differences between shaken and sound trees were as follows:

a) Shaken oaks had significantly wider rings and latewood (differences significant at $P < 0.10$ and $P < 0.05$ respectively). This was the same as the pattern found between trees in shake-prone woodlands and sound woodlands regardless of tree condition, and suggests that these wood structure patterns may be associated with the predisposition to shake.

b) Shaken trees had significantly smaller earlywood vessel (EWV) tangential and radial diameters (differences significant at $P < 0.05$) resulting in significantly smaller EWV cross-sectional areas (difference highly significant at $P < 0.01$). This was the opposite of the effect seen between oaks from shake-prone and sound woodlands, in which EWV radial diameters were greater in oaks from shake-prone woodlands. The smaller radial diameter of earlywood vessels of shaken oaks in sound woodlands was surprising, given that the rings were wider.

4.4.3. POSSIBLE CAUSES OF THE WOOD STRUCTURE PATTERNS FOUND TO BE ASSOCIATED WITH SHAKE IN OAKS.

The wood structure characteristics found in this study to be typical of trees in shake-prone woodlands, would seem to be influenced largely by environmental factors, although genetic variation no doubt plays a part in controlling response to the environment. The results of Chapter 3 showed a very strong association of environment (soil type especially) with shake incidence; wood structure evidence from this chapter 4.3 gives further support to this as follows:

WIDE RAY PROPORTIONS. Size of wide rays in latewood and percentage of wide ray in earlywood were greater in trees from shake-prone woodlands. The proportion of wide ray in oak has been shown by Maeglin (1974) to be much greater in trees on sites of low quality or site index; Williams (1942) showed that oak grown on dry sites produced broader rays. Thus the soil types associated with high incidence of shake have been independently associated with the wide ray characteristics of oaks which are more susceptible to shake. Results of Chapter 5 suggest that a high wide ray percentage is also associated with rapid growth rate, so part of the observed association with shake could be linked to the wider rings of the oaks from shake-prone sites. Myer (1922) concluded that within oak species, environmental factors have a stronger effect than genetics on ray volume.

EARLYWOOD VESSELS. EWV dimensions varied between oaks from shake-prone and sound woodlands. Other authors have shown that EWV tangential diameter is mostly under genetic control, while radial diameter is mostly under environmental control (Zasada and Zahner, 1970; Dodd, 1984). Studies of oak in a seed origin trial reported in Chapter 5 confirmed this. The oaks of shake-prone woodlands had significantly greater EWV radial diameters (presumably associated with the greater ring widths), but there was no significant difference in tangential diameters between woodland types. Thus again it seems that environmental factors had a strong influence on wood structure characteristics which were linked to shake incidence. Further work would be needed to investigate the apparently significant difference between tangential diameters (genetic control) in shaken and sound oaks within sound woodlands.

RING WIDTHS. Ring widths and late wood widths were significantly greater in oaks from shake-prone woodlands. It must be borne in mind that these patterns were not necessarily constant throughout the life of the tree and must be interpreted with care (section 4.4.2). The wider rings suggest that annual rainfall (or water availability) was greater in shake-prone woodlands than in sound (Section 2.2.2.2).

The wood structure patterns found in this study could thus indicate the nature of shake-prone woodland sites as being of low site quality: soils are nutrient-poor for topographical or geological reasons. Ring width and wide ray characteristics of oaks from shake-prone sites suggest that annual rainfall is high (promoting fast annual increment) but soil moisture retention is poor (causing leaching of nutrients). These conditions would corroborate the findings of the site surveys reported in Chapter 3.

4.4.4. COMPARISONS OF RESULTS FROM THREE STUDIES OF WOOD STRUCTURE ASSOCIATIONS WITH SHAKE IN OAK.

Only two other studies have investigated overall wood structure characteristics of shaken and sound oaks.

Savill (1986) measured earlywood and ring widths, wide ray size, wide ray frequency and proportion (i.e. percentage of ring), earlywood vessel frequency, and cross-sectional areas of earlywood vessels in a mixture of sessile and pedunculate oak. All his trees were from sites with a high incidence of shake. The samples were taken from the bases of 41 trees, and wood structure analyses were made in rings of cambial age 31 - 60 in one radius per tree. The wide ray size calculated was the width of the three widest rays in a 3 cm tangent to one ring per tree. EWV size was calculated from a single diameter of one vessel per ring.

Cinotti (1987) measured earlywood percentage, ring width, earlywood vessel area, EWV percentage of earlywood, and fibre percentage of latewood in frost-cracked and sound trees. He studied mixtures of sessile and pedunculate oak, sampled from two sites: one with a high incidence of frost-crack, the other unspecified (site effect was not assessed). Samples were taken 1 m above ground from seven pairs of oaks (pairs were adjacent trees of the same species, one frost-cracked and one sound). Wood structure was analysed in one radius per tree in five consecutive rings at 30% of the radius from the pith; it is estimated from his report that these rings were of cambial age approximately 35 - 40 years. Ring widths were measured in all rings across the disc, and EWV cross-sectional areas were measured by computerised image analysis.

Information from these studies is most comparable with the data from rings of cambial age approximately 45 - 70 years assessed in this chapter. Cinotti's frost-cracked oaks had greater ring-widths than sound oaks in early rings, followed by equal width then slightly smaller rings in the later years of growth. Savill found no significant difference in ring width between shaken and sound trees (though shaken trees had the wider rings). The study reported in this Chapter also found no significant differences in ring width between shaken and sound oaks (though ring widths were greater in mature wood of the middle to late years of growth of shaken trees).

Other wood structure characteristics analysed in all three studies are summarised in Table 4.8 below.

WOOD STRUCTURE CHARACTERISTIC	SHAKEN OAKS	SOUND OAKS	P	AUTHOR
Earlywood percentage	23%	28%	0.001	C
"	36%	29%	?	ExS
"	33%	43%	n.s.	H
EWV size (cross sectional area)	31410 um^2	27610 um^2	0.01	C
	81301 um^2	64942 um^2	0.001	S
"	44196 um^2	60098 um^2	n.s.	H
("	63408 um^2	63935 um^2	n.s.	Hs-p)
Wide ray % in latewood	8.2%	9.4%	n.s.	S
"	8.8%	6.9%	n.s.	H

Table 4.8. Comparisons of results of three studies of wood structure in sound and shaken oaks.

Samples were from rings of cambial age 30 - 70 years; trees were sessile and pedunculate oaks from both shake-prone and sound woodlands (details in Section 4.4.4 above).

P = significance of difference.
Authors: C = Cinotti (1987); S = Savill (1986); ExS = extrapolated from Savill (1986); H = this study; Hs-p = this study, oaks from shake-prone woodlands only (comparable with S)

Table 4.8 above shows much variation between the results from these studies. The wood structure characteristics in Cinotti's study were analysed in the only block of rings across the radius where ring widths were significantly different between cracked and sound trees: this would influence the differences between earlywood percentages and earlywood vessel characteristics. These differences are therefore not necessarily representative of the overall growth and wood structure characteristics of the tree.

The earlywood vessel data from the study reported in this chapter were derived from very few samples and the results can only suggest areas worth further investigation; they cannot be used to draw firm conclusions. They appear to contradict the results of Savill and of Cinotti, and suggest that in such studies it is important to take into consideration the influence of woodland type. Savill and Cinotti both found that shaken oaks had EWVs of greater cross-sectional area; this study found no significant difference in the vessel areas, but overall the mean size was greater in sound oaks. However, this study found that oaks from shake-prone woodlands (i.e. predisposed to shake, but not necessarily shaken) had earlywood vessels of larger radial diameter. This study suggested also that within shake-prone woodlands there was no difference between EWV size of shaken and sound trees, but within sound woodlands sound oaks had significantly larger EWV areas (both radial and tangential diameters being larger) (Appendix 4.3). Cinotti reported that the amount of variation due to 'pair' in analyses of variance carried out on his earlywood vessel data was very high. It is possible that this could have been differences in woodland type showing up; most of his samples were from a site with high incidence of frost-crack, the rest being from another site, of unspecified quality. All of Savill's samples were from shake-prone sites.

The lack of agreement in the results of these studies shows a need for further work using wider sampling within trees and between trees, including recognition of the influence of site type. Both radial and tangential diameters of earlywood vessels should be measured and considered separately from vessel area: area (if associated with susceptibility to shake) may indicate functional causes of shake, but variations in the two different diameters (again, if associated with shake) could suggest the means by which control of susceptibility could be effected. Use of green or dried samples should be specified, as anisotropy of shrinkage could result in dimension changes of earlywood vessels (oak of high density can have high anisotropy of shrinkage, or large volumetric shrinkage values (Nepveu, 1984c)).

4.5. CONCLUSION.

Wood structure patterns in the oaks of this study were found to be influenced largely by woodland type (i.e. whether the woodland in which the oaks grew had a high or a low incidence of shake), but only slightly by tree condition (i.e. whether the individual trees were shaken or sound).

It is proposed that the growing conditions and perhaps the genetic make-up of the oaks in shake-prone woodlands predisposed those trees to shake and was reflected in the wood structure. The wood structure characteristics typical of oaks predisposed to shake were mostly characteristics shown by other authors to be under environmental control. Whether these characteristics are a direct cause of shake, or a parallel effect of a common cause, is further discussed in Chapter 6. If any predisposing wood structure characteristic is under strong genetic control, this might allow artificial control of wood structure and therefore quality (susceptibility to shake) by selection and breeding as well as by site choice and silviculture. Chapter 5 reports a study of wood structure characteristics in trees from a replicated trial of different oak genotypes (seed origins).

CHAPTER 5.

GENETIC VARIATION IN WOOD STRUCTURE AND PROPERTIES OF OAK.

The overall aim of the research reported in this chapter was to quantify variations in wood structure and properties associated with differences in genetic origin of oak. The association of growth rate (ring width or tree diameter) with some of the wood structure characteristics was also examined.

Knowledge of the amount of variation in the characteristics of a species is of advantage when tree improvement is to be undertaken. The more variability that exists, the better the chance of selecting types which combine desired characteristics with a lack of the unwanted characters.

Knowledge of which particular characteristics are most clearly under genetic control is needed for selection or breeding programmes, although the preferred genotypes (in terms of survival, vigour or production of desired wood quality) may differ in phenotype (i.e. when modified by the eventual growing conditions of different sites or silvicultures).

This study aimed:

a) to assess the differences in wood structure and properties between eleven seed-origins from an established trial of sessile and pedunculate oak (*Quercus petraea* and *Q. robur*).

b) to identify which (if any) of the wood structure characteristics found to be associated with susceptibility of oaks to shake, might be under genetic control.

The knowledge of which particular structure and property characteristics were found to vary with genotype should also be of use for other considerations of controlling wood quality in oak.

5.1. MATERIAL AND EXPERIMENT DESIGN.

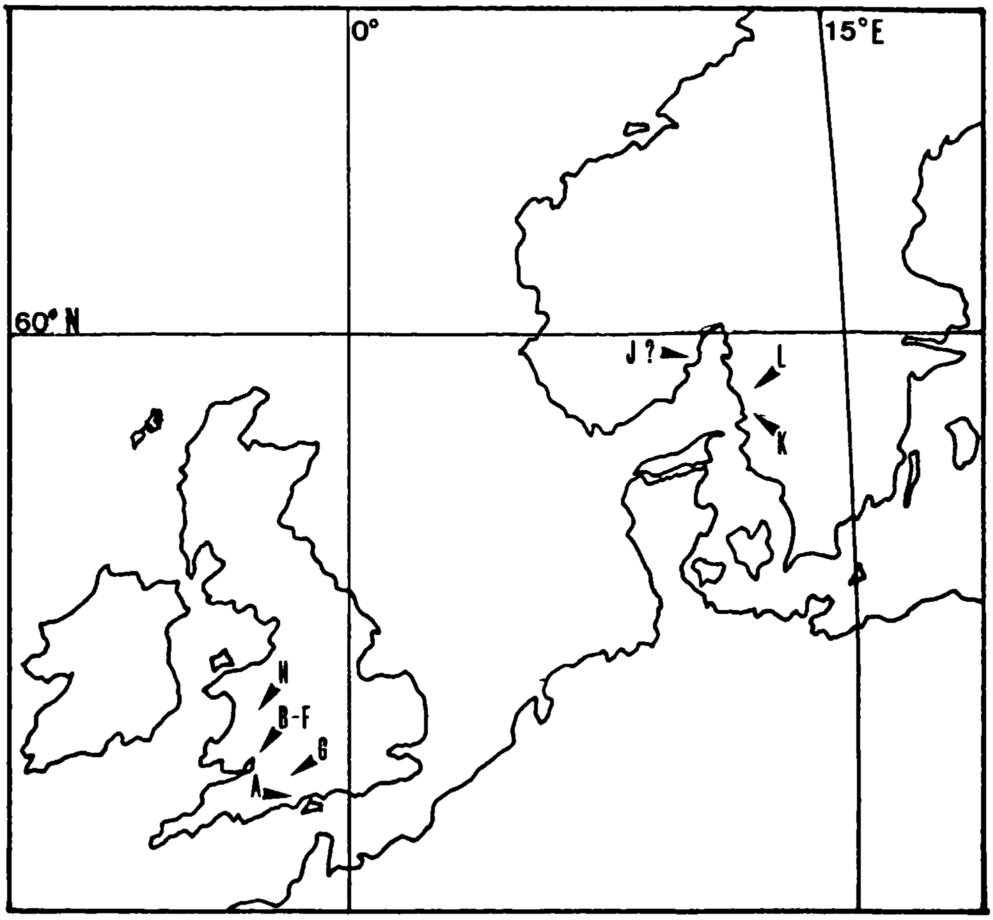
5.1.1. SOURCE OF MATERIAL.

PENYARD OAK PROVENANCE TRIALS. A set of "Race and Provenance" trials of oak were established by the Forestry Commission in 1954, in Penyard Wood, Forest of Dean (Grid Reference SO 613 223). The original object of the trials was "To compare the survival, rate of growth, form, yield, disease resistance and any other differential characteristics of a number of different origins of Oak mostly sessile but at least one lot pedunculate."; further notes from the experiment file of this project 232.12 are held in Forestry Commission archives at Alice Holt research station (FC File (AHL) S.Ex.PEN 1. P54).

Assessments of the trials were made at intervals until 1973 when the experiment was closed due to severe squirrel damage and to interaction of crowns in the un-thinned plots. The trial plots were thinned extensively in 1983 to be used for an underplanting experiment, and the thinned trees provided samples for this study of wood structure and properties.

The original project was entitled race and provenance trials because five of the eleven seed sources were not true provenances (in the forestry use of the term). These five were all from the Forest of Dean, and two of them were single plus-tree sources from within woods which also provided seed from the whole stand as a separate origin. Furthermore, the trials also tested species differences as they included the two oaks native to Britain. In this study, "seed origin trial" has been used as a generalised term to describe the treatments.

SEED ORIGINS TESTED AT PENYARD. The seed origins were listed and coded as in Figure 5.1 below; the original code letters have been retained. Lots 1 and 2, Sweden, were from the Goteborgs och Bohus lan area of SW Sweden. Latitudes and longitudes of 58°43' N/6°40'E and 58°9'N/6°51'E respectively are given in notes sent to the Forestry Commission after the seed was collected; these coordinates lie in Norway, but the same latitudes with longitudes of 11° N and 11° E would give positions which match verbal descriptions included in the same letters. It has not been possible to identify the Norwegian area 'Vestmorland'; the seed origin is therefore marked on the map with '?' in the Vestfold area - a low-lying coastal area which may be close to the origin of seed lot J.



SEED ORIGIN CODE LETTER	WOODLAND
A	Lodgehill, New Forest
B	Pritchard's Hill, Forest of Dean
C	Pritchard's Hill (Tree No.1), Forest of Dean
D	Hadnocks, Forest of Dean
E	Hadnocks (Tree No.1), Forest of Dean
F	Bond's Wood, Forest of Dean
G	Skilton's Paddock, Alice Holt Forest
H	South Side Wood, Powis Castle, Welshpool
J	In Vestmorland, Norway
K	Lot 1, Sweden
L	Lot 2, Sweden

Figure 5.1. Seed origins of sessile and pedunculate oak used in Penyard seed origin trial.

There was some confusion in the past Forestry Commission records as to the species of oak in the seed-source woodlands. Oak is notoriously variable in many of its characteristics, and distinguishing between Quercus robur and Q. petraea can be difficult; tree form and leaf size and shape can vary within species when trees are of different ages or grown under different conditions; there is also the possibility of hybridisation between these two species (Section 2.1.1.3). It was found during the Penyard study that seed origins linked by wood characteristics held in common, were not always linked by the original species attributions; therefore a study of leaf morphology was made on trees in the trial in order to try and separate the species types. The leaf morphometry work is described in a separate report to the Forestry Commission; the method involved the measuring of a number of leaf characters, assigning 'scores' to each leaf for each character, and deriving a "Hybrid Index" which ranked the tree or population between the hypothetical "pure" types of the two species.

Table 5.1 below shows the seed origins ranked according to the hybrid *index devised for this project, and includes* original assessments of species type (1952 experiment plan, and 1951 Identification Catalogue or 1951 Genetical Record Forms). In the case of the Swedish origins, only descriptions of form and stand name are given in the 1954 experiment file, but sessile-types were expected as the Swedish coastal area to latitude approximately 58°N has an indigenous population of sessile oak, although most oak in Sweden is pedunculate and the two often hybridise (pers. comm., L. Sennerby-Forsse).

THE PENYARD SITE. The experiment was grown on an even, gentle, convex slope of South West aspect, at an altitude of 104 m. The site is sheltered and the soil is a sandy loam over Old Red Sandstone (pH 4.6 to 5.6).

		a)	b)
SEED ORIGIN	HYBRID INDEX	ALLOCATED BY INDEX	SPECIES ALLOCATIONS OF 1951 AND (1952)
A	16.9	Pedunc.	? (Pedunculate)
H	18.6	Pedunc.	Pedunculate (Sessile)
G	22.2	Pedunc.	? (Sessile)
K	22.7	Pedunc.	? (Sessile)
L	27.5	Sess/Ped	? (Sessile)
J	29.8	Sessile	Sessile (Sessile)
B	31.0	Sessile	Mixed Sess/Ped (Sessile)
E	31.2	Sessile	Mixed Sess/Ped (Sessile)
C	31.6	Sessile	Sessile (Sessile)
D	32.1	Sessile	Mixed Sess/Ped (Sessile)
F	33.4	Sessile	? (Sessile)

Table 5.1. Allocation of each seed origin to species a) on basis of hybrid index used in this study, b) in F.C. records.

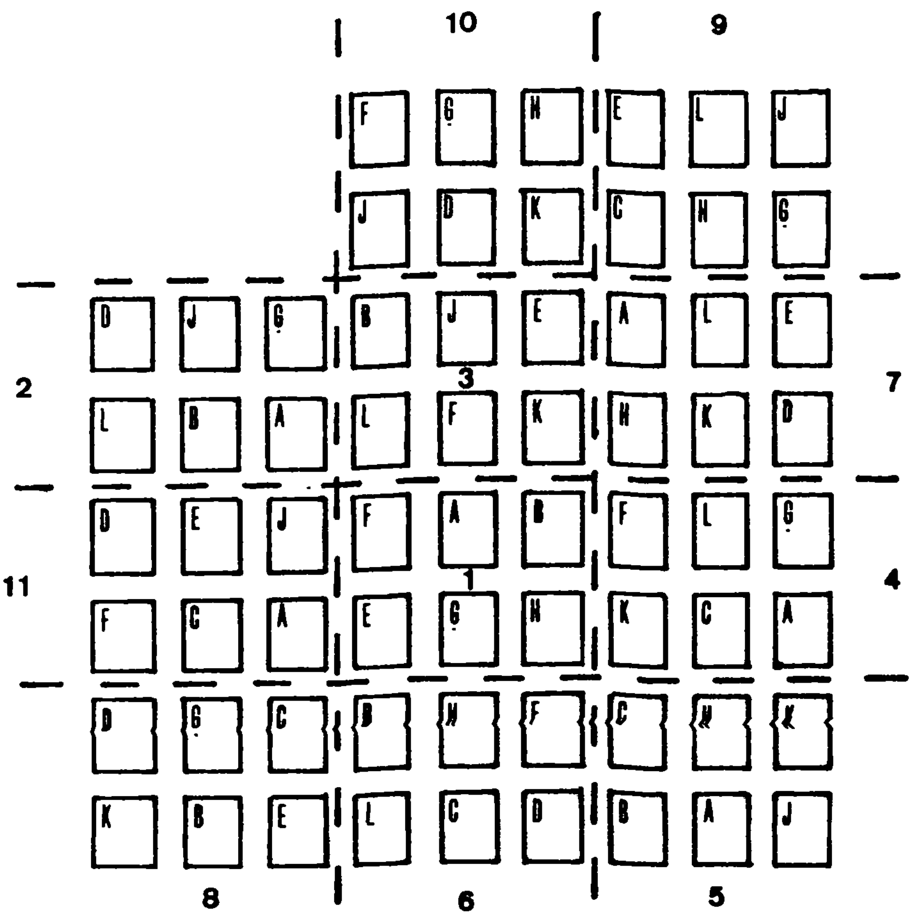


Figure 5.2. Penyard Wood experiment PEN 1, Forest of Dean.

Layout of blocks (numbers) and seed origin replicates (letters).

5.1.2. DESIGN OF SEED ORIGIN TRIAL, AND SAMPLING METHOD.

DESIGN OF TRIAL. The 1954 experiment was designed as an "intensive" trial of eleven seed origins, using a balanced incomplete randomised block layout with six of the seed origins replicated per block. The balanced nature of the design meant that any pair of seed origins appeared together within a block exactly three times.

Each seed origin replicate within a block consisted of thirty-six trees of that origin, in six rows of six trees. Figure 5.2 above shows the layout of the experiment.

SAMPLE SIZE. A sample of two trees per replicate (i.e. twelve per seed origin) was used for studying variations between seed origins. The four seed origins A, B, D and H (two pedunculate and two sessile) were selected for additional sampling to test growth rate effects within seed origins; an extra eight trees per replicate (48 per seed origin) were taken from these origins.

SAMPLE SELECTION. When the thinning was carried out in September/October 1983, the "best" two trees per replicate (i.e. the two of largest dbh, excluding wolf trees and those of exceptionally poor form) were to be grown on for further experiments. The samples for comparative studies of wood characteristics were taken from the remaining crop. The two trees chosen from each replicate, were what would have been the next "best" crop trees after those being retained on the site. Trees still showing signs of the 1970s' squirrel damage were rejected. Individual trees were identified by row and column number within the replicate; rows ran across the slope.

For the seed origins A, B, D and H, a total of ten trees per replicate (sixty per seed origin) divided evenly between five diameter classes (I - V) was sampled as follows:

a) breast height diameter (dbh) was measured for all trees in the replicate

b) the range for that replicate was divided into five equal-range classes of dbh

c) two trees were chosen from each 'diameter class' (mid-class diameters were preferred unless choice was limited by trees of poor form or with bad squirrel damage). Diameter class I contained trees which would have been dubbed 'wolf' trees in the whole-trial sampling; diameter class II contained trees corresponding to the "best" crop-tree pairs selected for the other seed origins in the whole-trial sampling.

Trees were selected and marked, dbh was recorded, and notes were made of crown form, presence of epicormics, and of damage or epiphyte growth (notes in Forestry Commission archives).

HARVEST AND SAMPLE REMOVAL. Sample trees were marked before felling, at 0.5 m from ground level and to show the North aspect of the tree; this ensured a consistent sample position within trees. On felling, a section of the trunk approximately 10 cm thick was cut from the 0.5 m level. Presence of rot, shake and squirrel damage was noted.

5.1.3 PREPARATION AND STORAGE OF PENYARD OAK SAMPLES.

After harvest, logs were placed immediately in black polythene bags and returned to the laboratory for processing within a few days at the most. Logs were cut on a large bandsaw, and notes were made of defects revealed by the sawing.

1 Half discs approximately 1 cm thick and containing the pith were cut from the logs. One was used for measurements of heartwood:sapwood; one was air-dried before further processing for X-ray densitometry.

2 A diameter strip approximately 1 cm wide was cut from a third half-disc from each log. This was preserved in FPA (formaldehyde, propionic acid and alcohol) prior to sectioning for light microscopy. The blocks were preserved from the fresh state to minimise distortion on drying.

3 The remainder of each log was stored under water (as reserve samples) to maintain the wood in as near the fresh state as possible. "Panacide" solution was added to the storage bins to discourage the growth of fungi and bacteria. This wood later provided samples for the knife test.

5.2. WOOD STRUCTURE ANALYSIS: METHODS

5.2.1. HEARTWOOD AND SAPWOOD MEASUREMENTS.

Measurements of heartwood and sapwood were made on a half-disc for each tree. The boundary was easily defined, being marked by a clear colour change in the wood. Measurements were made along two radii 180° apart, using Vernier callipers. Width of heartwood and sapwood was measured in millimetres, and number of rings of each were counted. For heartwood, the measurements were converted to percentages (of total ring number or of radial width) and a mean percentage was calculated for each pair of radii (i.e. each tree). Sapwood measurements are presented as actual ring number and radial thickness - a mean for the two radii per tree.

5.2.2. FINE STRUCTURE ANALYSIS.

5.2.2.1. PREPARATION OF MATERIAL.

The 1 cm wide blocks for microscopy samples sectioned satisfactorily without need for hot-water soaking or steaming. Transverse sections of 30 um thickness were cut using a Reichert sledge microtome. Sections were cut with the knife edge perpendicular to the rings, to reduce stretching and tearing in the earlywood. Sections were mounted unstained in glycerine gel.

5.2.2.2. SAMPLE SELECTION WITHIN TREES.

The oaks in the Penyard trial were 31 years old when harvested (trees of seed origin H, planted as 1 + 1 + 1 + 1, were 33). Oak wood has been reported to show marked juvenile characteristics for about ten to twelve annual rings from the pith, with fully mature wood not forming until at least twenty-five rings from the pith (Gasson, 1984). In trial investigations of the Penyard samples it was found that there would be time to measure tissue proportions and earlywood vessel data in only one ring per tree. A ring of at least average width was needed in order to sample the full development of latewood pattern (this seemed to become either truncated or compressed in unusually narrow rings), but rings of extreme width were avoided. Therefore, constrained by the fact that squirrel damage and crown interaction in the ten years before harvest may have been additional un-monitored influences on wood structure, and by the desire to choose a ring from as mature wood as possible, the 1971 ring was chosen for study. At 0.5 m above ground level, this ring had a 'cambial age' (number of years from pith) of about 15 years; this varied slightly depending on rate of early height growth.

5.2.2.3. RING WIDTH MEASUREMENTS.

The width of the 1971 ring in each tree was measured from the slides of thin sections, using Vernier callipers accurate to 0.01 mm. Two measurements per ring were made, on opposite sides of the tree diameter, and were averaged.

5.2.2.4. TISSUE PROPORTION MEASUREMENTS.

POINT SAMPLING. A method of counting percentages of cell-types within the annual rings was needed. A number of trials were made, all based on some form of point-sampling using a light microscope (Leitz Laborlux 12) and eye-piece graticule. The very marked changes in proportions and arrangements of cell-types occurring radially across the rings of oak wood, mean that cell-counts have to be made contiguously across the ring if whole-wood proportions are to be measured; if, for example, alternate fields of view were to be examined at x400, a complete axial-parenchyma band could be missed. Additionally, the large size and wide spatial distribution of the wide rays compared to the other tissue types, means that a large tangential spread (perpendicular to rays in T.S.) of sampling is needed within each ring. Trials showed that contiguous sampling across even one ring per tree was too time-consuming to use the method for all samples; also, that the point-sampling method was too small-scale to make accurate measurements of wide-ray proportions at the same magnification as other tissue-types.

To overcome these logistical problems, tissue proportions were measured separately within three distinct zones of the annual ring (as seen in T.S.), thus illustrating characteristic wood structure patterns rather than recording whole-wood tissue proportions. The three zones are shown in Plate 5.1 and Figure 5.3: they are earlywood (EW); latewood zone one (LWZ1), the central zone where the latewood-vessel flames are narrow and more or less parallel to the rays; and latewood zone two (LWZ2), where the latewood-vessel flames vary in pattern from narrow wedges to wide branches - patterns which have been described as characteristic of oak species (Walker,1978).

The wide rays were measured separately and at a lower magnification than the other tissue types in order to overcome the problem of scale. Point-sampling for the other tissues was then be carried out between the wide rays, with tissue proportions calculated as a percentage of the value remaining after subtraction of wide ray percentage for each zone. The narrow, uniseriate rays were sufficiently small and frequent to be point-sampled along with vessels, fibres and axial parenchyma.

WIDE RAYS. In other studies, wide ray proportions have often been measured as percentages of area of tangential longitudinal sections (TLS), because of the axially elliptical shape of these rays; their apparent width in TS depends on the level in their height at which they are sectioned. However, the rays of oak are not storied, so a single transverse section can pass through a number of rays at a variety of levels. Trials examining wide rays in tangential longitudinal sections from four trees cut from within the LWZ1 zone of the 1971 ring were carried out, but TLS measurements were found to be of no advantage over those from transverse sections because a) wide ray percentages were similar whether measured from TS or TLS of the LWZ1 of 1971 ring; and b) incorporation of results with those of the other tissues (which were measured from the TS) was difficult.

The wide ray percentage was therefore measured from transverse sections at x100 magnification within each of the three zones of the 1971 ring. Polarising filters were used because ray tissue in the unstained sections was found to be more distinct when viewed between crossed-polars. Total width of wide rays per section was measured with the eyepiece graticule laid tangentially (parallel to ring boundaries); and the percentage of the total section width was calculated. Frequency of wide rays (number per centimetre) was also calculated. Two measurements - one from each side of the diameter sample - were made per 1971 ring and averaged.

TISSUES BETWEEN WIDE RAYS. Proportions of vessels, fibres, uniseriate rays and axial parenchyma were assessed by point-sampling between the wide rays in each of the three zones of the 1971 ring. A field-of-view in the zone to be analysed was chosen at low power (at x40 it was not possible to judge on which cells the points would fall). Magnification was then increased to x400 and each cell-type lying under a point on the eyepiece graticule was scored. Initial trials used two different eye-piece graticules for point-sampling: a grid bearing 25 randomly scattered dots, and a linear scale of ten divisions (11 'points' formed by ends of scale lines). Tissue proportions calculated from the two methods were similar for the same total of points, but the 11-point scale was preferred as faster and less tiring (it was easy to lose one's place using the random dots).

Figure 5.3 shows the sampling positions used in each zone. In the early wood zone, the graticule was placed touching and parallel to the ring boundary. In the latewood zones, which were always distinct but very variable in width, the middle of the zone was centred in a low-power field-of-view. The graticule was then angled at 45° to the rays and the higher magnification selected. In this way the disadvantages of placing the line of sample points tangentially (points might fall wholly within or out of the tangential bands of axial parenchyma) or radially (inaccurate recording of narrow rays) were avoided. Number and thickness of LW parenchyma bands varied between trees, therefore angling the scale was most suitable for measuring these tissues also.

SAMPLE SIZE FOR POINT-SAMPLING. Trials to determine optimum total of sample points per ring, were carried out using randomly chosen trees from three different seed origins.

Cumulative results of tissue proportion calculations (up to sixteen fields of view - 176 points - per ring) were plotted. The sample size at which the graph for each cell-type in each zone levelled, was noted.

A sample rate of ten fields of view per ring - 5 from each side of the tree diameter was chosen. This gave 110 points per ring, exceeding optimum sample number for fibres, parenchyma, narrow rays (and sometimes for vessels) in LW, and corresponding to the minimum for all cell-types in EW and for vessels in LW.

IDENTIFICATION OF CELL TYPES: It was not possible to distinguish easily between fibres, fibre-tracheids and tracheids in the transverse sections; all these cell types were therefore recorded under the category of 'fibres'. Axial parenchyma cells were of similar cross-sectional area to many fibres and some practice was necessary to distinguish them confidently as cells of the 1971 ring no longer contained living protoplasts or starch grains; they were recognised by their thin walls and less angular shape, and a different light transmittance was very apparent at lower magnifications.

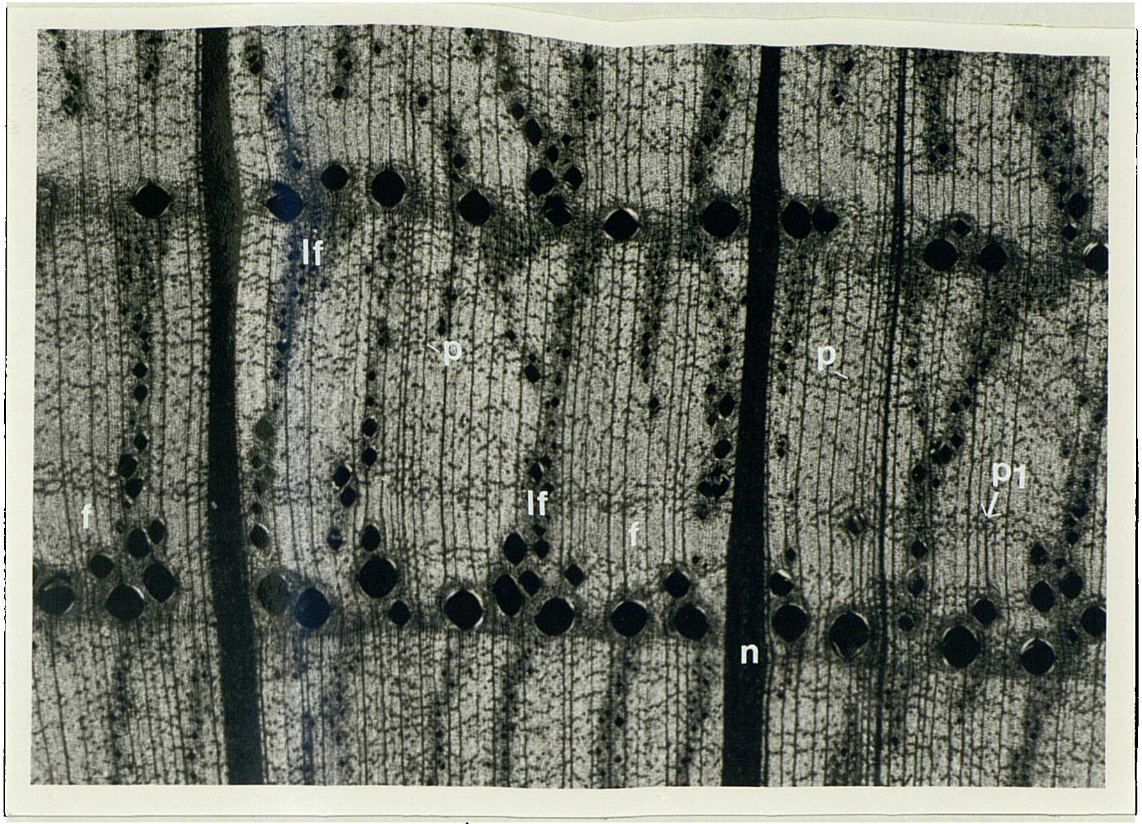


Plate 5.1. Cross-section of 1971 ring of oak. x 20.

Unstained section viewed between crossed polarising filters, to enhance contrast of ray and axial parenchyma. The plate illustrates the following features typical (though not always apparent) in the sessile and pedunculate oaks (Quercus petraea and Q. robur) analysed in this study.

f - Post-earlywood band of dense wood with high proportion of libriform fibres

p1 - wide band of diffuse-aggregate apotracheal axial parenchyma, which typically follows the dense fibre-band

p - later uniseriate bands of diffuse aggregate parenchyma and scatters of diffuse parenchyma; the presence and position of these was much more variable than of the first wide parenchyma band

n - noding of wide rays at ring boundaries

lf - latewood 'flames' of latewood vessels surrounded by thin-walled tracheids and fibre-tracheids

- high proportions of vasicentric tracheids in earlywood

Heartwood had not yet developed in this ring, therefore no tyloses were present in the earlywood vessels. The angular appearance of vessel lumina is an artefact of the polarised light.

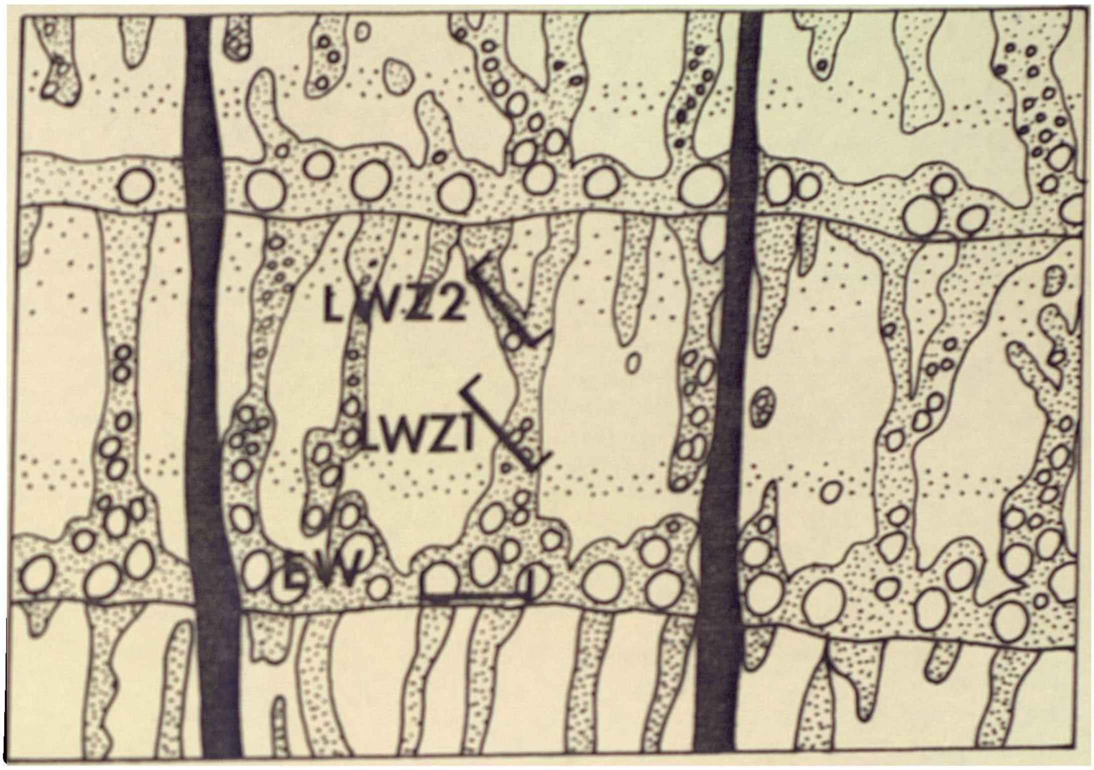


Figure 5.3. Sketch of Plate 5.1, illustrating the three zones per ring in which wood structure of oak from Penyard seed origin trial samples was analysed.

EW = earlyw d; LWZ1 = latew od z ne 1; LWZ2 = latewood zone 2

Scales sh w graticule position for point-sampling in each z ne.

5.2.2.5. EARLYWOOD VESSEL ANALYSIS.

A digitising table and associated computer software devised by Mr D A Davies at UCNW (Dept. of Animal Biology), were used to study earlywood vessel (EWV) characteristics. Tangential and radial diameter were measured from projected light-microscope images of transverse sections of the Penyard oak samples. This semi-automated image-analysis method allowed large numbers of vessels to be measured quickly and accurately, with the data entered directly into computer files. The aim was to determine the mean size, shape and frequency of EWV's, for each seed origin and to test the significance of any differences between seed origins.

CALCULATIONS OF VESSEL DIMENSIONS FROM DIGITISED DATA. Co-ordinate data recorded by the digitiser for diameter limits of each vessel were converted to vessel dimensions using specially written software (by D A Davies) on a Nimbus micro-computer. This calculated radial and tangential diameter in microns, cross-sectional area, and shape of each vessel. Cross-sectional area was calculated by assuming the vessel to be circular and using the formula for area of a circle, with radius given as a mean of tangential and radial radius for each vessel. Shape was calculated as the ratio of radial to tangential diameter: the higher the value, the more radially oval the vessel (round or radially flattened vessels were rare in these samples). Vessel frequency per centimetre was calculated as total number vessels measured per tree, divided by width of both sections per tree at the 1971 earlywood - excluding damaged edges.

ACCURACY OF DIGITISED MEASUREMENTS. Accuracy of the digitised measurements was tested on samples of vessels from twelve trees analysed in four separate digitising sessions. Digitised diameter results were compared with measurements of the same individual vessels made using an eye-piece graticule (crossed linear scales) in a light microscope. Digitised measurements of radial diameters were on average 1% greater than direct measurements; those of tangential diameters were on average 1% less than direct measurements.

SAMPLES ANALYSED. EWV's were studied in the 1971 ring of twelve diameter class II trees from each of the eleven seed origins. The same samples as used for tissue proportion measurements were used: 30 um, unstained, transverse sections taken from each side of a 1 cm-wide diameter strip from each tree. All vessels from the first vessel row of the earlywood were measured, with the exception of those excluded as follows. A standard method was adopted to deal with rings where extra vessel rows, or infrequent, unaligned vessels occurred: those not within 0.15 mm of the ring boundary were excluded; likewise, any occasional, unusually small vessels (less than 0.1 mm diameter) were excluded. More than 6 000 vessels were measured over all seed origins.

In a few cases, one side of the diameter was disrupted by wound tissue; in these cases, measurements were repeated on the sound side, giving a similar total of vessels to other samples, and incidentally providing a check on the accuracy of recording. The vessels at the edges of the sections were not measured in case they had been crushed or stretched in sample preparation.

Radial diameter was identified as the longest axis radially, which was usually parallel to the rays. Tangential diameter was perpendicular to the radial for each cell - this was not always parallel to the ring boundary.

SAMPLING RATE. Initial trials suggested an optimum sampling rate to be twenty vessels per tree, for an accepted error of 10% of the true mean for area (eighty-two for an error of 5%). All samples contained at least twenty vessels. A retrospective count showed that the mean number of vessels measured per tree was fifty.

ANALYSIS OF EARLYWOOD VESSEL DATA. Sets of data (two diameters, area and shape) for each vessel were transferred to the mainframe computer. A Fortran program written by Dr S Kalafatis at UCNW (Dept. of Forestry and Wood Science) changed the file into a suitable form for analysis by the SPSS-X package, and allowed keyboard entry of additional data.

The SPSS-X package was used to remove section code numbers, add details of seed origin, block, tree number and ring width for each vessel, and to break down data by seed origin, tree and ring width. Aggregate files of mean characteristics per tree were used to compute analyses of variance (section 5.4).

5.3. WOOD PROPERTIES ANALYSIS: METHODS.

5.3.1. X-RAY DENSITOMETRY.

X-ray densitometry was used to acquire detailed information of density variation across the radius of the oaks from pith to bark. The results reported here are for the density of the 1971 ring (that in which the wood structure analyses were made), and for the mean whole disc density at 0.5 m in the oaks of each seed origin.

X-ray images of radial strips of wood were made, and the developed films were scanned with a densitometer which recorded optical density (later converted to physical density) every 0.2 mm along the radius.

5.3.1.1. PRINCIPLES OF THE METHOD.

When an object is traversed by an X-ray beam (electro-magnetic radiation), individual photons are removed from the beam on interaction with the atoms of which the object is composed. The number of photons removed is thus determined by the thickness and chemical composition of the material. The attenuation magnitude is also dependent upon the strength of the radiation source. For a specific source of radiation, and a specific combination of elements, the attenuation co-efficient is constant. This is made use of in X-ray densitometry: any variation in the radiation transmitted through material of known, even thickness should be attributable directly to differences in density. In the X-ray densitometry of wood, 'soft' X-rays (i.e. of long wavelength, in the low frequency range) are used. This reduces the loss of definition which can occur due to scattering of higher frequency rays in tissues of very low density (particularly important in oak, where the beam can have an almost clear passage through the large earlywood vessels). The transmission of soft X-rays through the wood is recorded on photographic film.

Densities of wood samples are thus recorded initially as optical densities on photographic film negatives. Comparability between records of optical density is achieved a) by developing the films by a standard and exact process, b) by inclusion of a calibration device on each film exposed.

The film is analysed by a microdensitometer, which measures the amount of light transmitted through the negative images by scanning with a light beam and detector. The values of optical density are converted to physical density using regressions calculated from sub-samples of the wood under test; these are assessed both by X-ray densitometry and gravimetrically.

5.3.1.2. THE METHOD IN PRACTICE.

Radial strips of wood were cut from each of the air-dried half-discs (one disc per tree) described in section 5.1.3. The radii were chosen to provide clear specimens, therefore the positions round the half-disc from which they were taken, varied. The grain had to be very straight and parallel to the sides of the sample. The strips were 1 cm deep axially, 2 cm wide tangentially, and included the full radius from pith to bark.

Uniform moisture content and sample thickness are important for accuracy of densitometric analyses. Sample strips were conditioned to 12% moisture content, milled until exactly 5 mm deep and 5 mm wide, and kept in conditioning ovens to maintain a constant moisture content and prevent distortion.

Sixty-six test-specimens taken from fast and slow-grown material of all seed origins were chosen to represent the largest range of density likely to occur in the main sample. These test samples were used to determine the relationship between optical density and physical density for the oak wood.

Two radii per tree were sampled for the main analyses. Samples were prepared for trees of all diameter classes, but many were 'lost' during preparation because of lack of straight grain (even in such shallow samples), cracking on drying, or defects not seen in un-milled specimens.

The calibration device included with samples was a stepped wedge of 'Kemital', a polyacetal plastic which has an X-ray attenuation co-efficient very similar to that of wood, but which is homogeneous in density. The steps of the wedge are of known thickness and density. The image of the wedge was scanned by the densitometer at the start of each film analysis.

X-RAY EXPOSURE AND FILM DEVELOPMENT. The radiography used a stationary technique (some workers, e.g. Milsom (1979) use scanning radiography). The samples were laid in brass frames, along with the calibration wedge, and placed on top of a sheet of photographic film inside a lead-lined cupboard. The X-ray source was at 2.5 m from the film, giving an even 'dosage' over the samples and film. The samples were placed so that the transverse face of the wood was exposed to the beam. Beam strength and exposure time were the standard ones used by Oxford Forestry Institute where the work was carried out. The film (Kodak Industrex CX Readypack) was developed in DX80 developer for four minutes at a temperature of 68° F, washed once, stopped and fixed for 10 - 15 minutes.

DENSITOMETRY. The X-ray films were analysed on a Joyce Loebl Mark IIICS microdensitometer. The densitometer tracked the films along a straight line up the centre of each radial sample. Sample edges and ends were detected automatically from the large density difference between background film density and image. The slit through which the light beam passed was 50 um x 500 um; readings of the transmittance of this beam through the image of the samples were made at 'step' intervals of 200um. The calibration wedge was also tracked and adjusted readouts of optical density of the images were saved on computer files to be printed out as blocks of figures for each radius.

ANALYSIS OF DENSITY DATA. Positions of ring boundaries in samples are normally identified from adjacent extremes of high and low density figures in the densitometry readouts. This is satisfactory for softwood samples, but misleading patterns were common in the oak material due to the complex shape of the density trace (Figure 5.4). For example, the maximum density often occurs in the post-earlywood band of fibres, not at the ring boundary, and very low densities could occur part way across a ring if the beam passed through a large latewood vessel. Therefore all boundaries were confirmed by reference to the X-ray images (which were actual size) using the fact that five readings were equivalent to 1 mm length of sample.

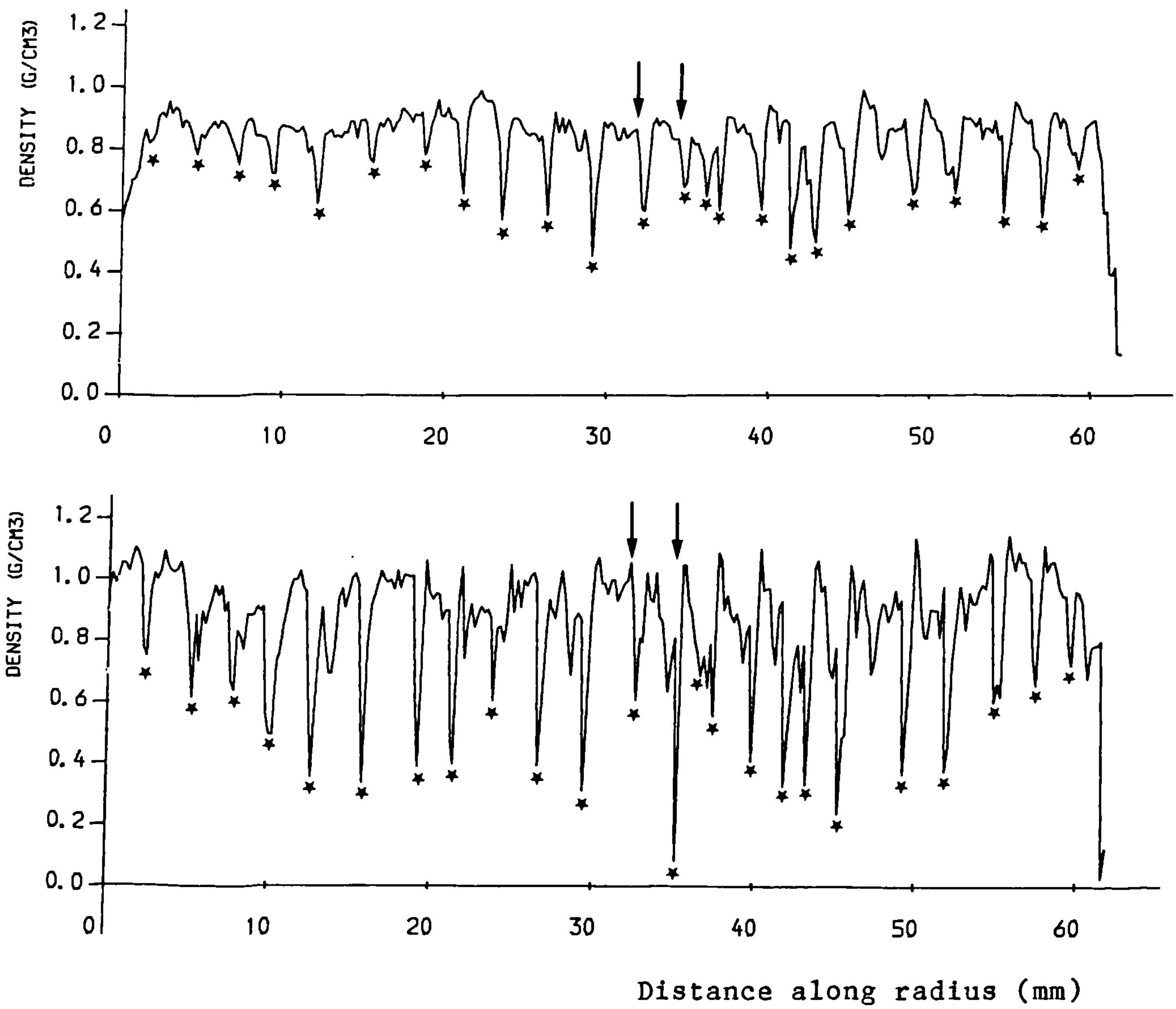


Figure 5.4. Examples of density traces of sessile oak (seed origin F) from densitometry of X-ray image.

Upper trace: wood 'viewed' through radial longitudinal face.

Lower trace: wood 'viewed' through transverse face.

Traces run from pith to bark (left to right). Arrows indicate boundaries of 1971 ring. Earlywood is characterised by low density followed by peak density of ring in post-earlywood band of libriform fibres.

* = annual ring boundaries

The regression of gravimetric on optical density of test samples gave an r^2 value of 84.6%. A maximum error of 0.05% is considered the limit for densitometry of most woods (information from 'X-raydens' program) but the complex structure of oak introduced many sources of error and the lower accuracy had to be accepted. For example, the fixed linear track of the densitometer viewing a transverse image of oak could result in a series of readings within a ring being taken along a wide ray or latewood vessel flame, giving a much higher or lower readout than the actual density averaged over the surrounding wood. Across a whole disc this is a less important effect because neither rays nor latewood flames are truly radial in orientation, but tend to be sinuous or angled.

The transverse section is the usual plane viewed in densitometry of other woods, but for oak the radial longitudinal section (RLS) would have been a better choice. It was found later that for the same test samples, the r^2 of the regression of physical density of the wood against optical density of the images viewed through RLS was 95.1%. The disadvantage of fixed-tracking by the densitometer described above would be avoided by analysis of radial sections, and the risk of 'flaring' of the beam through the lumina of large earlywood vessels would be reduced. For dendrochronological work where radial variations in density peaks must be recorded accurately, Fletcher and Hughes (1970) used RLS to avoid complications from rays, while Milsom (1979) analysed the TS because the orientation of the ring boundary and presence of rays caused alignment difficulties with the densitometer he used.

The program "X-raydens specification" written at the Oxford Forestry Institute used the densitometer output, the ring boundary positions and the details of the regression of gravimetric on optical density from the test-samples, to calculate ring width, ring area and wood density information for the main sample specimens. Rings were identified by year number.

The 'X-raydens' program calculated mean, minimum and maximum densities, weighted for ring area, separately for each ring of each radius per tree. Mean densities of the 1971 rings in the two radii per tree were later averaged to give a tree value for 1971 ring, which was used in analyses of variance of seed origins. 'X-raydens' also calculated a weighted mean disc density (weighted for ring areas) for each tree, using information from both radii.

The X-ray densitometry work was carried out at the Oxford Forestry Institute at the invitation of Mr F Hughes. Staff of the Wood Structure Section at the Institute carried out preparation of the samples (conditioning and milling), exposed and developed the X-ray films, and analysed the sub-samples for calculation of the relationship between gravimetric and optical density used in subsequent analyses.

5.3.2. KNIFE TEST OF SPLITTING STRENGTH.

Splitting strength parallel to the rays of oak wood in the 'fresh state' was tested. This was of interest in relation to the study of shake: it is possible that low natural splitting strengths could be an additional factor (with structural weaknesses caused by trauma or secondary weakening by pathogens) in the development of strains in the standing tree (combination of wood strength and growth stress) resulting in shake formation.

The knife test measured the force required to cause radial longitudinal splitting failure in small, clear specimens of oak. The force was compressive load.

PREPARATION OF MATERIAL. Sample blocks of oak for the knife-test were cut (using large and small band-saws) from half-logs from the Penyard trial, which had been stored from the fresh state under water (section 5.1.3) for 28 months after other samples had been removed. Tests were carried out on the saturated wood, being as near to the green condition as possible (lack of biodegradation had to be assumed, but the wood had been protected against this by addition of a biocide to the storage tanks).

Block dimensions were approximately 20 mm high (axially) and 25 mm square. Exact dimensions were measured to the nearest 0.1 mm for each specimen, using Vernier callipers. Straight grained samples, free from knots were chosen. Blocks were cut with the horizontal surfaces exactly perpendicular to the axial grain of the wood, and radial surfaces as parallel as possible to the rays. This latter requirement precluded use of wood close to the pith, where curvature of rings was noticeable within the block width; consequently, wood from the outer parts of the logs had to be used even though these contained some sapwood.

Only six of the seed origins (C, D, H, J, K and L) could be tested because insufficient material of the other origins remained.

TEST METHOD. The test machine was an Instron. A constant temperature of 20° C and relative humidity of 65% were maintained in the testing laboratory and the sample blocks were kept wet, but blotted before testing. A sample was placed under a blunt-edged 'knife' 30 mm long, which was orientated across the centre of the block, parallel to the rays. The load on the sample was increased slowly (0.08 mm/s) and a chart recorder traced the deformation of the block. From this trace, the force which caused the first sudden failure of the block was recorded. The radial longitudinal splitting strength of the block was calculated from the force causing the failure (F) and the total surface area (SA) of the plane of failure: $Nmm^{-2} = F/SA$.

5.4 STATISTICAL ANALYSES

Most of the statistical analyses were carried out on a Nimbus micro-computer, using a SNAP spreadsheet for data entry, and transferring data with SPAN for use with the SYSTAT package. Raw data were a single value of each variable per tree. Section 5.5 is a summary of the variables tested in the oaks from the eleven seed origins of the Penyard trial.

5.4.1. ANALYSES OF SEED ORIGIN INFLUENCES ON OAK WOOD STRUCTURE AND PROPERTIES.

ANALYSES OF VARIANCE. Normality of data distribution for each variable in each seed origin in turn, was assessed from a probability plot, before analyses of variance (ANOVAs) were carried out. The analysis of variance method used in the SYSTAT package was a one-way ANOVA which treated the experiment as a fully randomised design. The effects of seed origin were tested separately on wood structure and properties of twelve diameter-class II trees per origin.

Homogeneity of variances was tested with the Bartlett test before each ANOVA was run. This showed the variances of seed origin means for most of the variables measured to be homogeneous. The exception was axial parenchyma in the earlywood for which the test results could have been misleading because the data were not normally distributed and Bartlett's test is sensitive to this.

Tukey's HSD test (a critical and accurate multiple comparison test) was used to compare pairs of seed origin means following analysis of variance.

ANALYSIS OF VARIANCE OF EARLYWOOD VESSEL DATA. In order to take full advantage of the randomised block design of the Penyard experiment and apply a more precise test to the seed origins, a more complicated analysis of variance was required which would take account of the balanced incomplete nature of the blocks. This was done for the ring width and earlywood vessel data, which were stored on the VAX mainframe computer; the statistical package SPSS-X on the VAX could handle very large data files and be used to run complicated analyses to a stipulated design.

The designs of the analyses of variance investigating variation due to genetic type, used 'block', 'seed origin', and 'tree within seed origin by block' as independent variables. Missing values were given a code, and those trees with missing data were left out of calculations involving any variables for which data was missing. Adjusted means were calculated; these took into account the block effects (different for the different origins because of the incomplete design). Where the ANOVAs indicated significant differences between treatments, a modified version of Tukey's HSD test was applied to test the significance of the difference between pairs of adjusted means. This was a pairwise multiple comparison test; the method of calculating the effective error variance (everything below the square root sign) was taken from Cochran and Cox (1968) and takes account of the incomplete blocks:

$$D = Q_{.05}(k,df) \times \sqrt{RMS \times \left[1 + \frac{t - K}{t(K-1)} \right] \times \frac{2}{r}}$$

Two (adjusted) means were considered significantly different at $P < 0.050$ (the level chosen in tables of Q), if they differed by more than D.

The value of Q was taken from tables of the "Studentized Range Distribution" (Pearson, 1954) at the level of $P = 0.050$, with k = number of treatments and df = residual degrees of freedom (from ANOVA table). RMS = residual mean square, from

ANOVA table. Other figures in the equation are: number of seed origins (t = 11), number of blocks in which each seed origin appears (K = 6), number of trees in each seed origin (observations per treatment: r = 12). Thus:

$$D = Q_{.05}(11,38) \times \sqrt{RMS \times \left[1 + \frac{11 - 6}{11 (6 - 1)}\right] \times \frac{2}{12}}$$

The experiment design is equivalent to the Type V incomplete block design described by Cochran and Cox (1968). This uses Yate's method in which treatment means are adjusted for differences between the blocks, but no use is made of the inter-block information. In this design, t = b (b = block number = 11) and r = K (= 6); the two trees sampled per replication in the Penyard experiment make r = 12, but this is valid for the above procedure (Cochran and Cox, 1968).

It was found that for all earlywood vessel dimension data and for ring width of the 1971 ring, very little precision was gained by blocking in the experiment design (i.e. block effect was minor); this was indicated by the relative sizes of residual mean square and block mean square (Freese, 1980). It was then assumed that block effect was minor for all other parameters also, therefore these were tested only with the SYSTAT analyses of variance which treated the experiment design as though fully randomised. Little precision would have been lost by this method, and the procedure was far simpler than that using SPSS-X which necessitated lengthy re-coding of all data for analysis on the VAX computer.

ANALYSIS OF VARIANCE OF WOOD PROPERTY DATA. The statistical analyses of the X-ray densitometry data could be carried out only as though the experiment design was fully randomised because, by chance, blocks 5, 6 and 8 were not represented. Sample numbers for density variables were low in diameter class II of the seed origins in which wider sampling had been made (A, B, D and H) therefore these origins were represented by trees from both diameter class II and DC III.

For density and splitting strength data, sample numbers within seed origins varied (section 5.3.1), therefore the differences between means for these variables were tested using the t-ratio (rather than Tukey's test) following analysis of variance. The t-ratio was calculated using the standard error of difference:

$$SED = \sqrt{RMS \frac{1}{n} + \frac{1}{m}}$$

5.4.2. ANALYSES OF GROWTH RATE ASSOCIATIONS WITH VARIATIONS IN OAK WOOD STRUCTURE AND PROPERTIES.

Associations of growth rate with variations in wood structure and properties were studied by the intensive sampling within four of the seed origins: two sessile (B and D) and two pedunculate (A and H). Each replicate of each seed origin was divided into five equal diameter classes at harvest and two trees per diameter class sampled (i.e. ten per replicate). Thus sixty trees per seed origin with an even spread of diameters was sampled. Correlation co-efficients were calculated for:

a) diameter (dbh) - with heartwood percentage of ring number, heartwood percentage of diameter, sapwood width, sapwood ring number and wide ray proportions at mid ring (latewood zone 1) in 1971; and

b) 1971 ring width - with tissue proportions of the 1971 ring, and with earlywood vessel dimensions (tangential and radial diameters, size and shape).

The SYSTAT package was used to calculate Pearson correlations and the significance of each correlation was determined from the tables of correlation co-efficients at various levels of significance in Bailey (1964) and Freese (1980).

Initially, seed origins were kept separate for the analyses of growth rate association with wood structure and property variables. Earlywood vessel dimensions were an exception because being measured in diameter class II trees only, the sample numbers were too small for valid comparisons unless pooled; examination of the earlywood vessel data within seed origins showed that trends were the same in all four origins and that combining data was valid. The reasons for separate initial comparisons of most variables within individual seed origins were:

i) genetic differences between seed origins must control growth rate to some extent: significant diameter differences were found between the means of seed origins for trees of diameter class II in this study (diameter classes were relative to range in each seed origin replicate) and significant differences were found in growth rate of dominant trees in earlier assessments of the experiment (Evans, 1984).

ii) genetic differences influenced wood structure patterns (e.g. latewood flame shape) in a way which could have made the strength of the growth rate influence (if not its direction) differ between seed origins.

Correlations were then calculated using the combined data from all seed origins. Individual seed origin results are presented in Appendix 5.4; results from combined data are shown in Tables 5.3 and 5.4.

Data from the four seed origins were combined in order to calculate regressions of earlywood radial and tangential diameters on ring width, and sapwood width and ring number on tree diameter. There were too few trees per seed origin to analyse seed origins separately for earlywood vessels (which were studied in diameter class II trees only), but initial examination of the data within seed origins suggested that trends were the same in all four origins.

It should be borne in mind that within a seed origin also, genetic differences may have caused the observed differences in growth rate. Environment (site and spacing) of the Penyard plots was equal for all trees, yet large diameter ranges existed which were probably not entirely due to extrinsic controls. Genetic trials of wood structure have frequently shown that variation between trees is as great or greater than that between seed origins (Krahl-Urban, 1959; Polge, 1984).

5.5. SUMMARY OF WOOD STRUCTURE CHARACTERISTICS AND WOOD PROPERTIES ANALYSED IN OAKS FROM PENYARD SEED ORIGIN TRIAL.

Wood structure and properties of sessile and pedunculate oaks were studied. Eleven seed origins from a replicated trial were analysed. All samples were from one level in the tree (0.5 m above ground).

I. Influence of seed origin on the following characteristics was assessed in twelve dominant trees per seed origin:

1- diameter at breast height

2- heartwood and sapwood proportions

3- ring width of 1971 ring

4- proportions (by area in T.S.) of vessels, fibres, rays and axial parenchyma in three zones of the 1971 ring

Influence of seed origin on the following characteristics was assessed in twelve dominant trees per seed origin:

5- diameters, area and shape of earlywood vessels of the 1971 ring

6- density of 1971 ring

7- mean density of disc at 0.5 m

8- splitting strength of the wood

II. Association of growth rate with wood structure and properties within seed origins was investigated using four of the seed origins (two sessile and two pedunculate). Sixty trees per seed origin, representing an even spread across the range of diameters, were analysed. Correlations were calculated:

1- between diameter (bh) and heartwood, sapwood and wide ray proportions

2- between 1971 ring width and tissue proportions and earlywood vessel dimensions in the 1971 ring

5.6. RESULTS

PRESENTATION OF RESULTS:

All wood structure and property variables are summarised in a table of means per seed origin showing the significances of the analyses of variance, and noting which seed origins differ significantly from one another at the 5% level (normal type) and the 1% level (bold type) (Table 5.2a-h). This table also shows ranks of seed origin means; these are ranks of value only (1 = highest, 11 = lowest) and do not imply merit or quality. Notes to the table are in part 5.2.h.

Appendix 5.1 lists means and standard deviations of all variables measured. Appendix 5.2 lists analyses of variance of differences between seed origins for each variable.

Tissue proportions in each of the three zones of the 1971 ring are illustrated with pie charts (Figure 5.5).

Plates 5.2 and 5.3 illustrate wood structure patterns typical in the 1971 ring of two of the pedunculate seed origins, A and G. Plates 5.4 and 5.5 illustrate wood structure patterns typical in two of the sessile seed origins, C and D; seed origin D had sessile leaf characters, but the wood structure frequently differed from that of other origins of both species.

Associations of growth rate and wood structure and properties are summarised in Tables 5.3 and 5.4, and in Appendix 5.4.

SEED ORIGIN	SPECIES	TREE DIAMETER (cm) $\bar{x}$	origins differ	rk	HEARTWOOD (% of rings) $\bar{x}$	origins differ	rk	HEARTWOOD (% of diam.) $\bar{x}$	origins differ	rk
A	pedunc.	13.2		7	41.1	**H**	11	56.8		7
H	pedunc.	13.8		4	61.5	**A K C B J F G L**	1	46.7	**D L**	11
G	pedunc.	14.1	L	2	45.8	**H**	5	57.2		6
K	pedunc.	12.2	**D**	10	42.9	**H**	10	58.4		4
L	sess/ped	12.1	**D** G	11	47.6	H	4	62.0	H	2
J	sessile	12.5	**D**	9	45.3	**H**	6=	55.8		8
B	sessile	14.0		3	45.4	**H**	6=	59.1		3
E	sessile	12.8	**D**	8	51.0		2=	57.6		5
C	sessile	13.4		6	43.9	**H**	9	53.0		10
D	sessile	15.1	**L K J E**	1	50.7		2=	63.4	**H**	1
F	sessile	13.6		5	44.8	**H**	6=	54.7		9
Sig. of F		***			***			*		
Critical range		1.9			12.5			14.3		

Table 5.2.a. Differences between oak seed origin means for tree diameter and wood structure variables.

Pairs of origins which differ significantly at $P < 0.050$ are indicated in normal type; those which differ at $P < 0.010$ are in bold type. **Full notes to table are in part 5.2.h below.**

SEED ORIGIN	SPECIES	NUMBER OF SAPWOOD RINGS			SAPWOOD WIDTH (mm)			WIDTH OF 1971 RING (mm)		
		$\bar{x}$	origins differ	rk	$\bar{x}$	origins differ	rk	$\bar{x}$	origins differ	rk
A	pedunc.	13.7		2	25.3		6	2.4		11
H	pedunc.	12.8		7=	22.3	C F	9	2.8		10
G	pedunc.	13.2		4=	26.6	L	3	3.2		5
K	pedunc.	13.9		1	21.2	**C** F	10	3.0		8
L	sess/ped	12.7		9	20.4	**C F** G B E	11	3.3		3
J	sessile	12.8		7=	24.3		7=	3.4		1
B	sessile	13.2		4=	26.1	L	4	3.5		2
E	sessile	11.2		11	25.9	L	5	3.1		6
C	sessile	13.1		6	28.9	**L K** H	1	3.0		7
D	sessile	12.2		10	24.3		7=	3.2		4
F	sessile	13.4		3	28.3	**L** K H	2	2.8		9
Sig. of F		ns			***			ns		
SED					2.64 (df = 22)					

Table 5.2.b. Differences between oak seed origin means for wood structure variables.

SEED ORIGIN	SPECIES	LWZ1 WIDE RAY %			LWZ1 VESSEL %			LWZ2 WIDE RAY %		
		$\overline{x}$	origins differ	rk	$\overline{x}$	origins differ	rk	$\overline{x}$	origins differ	rk
A	pedunc.	6.5		3	11.0	B J	1	7.1		4
H	pedunc.	6.4		4=	7.6		3	8.0		2
G	pedunc.	8.1	K E D	1	7.4		4	9.0	K	1
K	pedunc.	4.3	G	11	6.6		5	5.2	G	11
L	sess/ped	5.6		6	6.5		6	6.6		6
J	sessile	4.8		8	5.5	A	10	5.6		9
B	sessile	6.9		2	4.6	A	11	7.8		3
E	sessile	4.5	G	10	7.7		2	5.8		8
C	sessile	6.4		4=	6.0		9	6.7		5
D	sessile	4.6	G	9	6.3		7	5.5		10
F	sessile	5.3		7	6.2		8	6.2		7
Sig. of F		**			*			**		
Critical range		3.4			5.2			3.5		

Table 5.2.c. Significant differences between oak seed origin means of tissue proportions in 1971 ring.

SEED ORIGIN	SPECIES	LWZ2 VESSEL % $\overline{x}$	origins differ	rk	EW WIDE RAY % $\overline{x}$	origins differ	rk	EW FIBRE % $\overline{x}$	origins differ	rk
A	pedunc.	11.4	**E** C	2	7.1		4=	27.4		10
H	pedunc.	9.7		3	7.8		3	32.3		6
G	pedunc.	12.1	**E C** B	1	9.8	**K E D** J	1	28.9		9
K	pedunc.	8.8		6	5.1	**G**	11	31.3		7
L	sess/ped	9.1		5	7.1		4=	36.3	J	1
J	sessile	7.2		8	5.7	G	8	24.7	L B	11
B	sessile	6.8	G	9	8.0		2	35.4	J	2
E	sessile	4.6	**G A**	11	5.4	**G**	9=	33.4		4
C	sessile	5.9	**G** A	10	7.0		6	33.2		5
D	sessile	8.7		7	5.4	**G**	9=	29.6		8
F	sessile	9.6		4	6.2		7	34.2		3
Sig. of F		***			***			**		
Critical range		5.2			3.6			10.2		

Table 5.2.d. Significant differences between oak seed origin means of tissue proportions in 1971 ring.

SEED ORIGIN	SPECIES	EARLYWOOD VESSEL %			EW VESSEL FREQUENCY (n/cm)			EW VESSEL AREA (um²)		
		$\overline{x}$	origins differ	rk	$\overline{x}$	origins differ	rk	$\overline{x}$	origins differ	rk
A	pedunc.	49.3		3	19.7	G F	9	35823		7
H	pedunc.	46.2		6	20.5	G	6	36127		5
G	pedunc.	46.7		5	23.8	B K A D L H	1	36347		4
K	pedunc.	47.4		4	19.6	G F	10	40108		2
L	sess/ped	41.4		10	20.3	G	7	34016		9
J	sessile	50.4		1	22.4	B	4	36842		3
B	sessile	40.2		11	19.1	G F E J	11	35805		8
E	sessile	44.6		8	22.6	B	3	32944		10
C	sessile	43.9		9	21.6		5	36084		6
D	sessile	49.4		2	20.0	G F	8	42889		1
F	sessile	45.5		7	23.2	B K A D	2	31002		11
Sig. of F		ns			*			*		
SED/Critical range:					SED 1.46 (df = 22)			12007		

Table 5.2.e. Differences between oak seed origin means of earlywood vessel characteristics in 1971 ring.

SEED ORIGIN	SPECIES	EWV TANGENTIAL DIAMETER (um) $\bar{x}$	origins differ	rk	EWV RADIAL DIAMETER (um) $\bar{x}$	origins differ	rk	EWV SHAPE (R:T diam.) $\bar{x}$	origins differ	rk
A	pedunc.	195		4	226		7=	1.18	F	9=
H	pedunc.	201	F	2	222		10	1.12	F K L	11
G	pedunc.	186		8=	239		3	1.30		4
K	pedunc.	192		7	255		1	1.35	H	2
L	sess/ped	180		10	233		4=	1.32	H	3
J	sessile	196		3	233		4=	1.20		7=
B	sessile	195		5	227		7=	1.18	F	9=
E	sessile	186		8=	220		11	1.20		7=
C	sessile	194		6	231		6	1.22		6
D	sessile	209	F	1	254		2	1.23		5
F	sessile	168	D H	11	226		7=	1.38	H B A	1
Sig. of F		***			ns			***		
Critical range		29.5						0.21		

Table 5.2.f. Significant differences between seed origin means of earlywood vessel dimensions (1971 ring)

SEED ORIGIN	SPECIES	DENSITY OF 1971 RING (g/cm³) $\overline{x}$	origins differ	rk	MEAN DISC DENSITY (g/cm³) $\overline{x}$	origins differ	rk	SPLITTING STRENGTH (N/mm²) $\overline{x}$	origins differ	rk
A	pedunc.	0.753	B **J** C F E	11	0.745	**C** B F **E** J	11	-		
H	pedunc.	0.822		6	0.813	C	6	9.80		3
G	pedunc.	0.786	**B J** C	9	0.771	**C B F** E	10	-		
K	pedunc.	0.785	**B J** C F E	10	0.780	**C** B F E	9	10.00		2
L	sess/ped	0.802	B J	7	0.790	**C** B F	8	9.32		5
J	sessile	0.878	**A K G** D L	2	0.816	A C	5	10.28		1
B	sessile	0.895	A **K G** D L	1	0.868	A **G** K L	2	-		
E	sessile	0.850	A K	5	0.832	**A** G K	4	8.60		6
C	sessile	0.876	A K G	3	0.886	**A G K L** D H J	1	9.50		4
D	sessile	0.795	B J	8	0.796	C	7	-		
F	sessile	0.853	A K	4	0.847	A **G** K L	3	7.50		7
Sig. of F		***			***			ns		

SED varied depending on sample sizes (and therefore degrees of freedom) in each pair of origins.
0.040 - 0.025 (df = 6 - 18)   0.034 - 0.022 (df = 6 - 18).

Table 5.2.g. Differences between seed origin means of oak wood properties.

NOTES: Seed origins are listed on each page in increasing order of leaf character index: origins with most pedunculate characters at top, to most sessile at bottom (indexes given in section 5.1.1, Table 5.1).

Differences between seed origins of oak (trees of diameter class II) from the Penyard experiment were tested for each variable by analysis of variance. ANOVA designs are described in section 5.4. Significance of F from the analyses of variance is symbolised as follows:
*** = $P < 0.001$; ** = $P < 0.010$; * = $P < 0.050$; + = $P < 0.100$; ns = not significant.

Analyses of variance of diameter, heart- and sapwood and tissue proportions were followed by Tukey's HSD test: critical ranges are given for differences between pairs of seed origins significant at $P < 0.050$.

Analyses of variance for ring width and earlywood vessel dimensions (but not frequency) were followed by a modified version of Tukey's HSD test (described in section 5.4). Critical ranges are given for differences between pairs of seed origins significant at $P < 0.050$.

Analyses of variance for all other variables were followed by t-ratio tests of differences between pairs of means. Calculations of standard error of difference (SED - significant at $P < 0.050$) are described in section 5.4. SEDs quoted in this table are for the majority of seed origins; SEDs were slightly different for a minority of origins in some variables, where data were missing for one or both origins of a pair and degrees of freedom were reduced.

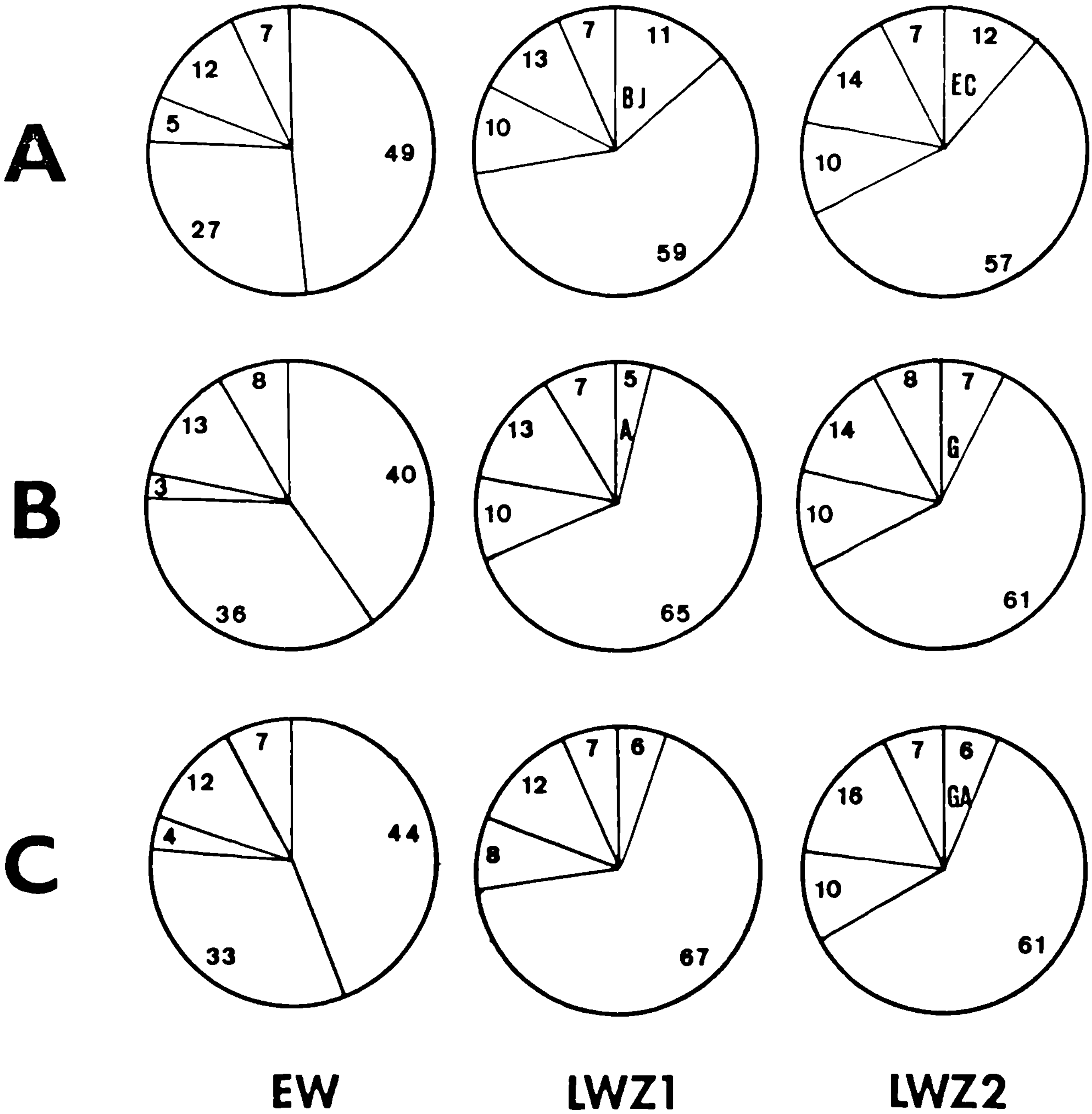
Seed origins which differ significantly from one another at $P < 0.050$ are indicated in the tables in normal type, those which differ at $P < 0.010$ are in bold type: the lists of seed origin codes ('origins differ' column) are in decreasing size of difference from the origin being compared.

Ranks of means (rk) are made with highest value = 1 and lowest value = 11; no implication of quality is included.

OTHER VARIABLES TESTED.

The differences between the means of seed origins for the following variables were also tested by analyses of variance, but no significant differences were found: percentages of fibre, narrow ray, total ray and axial parenchyma in latewood zone 1; percentages of fibre, narrow ray, total ray and axial parenchyma in latewood zone 2; percentages of vessel, narrow ray, total ray and parenchyma in earlywood.

Table 5.2.h. Notes to the Table 5.2. sections a - g, and summary of other variables tested.



Reading clockwise from the top of each pie:
V = vessel
F = fibre
AP = axial parenchyma
NR = narrow ray
WR = wide ray

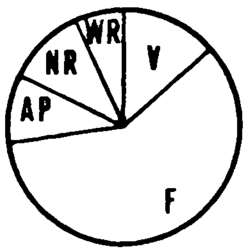
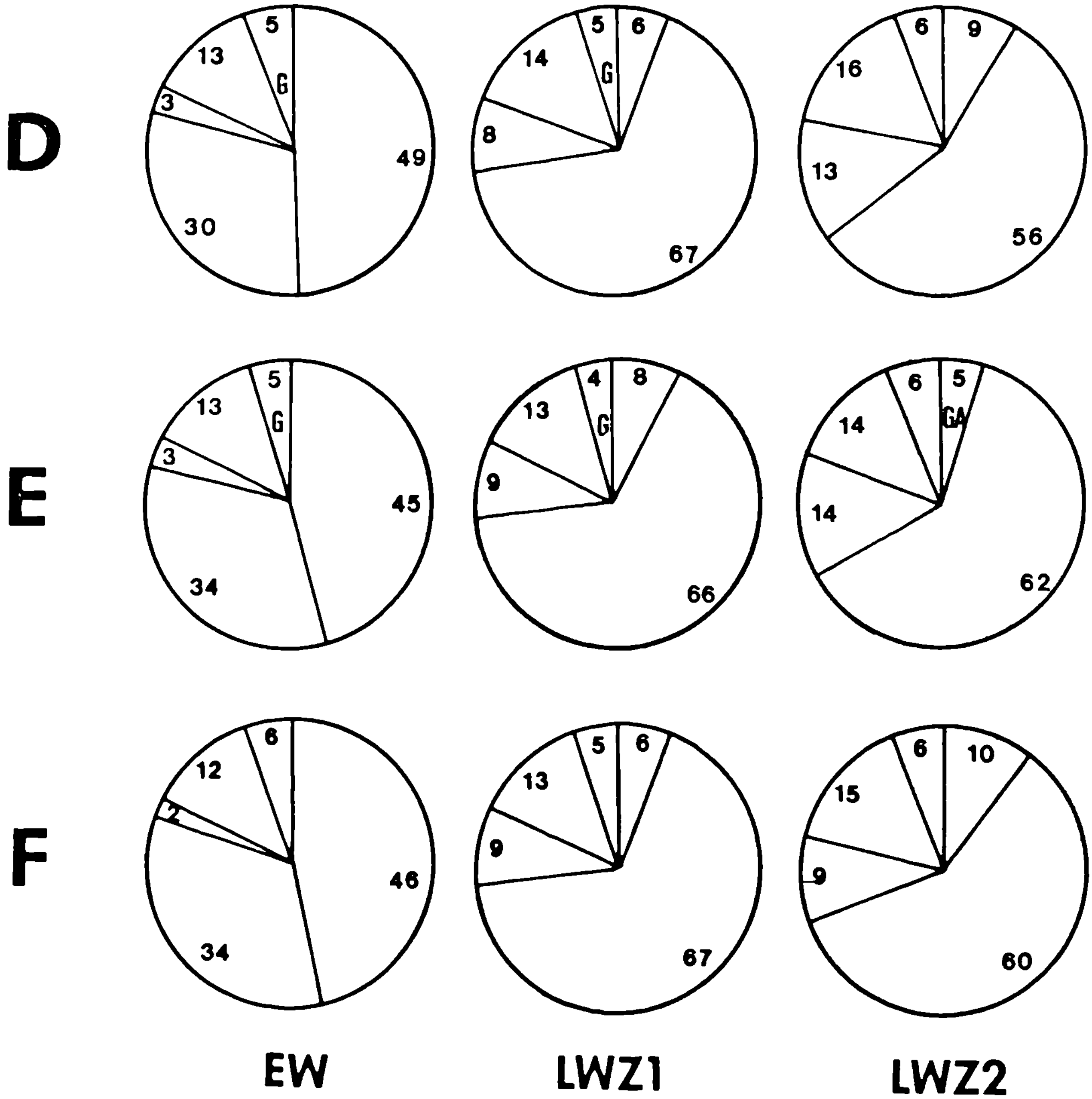


Figure 5.5. Tissue proportions in oaks from the Penyard seed origin trial. Continued overleaf; notes on p.263.

Cell types measured in earlywood and two latewood zones.



Reading clockwise from the top of each pie:
V = vessel
F = fibre
AP = axial parenchyma
NR = narrow ray
WR = wide ray

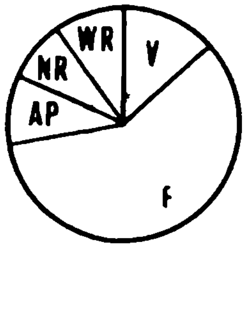
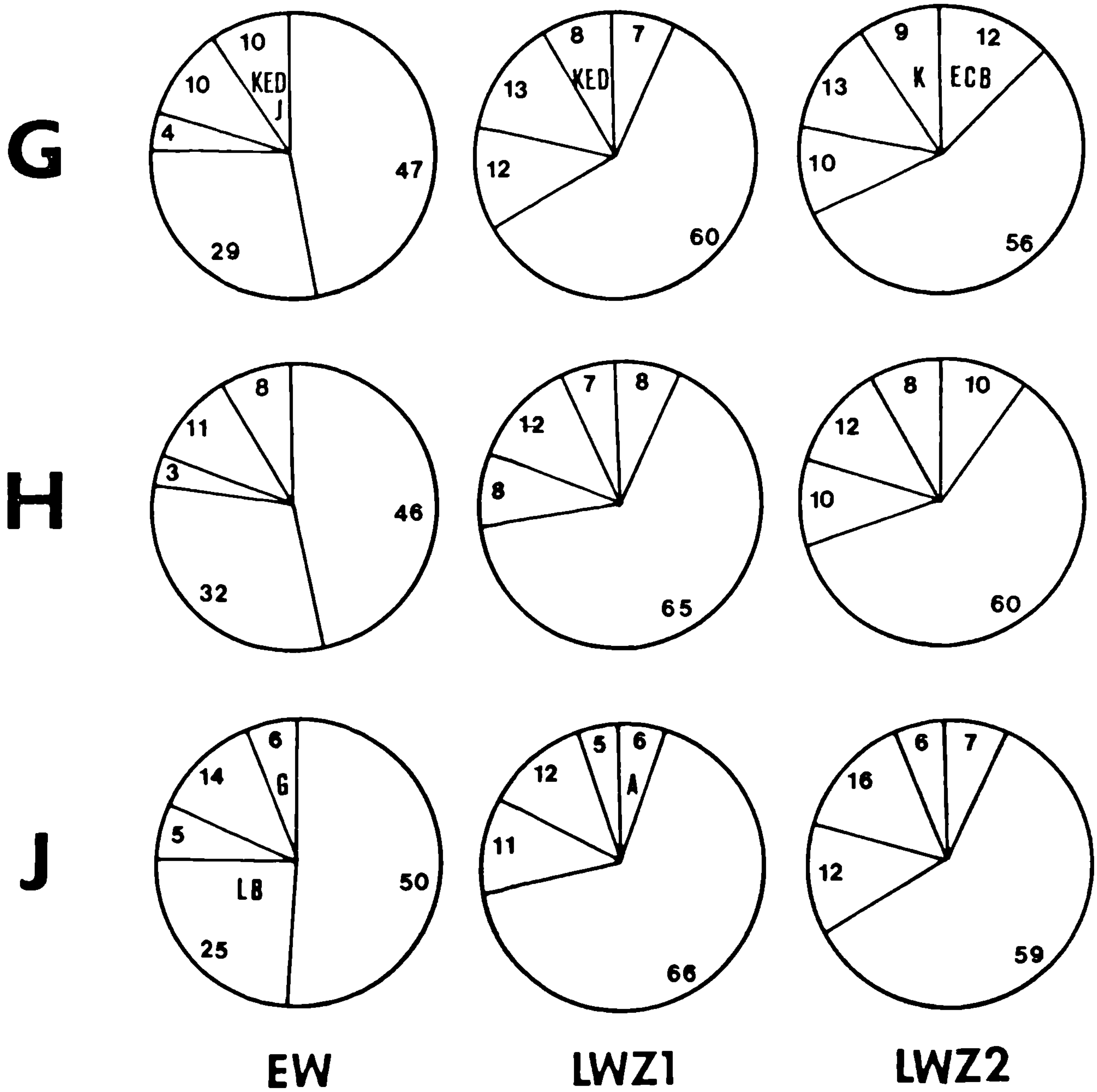


Figure 5.5. Tissue proportions in oaks from the Penyard seed origin trial. Continued overleaf; notes on p.263.

Cell types measured in earlywood and two latewood zones.



Reading clockwise from the top of each pie:
V = vessel
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WR = wide ray

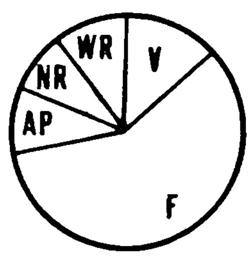

Figure 5.5. Tissue proportions in oaks from the Penyard seed origin trial. Continued overleaf; notes on p.263.

Cell types measured in earlywood and two latewood zones.

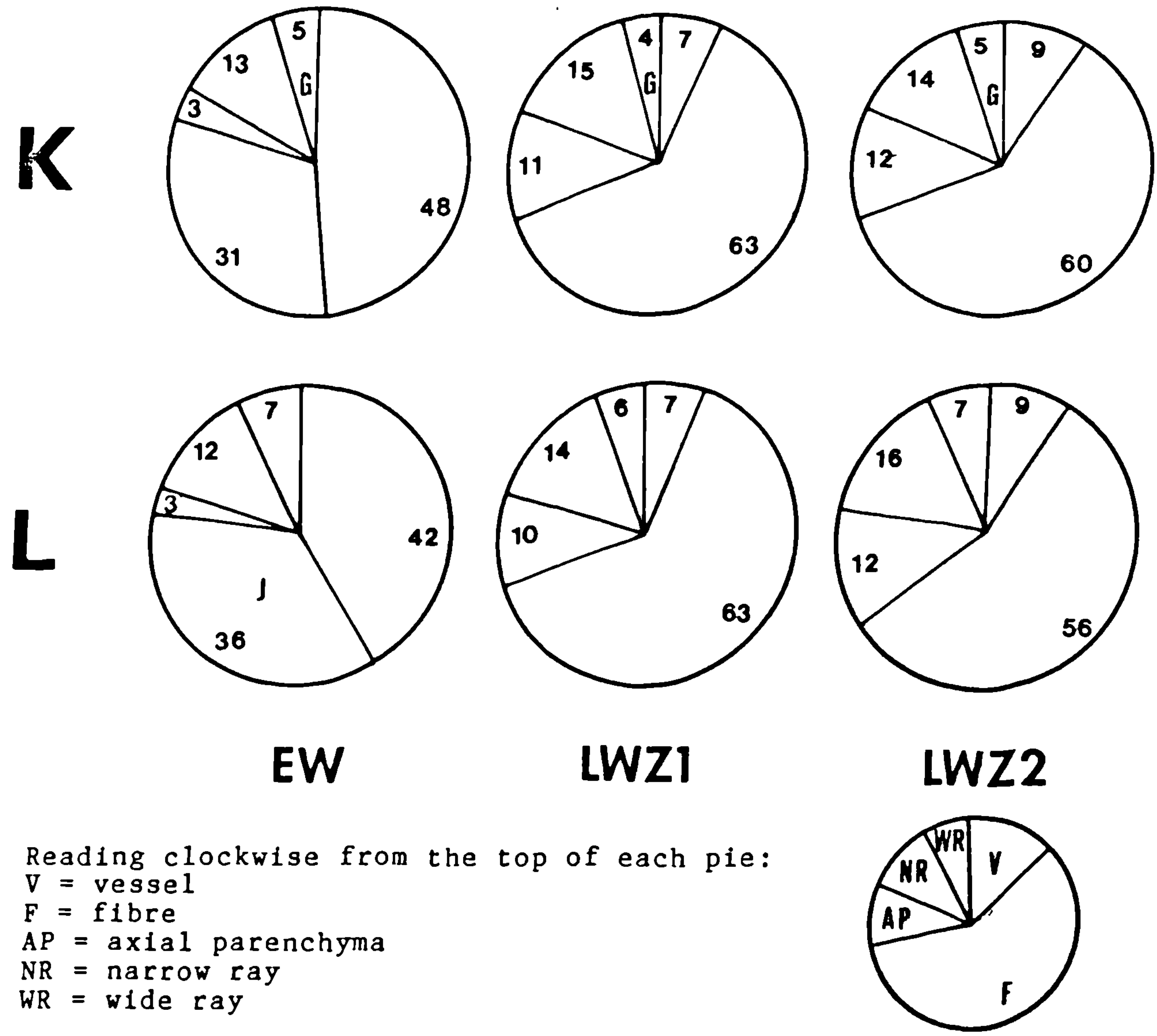

Figure 5.5. Tissue proportions in oaks from the Penyard seed origin trial.

EW = earlywood. LWZ1 = latewood zone 1. LWZ2 = latewood zone 2.

Pie sectors are mean percentages of cell types, measured in each of three zones of the 1971 ring at 0.5 m above ground.

Seed origins are identified by their code letters on the left of each row.

Seed origins which differ significantly from one another (Tukey HSD test at $P < 0.050$) are indicated by code letters in pie sectors.

TISSUE PROPORTIONS (%) AND CELL SIZES	ZONES IN WHICH TISSUE PROPORTIONS MEASURED: EARLYWOOD	LATEWOOD ZONE 1	LATEWOOD ZONE 2
	Co-efficient of correlation with ring width		
WIDE RAY	** 0.221	** 0.217	** 0.233
NARROW RAY	*** 0.291	*** 0.379	*** 0.338
TOTAL RAY	*** 0.392	*** 0.395	*** 0.415
VESSELS	0.131	0.102	** -0.191
FIBRES	*** -0.288	** -0.259	* -0.160
AXIAL PARENCHYMA	** -0.186	-0.129	0.007
EARLYWOOD VESSEL SIZE	* 0.313		
EARLYWOOD VESSEL SHAPE	*** 0.530		
RADIAL DIAMETER OF EWVs	** 0.441		
TANGENTIAL DIAMETER OF EWVs	0.060		

Table 5.3. Associations between growth rate (ring width) of oak, and tissue proportions and cell sizes.

Measured in 1971 ring of trees from seed origins A, B, D and H
Tissue proportions: n = 229 (significance of correlations based on df = 200). Earlywood vessel dimensions: n = 44.

WOOD STRUCTURE VARIABLES	CO-EFFICIENT OF CORRELATION WITH TREE DIAMETER
LATEWOOD ZONE 1 WIDE RAY	*** 0.360
HEARTWOOD PROPORTION (% of ring number)	*** 0.513
HEARTWOOD PROPORTION (% of disc diameter)	*** 0.502
SAPWOOD WIDTH	*** 0.257
SAPWOOD RING NUMBER	*** -0.383

Table 5.4. Associations between growth rate (dbh at 30 years) and wood structure in oaks.

Measured in trees from seed origins A, B, D and H. Heartwood and ray proportion: n = 229 (significance of correlations based on df = 200). Sapwood: n = 240.

5.7. DISCUSSION OF RESULTS OF WOOD STRUCTURE AND PROPERTIES ANALYSIS IN OAKS FROM THE PENYARD EXPERIMENT.

5.7.1. INFLUENCE OF SEED ORIGIN ON WOOD STRUCTURE AND PROPERTIES.

5.7.1.1. INFLUENCE OF SEED ORIGIN ON TREE DIAMETER.

Table 5.2.a.

The mean diameter at breast height (dbh) of trees from diameter class II (dominant but not wolf trees) in each seed origin, ranged from 12.1 - 15.1 cm. This range was a consequence of diameter class allocation at harvest being relative to the trees within each seed origin replicate. The rank of mean diameters was similar to that recorded in assessments of the experiment made in 1980, in which the six largest diameter trees per replicate were measured (Evans, 1984).

Seed origin had a strong influence on diameter of oaks in the Penyard experiment, this was mostly due to the significantly larger diameter (at $P < 0.01$) of origin D compared to the three Scandinavian origins, and to D's plus-tree E. Variation in diameter growth did not seem to be species related, the pedunculate origins were evenly distributed through the ranks of means of dbh.

5.7.1.2. INFLUENCE OF SEED ORIGIN ON HEARTWOOD AND SAPWOOD.

Table 5.2.a & b.

Heartwood proportion as a percentage of ring number in seed origin H was significantly greater than in seven other origins (difference significant at $P < 0.01$ for all noted in Table 5.2 except L which was significant at $P < 0.05$). However, when heartwood proportion was measured as a percentage of distance across the disc diameter, then H was significantly different from D only. Ranks of means suggested no association of heartwood proportion with species (sessile or pedunculate).

There was no significant difference between seed origins in the number of sapwood rings; but the sapwood width was significantly different between several seed origins (significant at $P < 0.01$ for differences of C from K and L and of F from L; significant at $P < 0.05$ for other pairs). The relative constancy of numbers of sapwood rings in oak is a factor relied upon by dendrochronologists; Baillie (1973) quotes a figure of 32 +/- 9 rings, which is much greater than the numbers recorded in the Penyard oaks, as was the range of 18 - 22 sapwood rings measured in mature oaks by Deret-Varcin (1983), but this may be because the Penyard trees were not fully mature. Hollstein (1970, quoted in Trenard, 1982) gave a list of different sapwood ring numbers for oak, depending on tree age. In trees 50 - 100 years old, the number of rings of sapwood was 16 +/- 4 years, whereas in trees over 200 years old the number was 26 +/- 7.

Ranks of seed origin means of sapwood proportions did not appear to be influenced strongly by species (sessile or pedunculate oak), though the three lowest mean widths were all from pedunculate types. Deret-Varcin (1983) found a more distinct species influence: sapwood thickness of sessile oak was highly significantly greater than that of pedunculate oak from the same site in N France (the number of sapwood rings was also greater in sessile oaks).

Associations between seed origins, growth rates (section 5.7.2) and heart/sapwood proportions were complex. Consequently, ranks of means for these characters sometimes appeared to be contradictory. For example, origin A, (low mean height growth in the 1980 assessments (Evans, 1984)) had the smallest ring number at 0.5 m and thus gave a low result for heart wood expressed as percentage of total rings, even though its percentage of disc diameter was not low.

Anomalous patterns in the sapwood and heartwood proportions of seed origin H were a consequence of the fact that the trees of this origin were two years older than other stock when planted, but were checked for many years so that by 1980 H ranked only in the middle of the means of height growth; this affected total ring number at 0.5 m, thus heartwood as a percentage of ring number.

5.7.1.3. INFLUENCE OF SEED ORIGIN ON 1971 RING WIDTH.

Table 5.2.b.

Analyses of variance of ring width (Appendix 5.2) showed variation in ring width between seed origins to be greater than that between trees within origins and much greater than that due to block effect.

However, there were no significant differences between seed origins in the width of the 1971 ring.

The lowest mean 1971 ring width was in a pedunculate seed origin (A), but other pedunculate origins (G, H, K) were scattered through the rank of means.

5.7.1.4. INFLUENCE OF SEED ORIGIN ON TISSUE PROPORTIONS.

INFLUENCE OF SEED ORIGIN ON TISSUE PROPORTIONS IN EARLYWOOD.

Table 5.2.d & e; Figure 5.5.

EW WIDE RAY %. Seed origin G was significantly different from origins K, E, and D at $P < 0.01$, and from J at $P < 0.05$. No clear association with species was apparent from the ranks of means.

EW FIBRE. Seed origin J differed significantly from L and B. The ranks of means show the four pedunculate types plus D and J to have the lowest fibre proportions for this zone. This is a reciprocal pattern of ranks to that for earlywood vessel proportion.

OTHER CELL TYPES. There were no significant differences between seed origin means of vessel, narrow ray, total ray or axial parenchyma proportions in the EW.

INFLUENCE OF SEED ORIGIN ON TISSUE PROPORTIONS IN THE LATEWOOD ZONE 1.

Table 5.2.c; Figure 5.5.

LWZ1 WIDE RAY. Pedunculate origin G had a significantly greater proportion of wide ray in this zone than did origins K, E and D. This result was the same as that for wide ray in the earlywood, although in the earlywood the significance of the differences was greater and mean of G was greater than J also; this may have been because the high EW wide ray proportion in G was due to wider rather than more frequent rays, and noding in the earlywood exaggerated the difference. No association of species or of geographical origin with wide ray proportion was apparent in the ranks of means.

LWZ1 VESSEL. Seed origin A, having the highest percentage of LWZ1V, differed significantly from B at $P < 0.01$ and from J at $P < 0.05$. Although differences between other seed origins were not significant, pedunculate seed origins and the sessile origin E, ranked highest for vessel proportion in this zone.

OTHER CELL TYPES. There were no significant differences between seed origin means of fibres, narrow ray, total ray or axial parenchyma proportions in the latewood zone 1. However, pedunculate types A, G, and K had some of the lowest fibre proportions in this zone.

INFLUENCE OF SEED ORIGIN ON TISSUE PROPORTIONS IN LATEWOOD ZONE 2.

Table 5.2.c & d; Figure 5.5.

LWZ2 WIDE RAY. Pedunculate seed origins G and K differed significantly from one another. Ranks of means were similar to those for wide ray in the other two zones of the ring.

LWZ2 VESSEL. Vessel proportions in this zone were significantly greater ($P < 0.01$) in pedunculate origins G and A than in sessile origins C and E; G was also significantly greater ($P < 0.05$) than sessile origin B.

The greatest proportions of LWZ2 vessels were found in the pedunculate oak types, plus sessile origin F. The latewood pattern of A was a classic pedunculate pattern of wedge-shape latewood flames broadening continuously through the latewood and giving rise to the large LWZ2 vessel proportions (Plate 5.2). The high percentage of vessels in this zone in trees of origin G was due to branching of vessel flames and the large size of latewood vessels within the flames (Plate 5.3).

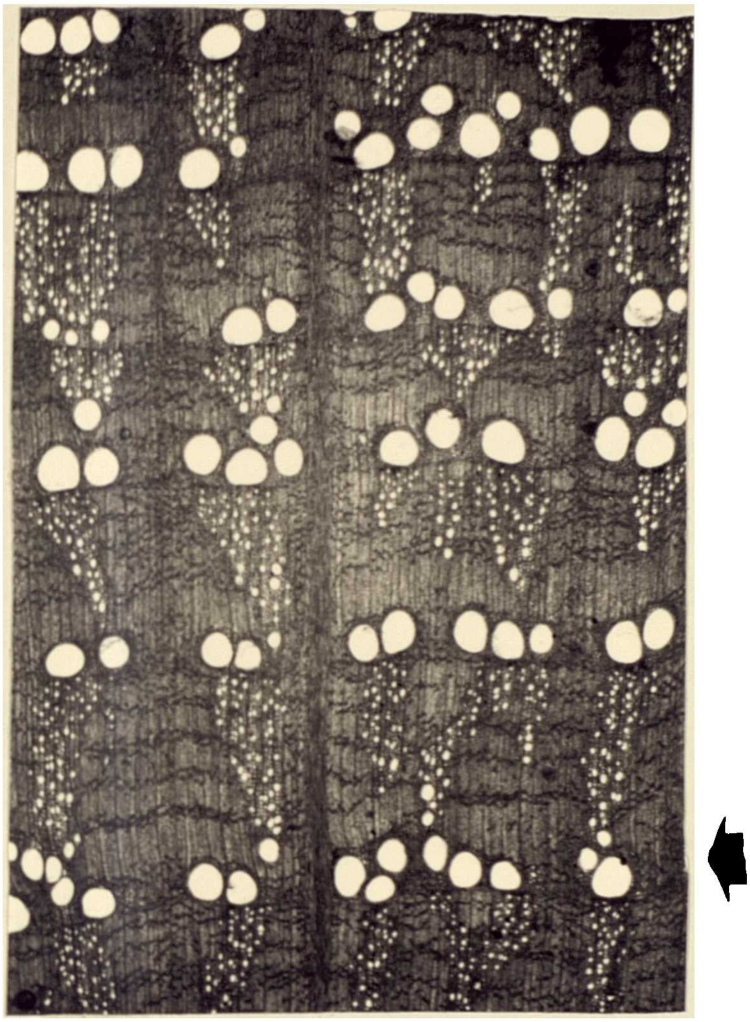

Plate 5.2. Unstained cross-section of 1971 ring of *Quercus robur* (pedunculate oak) typical of seed origin A. x 16.

Leaves of this seed origin were the most pedunculate in character of all eleven seed origins. T.S shows wedge-shaped latewood flames with high proportions of vasicentric tracheids. These, together with the single row of crowded or irregularly shaped earlywood vessels and the discrete bands of axial parenchyma in the latewood, make the wood structure pattern similar to the pedunculate type of Huber *et al.* (1941) figure 9, shown in Walker (1978).

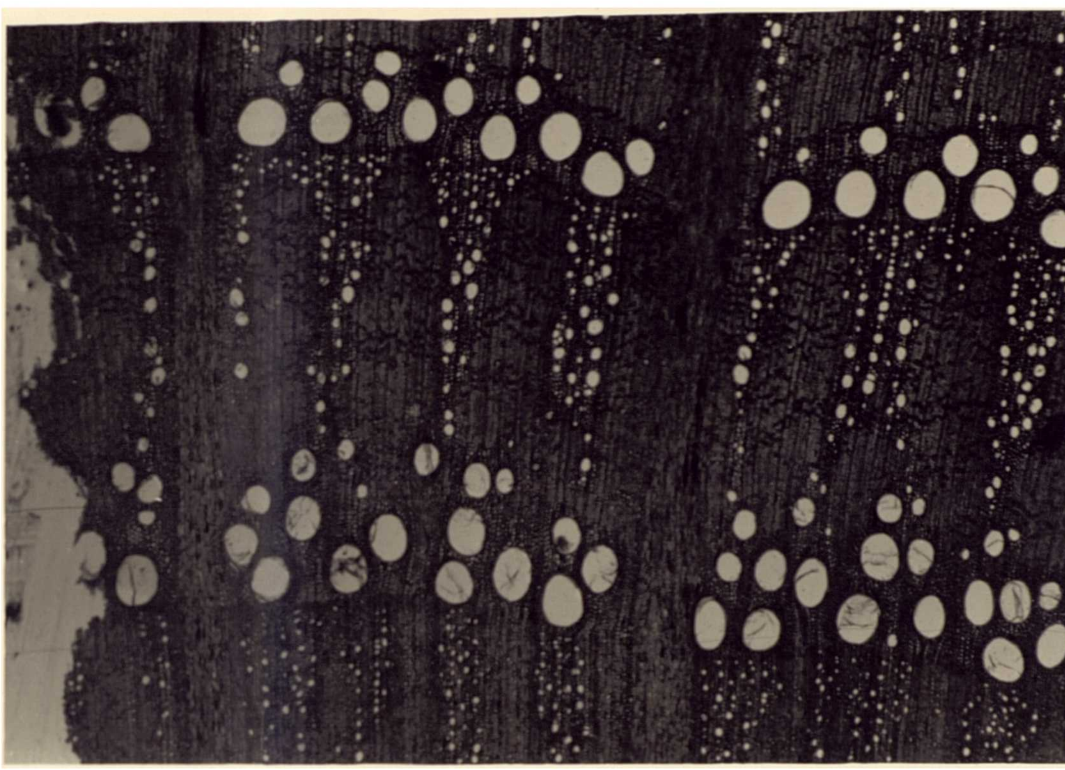

Plate 5.3. Unstained cross-section of 1971 ring of pedunculate oak typical of the majority of trees sampled from seed origin G. x 20.

Earlywood vessels are crowded and oval (as described for pedunculate oaks in Walker (1978)); latewood flames are wedge-shaped in zone-2 (were branched in several samples), and latewood vessels are large. The earlywood vessel and latewood flame patterns and more scattered axial parenchyma of this seed origin are similar to the pedunculate type in Figures 7 and 8 of Huber _et al._ shown in Walker (1978).

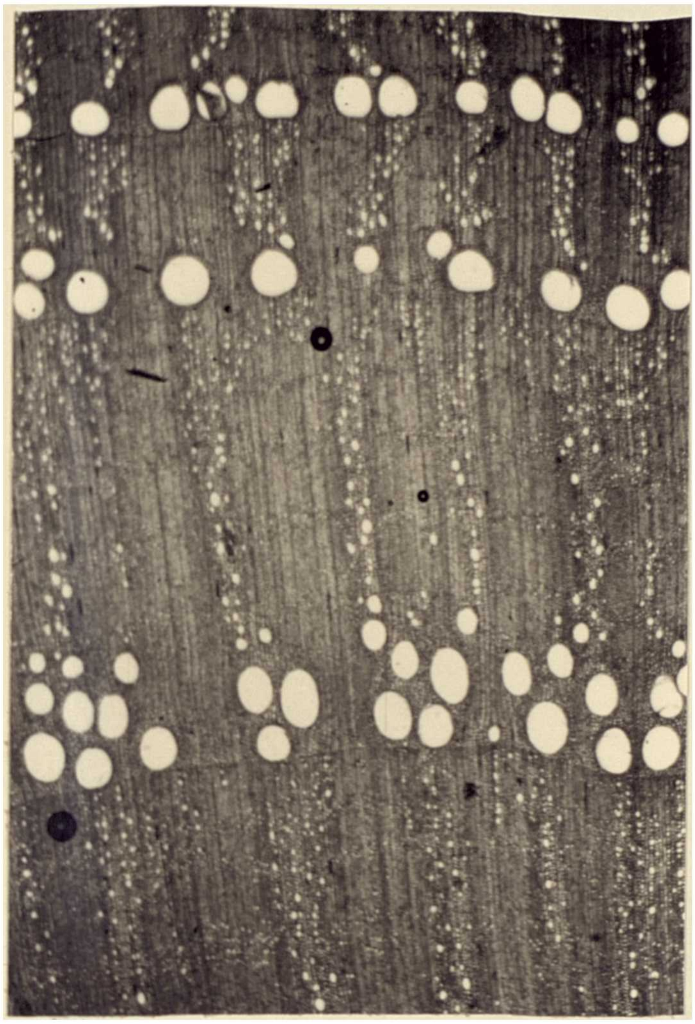

Plate 5.4. Unstained cross-section of 1971 ring of *Quercus petraea* (sessile oak) typical of seed origin D. x 16.

Earlywood vessels are large compared to the other ten seed origins; latewood flames are narrow with small vessels. The two upper rings in the section have markedly less oval earlywood vessels which were more usual in narrow rings in this seed origin; the tangential diameter was still large, even in narrower rings.

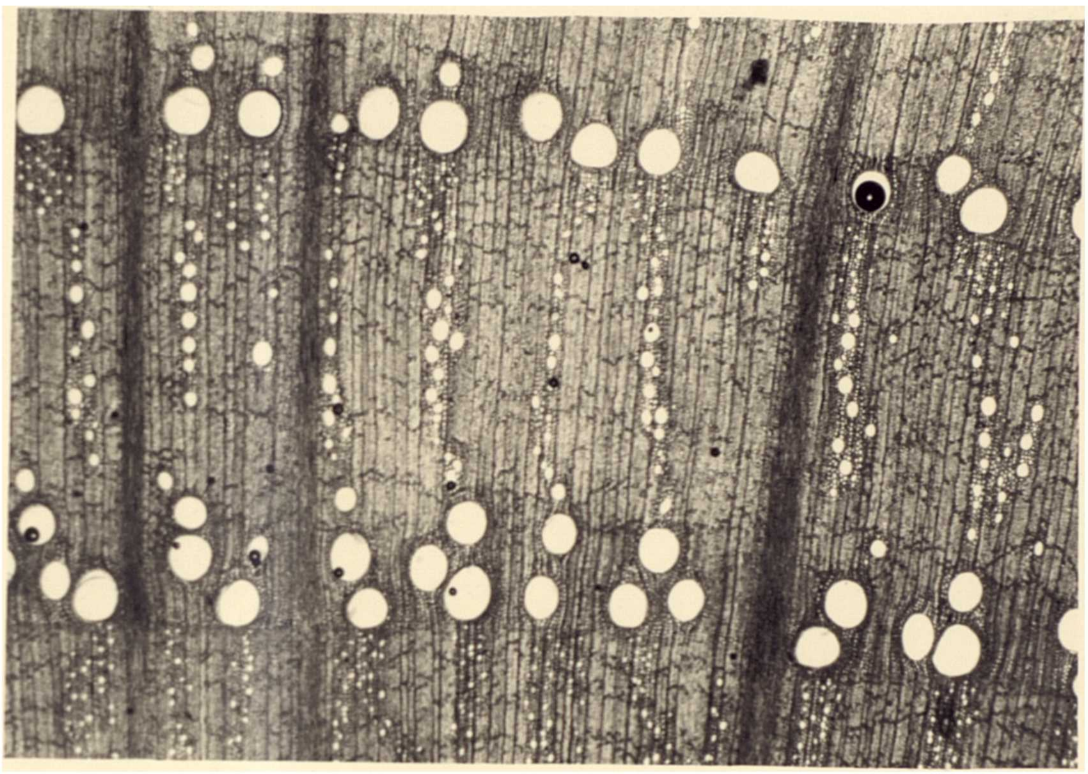

Plate 5.5. Unstained cross-section of the 1971 ring of sessile oak typical of seed origin C. x 20.

Earlywood vessels fit Walker's description of sessile oak vessels best of all the seed origins studied: they are well-spaced, and round in shape. There were two earlywood vessel rows in the 1971 ring of this tree, but one row was more usual in seed origin C (as in the upper (1972) ring).

The high vessel proportion in LWZ2 of F was a surprising result, as F was markedly sessile-like in its characteristics. Examination of the samples showed that although the latewood flames in origin F were narrow and strap-like, the zone-2 ends of the flames broadened slightly, the vessel numbers within the flames were high and the flames were frequent in occurrence across the tangent to the ring.

LWZ2 OTHER CELL TYPES. There were no significant differences between seed origin means of fibre, narrow ray or total ray proportion in this zone.

TISSUE PROPORTIONS IN THE PENYARD OAKS COMPARED TO RESULTS REPORTED BY OTHER AUTHORS.

Wide ray proportions ranged from 4 - 10%. It has been suggested by other authors (reported in section 2.2.2.2) and by this study (section 5.7.2) that wide ray proportions are influenced mainly by site index and by growth rate, effects which would have been minimised by the present comparisons of the same annual ring in trees on the same site.

Mean vessel percentages ranged from 40 - 50% in earlywood, 5 - 11% in latewood zone-1, and 5 - 12% in latewood zone-2. Maeglin (1974) summarises studies of oak in Europe and America and the wide ranges of vessel proportions reported; he quotes as the largest range, figures of of 22 - 85% for sessile oak reported by Pechmann and Aufsess (1973, reported in Maeglin, 1974). The range would be extended beyond that seen in the Penyard oaks, if rings of extreme width and narrowness were examined.

Fibre percentages over the three zones of the 1971 ring in the Penyard oaks ranged from 25 - 67%, similar to the range reported for sessile oak (20 - 60% in plantation grown trees) by Pechmann (1956) but greater than the 3 - 35% reported by Courtois _et al._ (1964) for both species. The differences in these results could be due largely to the inclusion of tracheids with fibres (as this study) or with vessels (as Courtois et al.) in analyses of tissue proportions. The importance of stating method of fibre and tracheid assessment, for comparability of results, is thus indicated.

Mean axial parenchyma percentage ranged from 3 - 14%, spanning the average of 10% reported by Courtois et al. for sessile and pedunculate oaks (also measured by cross-sectional area).

Mean narrow ray proportions ranged from 10 - 16% over the three zones of the 1971 ring in all seed origins; total ray ranged from 17 - 24%. Ranges of ray and axial parenchyma are small compared to those of vessels and fibres, a pattern observed in oak by Taylor and Wooten (1973) also. Taylor and Wooten also reported that variation of vessel and fibre percentages with height in oak was not significant; Hamilton (1961) found that specific gravity, tissue proportions and ray size of oak were not significantly affected by combined influences of height in tree and cambial age. Therefore it is reasonable to expect that the results reported from the Penyard study for tissue proportions measured at 0.5 m will be representative of most of the bole. However, Hamilton showed that 70% of variation recorded in earlywood vessel diameter was due to the combined influences of height in tree and cambial age; earlywood vessel dimension results should therefore be compared with other studies with care.

5.7.1.5. INFLUENCE OF SEED ORIGIN ON EARLYWOOD VESSEL CHARACTERISTICS AT 0.5 M ABOVE GROUND.

Table 5.2.e & f.

Multivariate analyses of earlywood characteristics (Appendix 5.2) showed the effect of seed origin to be greater than the effect of block, and much greater than the effect of tree within seed origin by block for earlywood vessel radial and tangential diameter, area and shape. Variation due to block and tree effects was not significant for any of these variables, but was particularly low for vessel shape.

EWV FREQUENCY. There were significant differences between the means of earlywood vessel frequency (number per centimetre along first EWV row), for several seed origin pairs: in particular, origins G (pedunculate) and F (sessile) had a high frequency of vessels, while K (pedunculate) and B (sessile) had a low frequency. The differences of G from B and from K were significant at $P < 0.01$.

Thus there was no association of vessel frequency with species. Walker (1978) described 'crowding' of vessels in pedunculate oak (Plate 5.3), and Deret-Varcin (1983) reported a higher vessel number per 5 mm tangent in pedunculate than sessile oak, but these two studies included the vessels of all earlywood vessel rows in a ring (which the authors therefore confirmed to be more numerous in pedunculate oak), whereas this study of the Penyard oaks assessed vessels of the first row from the ring boundary only.

Earlywood vessel frequency was plotted against vessel size for all seed origins and found to be un-related; calculations of seed origin means for vessel dimensions did not need to be weighted for vessel frequency therefore, even though all vessels per section width were sampled and sample numbers were consequently dependent on vessel frequency.

EWV RADIAL DIAMETER. There was no significant difference between seed origins in radial diameter of earlywood vessels. Neither the species, nor geographical origin seemed to influence the ranks of means. The range of diameters was fairly wide, but variation within seed origins was high; this was probably because the radial diameter was more strongly influenced by growth rate than by genotype (Section 5.7.2).

Courtois <u>et</u> <u>al.</u> (1964) found no significant difference between the radial diameters of sessile and pedunculate oak, but reported influences of ring width and cambial age on this characteristic.

EWV TANGENTIAL DIAMETER. The sessile origins D and F had the largest and smallest mean tangential diameters of earlywood vessels respectively; the means were significantly different at $P < 0.01$. Origin F also differed significantly from origin H. Ranks of means did not appear to be influenced by species or geographical region of seed origins.

EWV AREA. There were no significant differences in earlywood vessel area between means of any seed origins. Extremes of the range, not quite significantly different at $P < 0.05$ were D (large) and F (small); both are sessile origins and there was no grouping of species in the rank of origin means between these two.

Deret-Varcin (1983) studied oaks from the North of France and also found no significant difference in size (cross-sectional area measured by image-analysis) of individual vessels between sessile and pedunculate oaks.

EWV SHAPE. Mean vessel shapes in the 1971 ring (ratios of radial to tangential diameters) were all greater than 1.0 (i.e. slightly to markedly oval). The most oval vessels were in sessile seed origin F, which differed significantly at $P < 0.01$ from the rounder vessels of pedunculate seed origin H. This appeared to contradict the shapes described by Walker (1978), though he did note that some sessile oaks had oval vessels, and in these cases were distinguished from pedunculate by the rarity of either crowding or distortion (a feature which was characteristic of the oval earlywood vessels in sessile origins from the Penyard experiment).

5.7.1.6. INFLUENCE OF SEED ORIGIN ON PROPERTIES OF OAK WOOD.

1971 RING DENSITY. Table 5.2.g. The highest ring densities were in sessile seed origins, and the lowest in pedunculate seed origins. Significant differences existed between many pairs of origins, the greatest differences ($P < 0.01$) being J denser than A, K and G, and B denser than K and G. Density of D was much lower than that of other sessile origins despite its moderately large ring width; the very large earlywood vessels of D contributed to this result. The density of H was higher than that of the other pedunculate origins despite a mid-range earlywood vessel size and relatively high latewood vessel proportions. Perhaps the method of combining tracheids in fibre counts influenced this result: if the latewood flames of H contained relatively few tracheids, this could result in a greater density of the wood despite high latewood vessel proportions. It is suggested that separate analysis of tracheids (though difficult in cross-section) would be important for studies of density correlations with microscopic structure of oak; use of polarising filters in microscopy may help to identify these cells more easily, at least at low power (Plate 5.1).

MEAN DISC DENSITY. The pedunculate seed origins and sessile origin D had the lowest disc densities. These results confirm those of Deret-Varcin (1983) who found that specific gravity was significantly greater in sessile than in pedunculate oaks from Morimond in N France (a highly significant difference in mature wood of the trees), and of Nepveu (1984b).

The ranks of seed origin means for disc density were very similar to those for 1971 ring density, with the exception of J which showed a higher ring density.

SPLITTING STRENGTH. No significant differences were found between the seven seed origins tested for splitting strength in the radial plane of 'green' wood, though two sessile origins (E and F) had much lower mean strengths than the other origins. FPRL (1936) reported differences between species in splitting strength in the radial failure plane, found in three parcels of pedunculate oak and one of sessile; the average value for green wood of sessile oak was equal to the lowest of the pedunculate parcels. For air-dry timber, the strength of the sessile oak was much lower than that of the pedunculate.

5.7.1.7. INTENSIVE SAMPLING OF FOUR SEED ORIGINS.

Extra samples were taken from seed origins A, B, D and H in order to study wood structure and properties over the full range of diameters. Sixty trees were sampled per seed origin, representing an even spread over the five diameter classes.

Appendix 5.3 lists means and standard deviations of wood structure and property variables measured over trees of all diameter classes in each of the four seed origins (n = 58 due to missing data). The relative ranks of these means were almost always the same as in the main study (of all eleven origins) which used only twelve dominant trees per seed origin. The differences between means were more often statistically significant in the larger samples however.

The only variables for which means of all diameter classes of A, B, D and H ranked differently from means of DCII samples were sapwood proportions. Differences in sapwood ring number and sapwood width of A, D and H were of the same order as seen in DCII samples, but both ring number and width means of origin B were much greater when measured over all diameter classes.

5.7.1.8. PLUS-TREE PROGENY AND ASSOCIATED SEED ORIGINS.

Seed origin C was a single plus-tree in the woodland of seed origin B; likewise, seed origin E was a plus-tree from the woodland of seed origin D. The plus-tree origins were in effect two families of half-sib progeny from open pollinated mother trees.

HEARTWOOD PROPORTIONS. In the rank of seed origin means of heartwood as a percentage of diameter, the plus-tree progeny were not linked to their associated origins; however, D and E had equal proportions of heartwood measured as a percentage of rings.

TISSUE PROPORTIONS. In analyses of tissue proportions, the plus-tree progeny were found to be representative of their associated seed origins only rarely; means for most characteristics of D and E ranked very differently from one another. Variation within the plus-tree origin E (as indicated by standard deviation of variables) was as great as that within D. Origins B and C were more often similar to one another, though only in variables which did not differ significantly between any seed origins. Variation within C was low for many variables.

EARLYWOOD VESSEL DIMENSIONS. Origins D and E ranked at opposite extremes for all earlywood vessel dimensions; B and C were similar to one another for tangential and radial diameter of earlywood vessels.

Kanowski *et al.* (in press) studied sessile and pedunculate oaks from clonal and from half-sib progeny trials, and found that vessel size was under strong additive genetic control; but vessel size was calculated as cross-sectional area from a single unspecified diameter per vessel, so cannot be compared directly with the Penyard results.

DENSITY. Seed origins B and C were similar in ring and disc density; D and E again differed greatly in value (though not in rank) for both these variables.

5.7.1.9. SCANDINAVIAN SEED ORIGINS.

The three Scandinavian origins (J, K and L) had the lowest mean diameter at breast height (diameter class II trees) of all the seed origins in the trial; the other eight origins were all from the South of Britain (Figure 5.1), these were from planted (rather than semi-natural) woodlands, but were from areas traditionally afforested with oak and where the likelihood that local (or at least British) seed was used is high.

No grouping of the Scandinavian origins occurred in the ranks of means for any of the other variables measured. There was a suggestion of greater splitting strength, but no significant differences between these and other origins, and poor sample sizes limited validity of comparisons.

5.7.2. ASSOCIATIONS BETWEEN GROWTH RATE AND VARIATIONS IN OAK WOOD STRUCTURE AND PROPERTIES.

5.7.2.1. ASSOCIATIONS BETWEEN TREE DIAMETER AND HEARTWOOD AND SAPWOOD PROPORTIONS.

Table 5.4.

There were highly significant positive correlations between tree diameter and heartwood proportions, whether expressed as a percentage of ring number, or as a percentage of disc diameter. When the four seed origins A, B, D and H were examined individually (Appendix 5.4), the same pattern was seen for all (though the correlation with heartwood as a percentage of diameter in origin B was of lower significance).

There was a significantly positive correlation between tree diameter and sapwood width, but a highly significant negative correlation between tree diameter and sapwood ring number. This suggested that the width was regulated to some extent, such that fewer wide rings were retained as sapwood, than narrow rings.

5.7.2.2. ASSOCIATIONS BETWEEN RING WIDTH AND TISSUE PROPORTIONS.

Table 5.3. Associations were calculated between tissue proportions and growth rate (ring width) of the current ring.

RAYS.

Ray proportions were significantly positively correlated with growth rate of the ring in which they were measured. Associations of narrow rays with ring width were the most significant, and affected total-ray results. Wide ray percentage was significantly associated with ring width when all seed origins were combined. However, examination of data for each of the four seed origins separately (Appendix 5.4) shows that the result was due to the highly significant positive correlation of wide ray percentage and ring width found in seed origin D, but that in general the wide ray proportion did not vary significantly with ring width (though the correlation was always positive).

Wide ray correlation with tree diameter was calculated because this should give an indication of the association between wide ray proportions and the long-term vigour of the tree (Table 5.4; Appendix 5.4). Wide ray correlation with tree diameter was significantly positive for individual seed origins as well as for the combined data (origin D again showed the strongest associations of these variables).

The tendency for increased total ray proportions with increased growth rate agreed with the findings of other authors (Section 2.2.2.2). However, little variation between seed origins was found in total ray proportion (Section 5.7.1), and little variation between seed origins or with diameter differences was found in wide ray proportion; this also agreed with the results reported by others (Section 2.1.2.1; work on American oaks).

VESSELS.

Vessel percentage in earlywood and latewood zone 1 was positively related to ring width, but the correlation was not significant when calculated from the combined data of all seed origins. Seed origin A alone showed a significant correlation between ring width and these variables (Appendix 5.4); this seed origin had wedge-shaped latewood 'flames' which started widening early in the ring (Plate 5.2) and a tendency to sample further into the ring (thus into this wedge) in wider rings may explain the latewood zone 1 result.

Vessel percentage in latewood zone 2 was negatively correlated with ring width; this was significant for the combined data, but not significant when calculated within each seed origin separately. At first the negative correlation seemed surprising, given the tendency for latewood flames to widen towards the end of the ring, but if Plates 5.1 - 5.5 are examined, it appears that the reason is a combination of wider distribution and decreased size of vessels at the end of the ring. The cells which increase in number at this point and enhance the flame-widening effect, are the tracheids (which were assessed as 'fibres' in tissue proportion analyses).

FIBRES.

Fibre proportions in all three zones of the ring were significantly negatively correlated with growth rate (ring width). In latewood zone 2 the result was heavily influenced by seed origin D (Appendix 5.4), otherwise the correlation was not strong; since the vessels in this zone were also negatively correlated with ring width and tracheids were counted as fibres, it seems that the larger ray proportions in this zone of wider rings account for the balance in tissue proportions. In earlywood and latewood zone 1, vessels and fibres were negatively correlated.

AXIAL PARENCHYMA.

Axial parenchyma proportion of the earlywood was significantly negatively correlated with ring width, but parenchyma proportion in the latewood zones was not correlated with growth rate. The earlywood result was due to the influence of seed origin A alone, and much variability was evident between zones and between seed origins (Appendix 5.4), so it seems that there was no simple association between ring width of the current year and axial parenchyma proportions.

5.7.2.3. ASSOCIATIONS BETWEEN RING WIDTH AND EARLYWOOD VESSEL DIMENSIONS.

Table 5.3.

Earlywood vessel size (cross-sectional area) was significantly positively correlated with ring width at $P < 0.05$. Earlywood vessel shape (R:T diameter ratio) was highly significantly positively correlated with ring width: more oval vessels were associated with wider rings.

Results in Tables 5.2 and 5.3 show that radial diameter of earlywood vessels was strongly associated with ring width but was not under strong genetic control, whereas tangential diameter was not associated with growth rate (ring width of the current ring) but, although varying very little, did appear to be under genetic control (there were significant differences between means of seed origins F and D, and F and H).

Dodd (1984 - work on Acer) and Zasada and Zahner (1970 - work on Quercus rubra) also reported that radial and tangential diameters of vessels vary independently. Dodd suggested that radial diameter is influenced at the time of vessel expansion, but variation in tangential diameter may be due to influences at the cambial stage. Zasada and Zahner showed that site had little to do with tangential diameter of vessels and explained that this was because the vessels expand freely at early stages in ring formation, into tissue which yields readily, so that tangential diameter is independent of growth rate and vigour; whereas radial expansion must concur with the radial growth of all cells in the tangential band. On poor sites therefore, where radial growth is slower, enlarging vessels lignify earlier (at smaller radial dimensions) and radial diameter is therefore smaller than on sites where growth is fast.

5.7.2.4. ASSOCIATIONS BETWEEN GROWTH RATE AND WOOD DENSITY.

Sample numbers were too small for valid studies within seed origins of associations between growth rate and ring or disc density. When data for seed origins A, B, D and H were combined, non-significant negative correlations were obtained between ring width and ring density (1971 ring) and between tree diameter and disc density. However, examination of data for the four seed origins separately suggested that the correlation may be positive for some seed origins and negative for others, or that the relationship may not be a straight line. The different patterns of latewood zone 2 vessel distribution with seed origin seen in these studies (for example as shown by Plates 5.1 - 5.3), could contribute to such variation with ring width, taking into account also: predominance of low density earlywood in very narrow rings, variations in fibre cell-wall thickness (tend to be thinner in fast-grown hardwoods (Zahner, 1971)), and abundance of vasicentric tracheids in latewood flames, all of which would complicate the pattern. No results are presented here as further work using larger sample numbers is needed.

5.8. CONCLUSIONS FROM THE STUDY OF THE PENYARD OAK SEED ORIGIN TRIAL.

Variations in wood structure and properties of oaks from the Penyard seed origin trial were quantified, and the influences of seed origin and of growth rate were analysed.

I.

Analyses of variance of seed origin data from the replicated trial of eleven origins, showed which of the wood structure and property variables could be assumed to be under genetic control. Wood density was the characteristic which differed significantly between the greatest number of seed origin pairs. Sapwood width also differed significantly between many seed origins, but evidence of a good juvenile-adult correlation in this character would be needed before this information could be used as a selection criterion (the strong influence of growth rate would also have to be borne in mind). For the finer wood structure variables measured, fewer seed origins differed significantly from one another; however, vessel proportions in zone 2 of the latewood, and earlywood vessel frequency and shape, differed between several seed origins.

In most tissue proportions for which analysis of variance showed a significant difference between seed origins, the difference was due to one or two origins with extreme values differing from from one or two (rarely, all) of the rest: this was the case for proportions of wide rays and fibres, vessel proportions in latewood zone 1, and for tangential diameter of earlywood vessels.

Although pairs of seed origins might not differ significantly for single wood structure variables, combinations of variables can characterise each origin more clearly. Density represents such a combination of structure variables: it is influenced by tissue proportions (which will vary with both genotype and growth rate as has been shown) and by the wall thicknesses of cells. Seed origins, as has been noted, were best characterised by their differences in wood density.

Pedunculate and sessile genotypes were separable on the basis of the following characteristics:

a) vessel percentage in both latewood zones; this was greater in pedunculate oaks (and sessile origins E for zone 1 and F for zone 2);

b) earlywood vessel percentage tended to be larger in pedunculate oaks (though not significantly so), but the largest earlywood vessels of all were in sessile types J and D; selection for earlywood vessel size should not be based on species choice therefore;

c) density; this was lowest in pedunculate oaks (plus sessile origins D and J which had unusually large earlywood vessels), and might be expected given the greater vessel proportions in these trees;

d) the three lowest sapwood widths were found in pedunculate oaks, but not all pedunculate types had low values for this characteristic; it is therefore not safe to use species as a single criterion for selection of desired sapwood widths.

Gasson's (1984) contention that earlywood vessel shape is not a reliable diagnostic character for pedunculate oak was supported, not only on the basis of variability with growth rate (his argument), but also when measured in directly comparable rings. The species-diagnostic system of Huber et al. (1941) modified by Walker (1978) relied on the usual presence of characteristic shape (oval for pedunculate) in combination with other diagnostic characters; however, similarities seen between qualitative patterns of structure in their studies and the present study might be a better means of separating types. There appears to be a pedunculate type which combines more than one row of crowded, oval earlywood vessels with branching latewood flames, and another which combines a single row of round or tangentially flattened earlywood vessels with rapidly broadening wedge-shaped flames. The latter type had leaves which were the most pedunculate in character in the present study. Sessile types examined in this study were more usually characterised by narrow latewood flames with single files of vessels, at least in zone 1 of the latewood.

II.

A strong association of growth rate was found with a number of the variables measured. Heartwood proportions and sapwood width were positively associated with growth rate (growth rate being represented by tree diameter at equal age and height of oaks). Sapwood ring number was strongly negatively associated with growth rate.

High proportions of all rays (wide and narrow) were associated with greater tree vigour.

Fibre proportions in all three zones were negatively associated with ring width. No significant association of vessel proportions with ring width was found in earlywood and latewood zone 1, but wider rings were associated with lower vessel percentage in latewood zone 2.

Earlywood vessel radial-diameter and shape were strongly affected by current growth rate (increased diameter and radial elongation of vessel, with increased ring width). Earlywood vessel area (which was calculated from radial and tangential diameters) also increased with growth rate, but the influence was less strong because of the incorporation of tangential diameter which was not affected by growth rate.

III.

Some of the characteristics which were found to be most strongly under genetic control (in diameter class II samples) also varied with growth rate. These were vessels of latewood zone 2, density, and sapwood width. Examination of the relative ranks of these characteristics and appropriate indicator of growth rate (ring width or tree diameter) suggested that for latewood zone 2 vessels, growth rate is the observed 'seed origin' effect. This may be so for density also, but this is less probable because density is due to a combination of so many factors under differing controls; genotype seems to be the dominant influence on sapwood width.

IV.

Variables which showed no significant influence of growth rate (1971 ring width) were few; they were the vessel proportions in earlywood and in latewood zone 1, axial parenchyma proportions in latewood, and the tangential diameter of earlywood vessels.

Of these variables, LWZ1 vessel proportions and tangential diameter of earlywood vessels appeared to be under genetic control, though the number of differing origin pairs was low. Selection for either of these characteristics from significantly different seed origins should be successful, and little influenced by subsequent silvicultural treatment.

V.

The results of this chapter are of value in the study of shake, as they indicate:

1. what might have been the cause of wood structure patterns found in shake-prone oaks (Chapter 4), and thus:

2. which of the variables found to be associated with shake and suspected to be causal (rather than parallel effects of a separate cause of shake) might be controlled in future crops by tree selection and/or silviculture (influencing growth rate or site type).

VI.

The results of this chapter are also of interest in other aspects of oak wood quality. It seems that the prospects for improving stock for the following characteristics are good:

1. Density: which affects shrinkage (Nepveu, 1984) and workability (Farmer, 1970).

2. Texture: (i.e. the homogeneity of vessel and fibre proportions across the ring) which affects veneer and other high quality end products (Marchal, 1983).

3. Sapwood width: which affects the usable volume of logs.

Wide ray proportions varied very little overall, but one seed origin (G) did differ greatly from the rest. This was due to a ray proportion which was very high however, and as other authors have shown increased wide ray proportions to result in increased density and shrinkage of oak wood (Section 2.2.2.1) this is a feature that would generally be selected against rather than preferred. However, if this occasional extreme type exists, it may be that other seed origins could be found with unusually low, heritable wide ray proportions.

VII.

The following chapter (Chapter 6) collates the evidence of site surveys and of wood structure variations in shake-prone oaks, together with the information collected in this chapter on control of wood structure and properties, to complete the proposed model of shake development in oak and make recommendations for growing future oak crops with a reduced incidence of these defects.

CHAPTER 6.

SHAKE IN OAK: FINAL DISCUSSION AND CONCLUSIONS.

6.1. CAUSES OF SHAKE IN OAK.

In Chapter 3 it was proposed that the development of shake in oak is a gradual process involving some or all of a number of factors. The causative factors were divided into two main groups: predispositions to shake, and triggers of shake (Figure 6.1).

Figure 6.1. Model of shake development in oak. Stage I.

A predisposition to shake is a weakness in the wood; a trigger is some form of mechanical stress. Increased predisposition (i.e. decreased strength of the wood) plus increased influence of trigger (i.e. increased stress) results in increased strain which can lead to failure of the wood. If predispositions exist without the influence of a trigger, or vice versa, then shakes are unlikely to develop.

This model is now expanded to incorporate the findings of the wood structure analyses with those of the site surveys. Also included are the roles of bacterial degradation, wound response and growth stresses (researched by other authors, and for which evidence was found during site surveys: Sections 2.3.3.4, 2.3.7.4. and 3.2.4.3).

Site surveys showed that environmental influences were very important in the development of shake in oak; wood structure patterns in shaken and sound trees from shake-prone and sound woodlands supported this. However, genetic variation between trees must also play a role: a) indirectly by influencing tree response to the environment, or susceptibility to environmental effect; and perhaps b) directly by controlling wood structure patterns and wood chemistry, and therefore natural growth stress levels and wood strength. Figure 6.2 shows the next stage in expansion of the model of shake development.

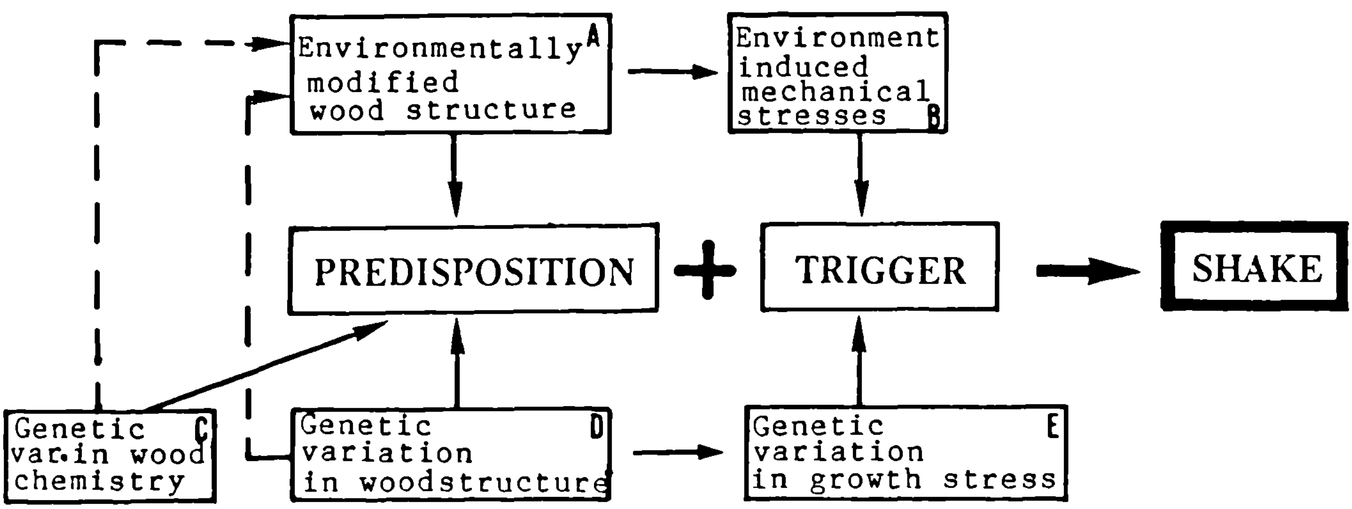

Figure 6.2. Model of shake development in oak. Stage II.

⟶ = causes   - - - - → = modifiers

ENVIRONMENTAL MODIFICATIONS OF WOOD STRUCTURE (Box A in Figure 6.2).

These wood structure modifications either could occur at the time of wood formation, or could be secondary changes developing some time after the wood was formed. Factors predisposing oak to shake by modifying wood structure are described below.

1/ Injury to the cambium. This leads to formation of a barrier zone, wall-4 of which develops in newly forming wood. This is a structurally weak zone, though strong in chemical and ultrastructural defence against pathogenic fungi and bacteria; the response can occur for some distance tangentially and axially from the wound.

Injuries leading to such modifications could be due to silvicultural operations (for example accidental injury during thinning, or deliberate action such as pruning); or to pest damage (for example bark-stripping by mammals, and possibly wood pecker damage); or to fire scorch, or possibly to severe frost damage. Wounds which expose the wood and are repaired by gradual in-rolling of subsequent rings until the cambium is again a complete sheath round the tree, could also leave a line of radial weakness where the inroll edges meet.

Wound repair and defence response require extra substrates for new growth and protection against infection; concentration of elements, particularly calcium (but also magnesium and potassium amongst other inorganic substances), has been reported from such zones (McGinnes and Wu, 1973). Consequently, oaks with poor nutrition (due to poor nutrient supply in soil, or debilitated roots) may be more prone to weaknesses in these zones than are those with abundant supplies of such minerals.

The consequences for timber quality, of all such injury, will be worse if the injuries are sustained by young to mid-rotation age trees:

a) even though a ring shake formed in a very early ring affects only the centre of the tree, and cannot extend higher in the bole than the vertical extent of that ring (i.e. the height of the tree in the year the ring was formed), radial splits usually develop from ring shakes and these may extend much further through the length and diameter of the bole.

b) rings which are predisposed to shake when formed in pole-stage crops may be the site of a ring shake with the potential to extend through most of the timber height of the tree.

c) structural predispositions to shake, formed at an early age will exist in the wood for many years during which aggravation of the weakness by bacteria invading at the same time (see 3/ below) will have time to develop.

d) weaknesses near the centre of the bole will, when the tree becomes older, be subject to the strongest triggers of shake.

e) Butin and Shigo (1981) suggested that if injury is sustained by a young, vigorously growing tree shake would be more likely to develop.

In end-of-rotation trees, such injuries would be less important because the effects seem to travel from the inside outwards, thus only the sapwood would be affected, bacterial aggravation will not have so long to develop, and growth stresses triggering the shakes would be at their lowest in the outer portions of the bole (frosts severe enough to cause frost-cracks in outer wood are rare in most of Britain). On the other hand, wound healing may be less efficient in older trees, when rot becomes a problem instead.

2/ Environmental modifications of wood structure at the time of formation can also result from physiological change or stress other than from direct injury to the cambium. Drought, defoliation and sudden change of environment due to silvicultural operations such as late-thinning or coppice removal can alter the balance of water-relations, hormone levels and growth substrates in the tree.

Consequent changes in ring width are apparent, and on sites where mineral nutrients are in short supply, weaker cell wall structure or bonding might accompany this (soil analysis results from site surveys combined with wood structure analysis results suggested that periods of fast growth in oaks on impoverished soils might increase susceptibility to shake). Calcium in particular is important for strength of bonding between cells: calcium pectate is the major constituent of the middle lamella. Wood strength is determined by the physico-chemical nature of the cell wall as well as by anatomical structure (this is demonstrated in ash wood which has toughness and bending qualities which are not explained specifically by its anatomical structure (Clarke, 1935; Wilson and White, 1986).

Longer term physiological stresses such as competition for nutrients in short supply, and gradual decline in growth rate might also be important in development of weak wood. In this context, use of 'hungry' species such as larch (which uses much calcium) in mixture with oak might lead to problems on poor quality sites, although there is no direct evidence for this; a study of competition for nutrients in short supply would be interesting, but interpretation of such studies can be difficult.

3/ A modification of wood structure which occurs after wood formation and results in a predisposition of oak to shake, is the degradation of the wood by anaerobic bacteria associated with wetwood. This microbial activity tends to be concentrated at the edge of barrier zones formed at the time of infection, therefore vertical and horizontal spread often matches the pattern of the wetwood boundaries.

Not all ring shaken trees seen in the site surveys appeared to contain wetwood, although American researchers claim that shake never occurs without wetwood (Ward, 1983). It may be that mild cases of wetwood were not recognised in the site surveys; however, rot was often associated with presence of ring shake in oaks from site surveys (presumably due to a common wound source) suggesting wetwood was not present in these zones. Wetwood is perhaps more important in the development of radial weaknesses which lead to star shakes.

Anaerobic bacteria are reported to invade from the soil via lesions in tree roots, and may enter stem wounds also. Root lesions are usually caused by root pathogens (such as honey fungus) which attack trees already under physiological stress. Such stress may be the result of damage to aerial parts of the tree (defoliation or lightning strike, for example) or can be due to poor rooting conditions (drought, waterlogging, or high levels of potentially toxic elements such as aluminium when required elements such as calcium are in short supply).

ENVIRONMENTALLY INDUCED MECHANICAL STRESSES (Box B in Figure 6.2).

Such stresses could be internal growth stresses or externally imposed stresses. Natural growth stresses in oak were not investigated during these studies, but the work of other authors is reported in Section 2.3.7.4. Growth stresses result from modifications of wood structure at the time of formation, with a cumulative effect as tree diameter increases. Growth stresses in other temperate hardwoods are partly influenced by silviculture, being higher both in un-thinned stands and in stands subject to sudden delayed thinning. Growth stresses may also be higher in trees with high proportions of tension wood, a characteristic of trees grown on steep slopes.

Mechanical stress generation due to tension forces in the sap-stream might have a minor and transitory role as an additional trigger of shake in oaks on droughted soils. Only the outer ring of the tree would be directly affected, but this might supplement axial tension forces of the usual growth stresses.

Externally imposed stresses could result from torsion and bending of the stem in wind, and (rarely in Britain) rapid changes of temperature extremes as a result of insolation during times of severe winter cold.

GENETIC VARIATIONS IN WOOD STRUCTURE, GROWTH STRESS AND CHEMISTRY (Boxes C, D and E in Figure 6.2). Genetic variations in these groups of variables could take effect as direct influences on wood strength and natural growth stresses; some authors believe that genetic influences on internal growth stresses are stronger than environmental effects. Otherwise, genetic influences could be indirect, through modifications to tree response to environmental factors. For example, by influencing the tangential and axial extent of barrier zones beyond the wound area; through suitability of internal atmosphere and chemistry for bacterial colonisation; through suitability of cell structures for bacterial colonisation or spread (perhaps pitting, or cell sizes or distributions).

Figure 6.3. overleaf is a more fully expanded model of shake development in oak, which summarises the main factors associated with shake and discussed above.

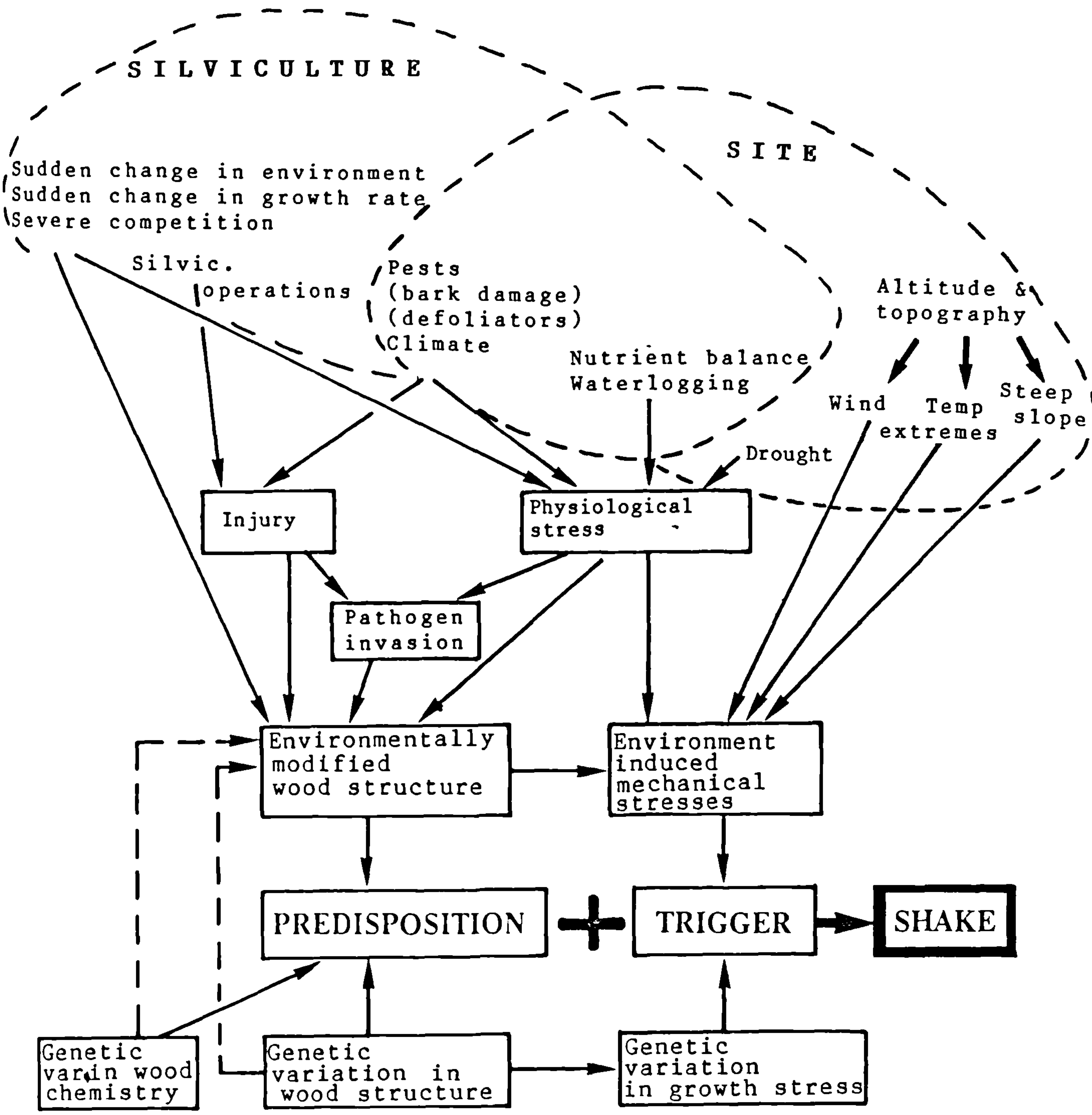

Figure 6.3. Model of shake development in oak. Stage III.

It should be noted that genotype could modify other aspects of tree response to environment. For example, onset of physiological stress could depend on tolerance of waterlogging or drought, and this varies between species and varieties of oak (2.1.1.2). Such tolerances could be due to numerous factors including root physiology and wood structure variations (e.g. size and number of vessels, affecting water carrying capacity of xylem and thus influencing transpiration rates), but such variations are in turn also affected by water potential and hormone levels within the tree. Interpretation of physiological effects of vessel size and distribution must be made with care (Gasson, 1985) there is great variability in association of structure and function, both within and between woody species.

There remains one aspect of the study of shake in oak which is not incorporated specifically in the proposed model of shake development. Savill (1986) and Cinotti (1987) found that in the shaken (or frost-cracked) oak samples they examined, mean earlywood vessel size was greater than that in sound trees. The data for earlywood vessel dimensions collected in the present study did not support this finding, and it is suggested that the question of whether vessels are larger in shaken oaks or shake-prone oaks needs further research. Savill and Mather (1990) suggested that the importance of vessel size in shake formation is a matter of structural strength, crack propagation under tension stresses being greater in cellular solids with larger cells. However, a role in the physiology of the tree would seem more probable: either as a factor related to a separate cause of shake, or as a direct predisposition to shake.

The association of shake with large vessels might be a parallel effect of a common cause if for example, the observed variations in vessel size were due to high auxin levels in physiologically stressed trees, to fast growth rates on poor soils, or to poor root:shoot ratios. Savill and Cinotti both measured vessel areas without specifying diameter differences;

their results may have been reflecting greater radial diameters of vessels, which would indicate a faster growth rate in the shaken trees (a result reported by both authors).

A more direct role of larger vessels in the development of shake could be through an increased susceptibility of oaks with larger vessels to drought stress, to cavitation of the vessels (Zimmermann, 1983), or to tracheomycosis. Evidence for the latter is given by Elgersma (1970, quoted in Savill, 1986) who showed that elm varieties resistant to Dutch elm disease had smaller vessels. Gensi (1988) reported that some varieties of Hungarian oaks were more resistant to tracheomycosis despite the large vessels typical of the species, because they could control the problem by osmoregulation. The importance of earlywood vessels as a route for spread of pathogens is also suggested by the fact that red oak species (having few tyloses in vessels, except in traumatic wood) have a higher incidence of wetwood (Ward et al.) and of shake (McGinnes, 1965) than do white oaks (which develop tyloses as characteristic of normal wood structure).

If large earlywood vessels do prove to be directly associated with shake, then the results of Chapter 5 suggest that control of shake development might be exercised by selection of oak genotypes with small EWV tangential diameter, which are then grown in a silvicultural regime fostering a slow to moderate growth rate (to maintain small radial diameter earlywood vessels).

The model of shake development could be more precise if the reasons for variations between tree species in susceptibility to shake could be understood. It has been suggested that shakes are somehow related to the large earlywood vessels in the ring porous species oak, elm and sweet chestnut (Savill, 1986); yet ash which has a similar ring porous nature never develops shake, and ring shakes form in the diffuse-porous species horse chestnut and poplar. The wide rays of oak would seem a possible site of weakness leading to star shakes (not seen in sweet chestnut, which has no such rays), and Butin and Shigo (1981) state wide rays to be the site of star shakes; yet star shake usually accompanies ring shake in yew, a species in which rays are not so high as those of oak, and no higher than several species of softwood and hardwood which do not shake.

Growth stresses as triggers, despite being part of the process of shake development, do not seem to explain species differences in susceptibility to shake: although growth stress in American ash is very low, beech (not prone to shake) often has very high growth stresses, and oak is middle of the range of all species for growth stress (Kubler, 1987).

Susceptibility to wetwood formation and bacterial degradation in the standing tree may be the explanation of species differences in susceptibility to star shake. Rol (1948) listed oak, elm, poplar and "certain firs" as particularly susceptible to frost-crack. These are the species which are most prone to develop wetwood. Wetwood bacteria are favoured by anaerobic conditions in wood of a high moisture content, and are circumstantially linked with high calcium levels. Very high moisture contents of green wood are found in oak and elm (shake-prone), whereas moisture content of ash (not shake-prone) is much lower than most other British hardwood timbers (FPRL, 1936; sweet chestnut was also listed as having a high moisture content). Differences between species in functional organisation of vessels and tracheids described by Bell and Coombes (1965) may explain these differences: in sweet chestnut, oak, elm and walnut both tracheids and vessels are involved in conduction of water, in horse chestnut vessels conduct water and tracheids serve as reservoirs, in sycamore and ash conduction is confined to the vessels and all matrix fibres are filled with air. Finally, differences in wood chemistry may also favour bacterial colonisation: poplars usually contain calcium carbonate deposits, <u>Abies</u> species contain crystal inclusions of calcium oxalate.

6.2. CONTROL OF SHAKE IN BRITISH OAKS.

The model of shake development presented in Figure 6.3 indicates that control of shake in future oak crops can be exercised through careful site choice and silviculture. Further methods of control may be through selection of genotypes which modify response to environment in such a way as to reduce formation of predispositions caused by environmental factors. This would allow use of a wider range of site-types for growing high quality oak timber, but further work would be needed to identify the appropriate genotypes. Characteristics which might be of advantage are a) tolerance of poor soil conditions without root distress (sessile oak types may be most suitable), b) a barrier-zone response to wounding which neither 'over-reacts' (greater potential for ring shake), nor 'under-reacts' (so that rot or wetwood spread is not contained), c) discouragement of the colonisation or spread of bacteria associated with wetwood (this might depend on wood structure or chemistry characteristics).

Meanwhile, the following prescriptions can be made for growing future oak crops with a lower incidence of shake:

I. SITE CONDITIONS.

The following site conditions are recommended:

1. SOIL TYPE

- Good nutrient supply (calcium, magnesium and potassium levels appear to be important, calcium particularly so; calcium availability of more than 1.0 me/100 g is recommended.
- High clay fraction (more than 20% by Avery soil texture classification).
- Deep soil

1. SOIL TYPE (continued)

- Good moisture retention (may be due to higher clay and/or organic matter contents).

Gravels and nutrient-poor stony soils where uptake of nutrients by roots might be difficult, should be avoided. Moist soils are ideal, but drier sites may be suitable if the water table is naturally stable or artificially stabilised by drainage throughout the life of the crop. Waterlogging or periodic severe drought should be avoided. If sandy soils are planted, the water table should be constant, and the calcium availability high. A further constraint (though perhaps of lesser importance where other conditions are fulfilled) would be high aluminium content of soil, particularly on acid/low calcium sites.

2. TOPOGRAPHY.

- Level or slightly sloping site.
- Avoid frost hollows.
- Avoid extreme wind exposure.

II. SILVICULTURAL PRACTICES.

The following silvicultural practices are recommended:

1. PROTECTION.

- Avoid un-necessary damage during forest operations.
- Protect from animal damage (bark-stripping, etc.), especially in young crops.

1. PROTECTION. (continued).

- Protect from fire.
- If pruning, prune with care to minimise wound infection (follow recommendations of Shigo, for example Shigo (1984b).

Protection from attack by root pathogens, although desirable is not feasible except by choice of site conditions (above) which reduce physiological stress of root systems. Advice for tree planting on sites of known honey fungus (Armillaria) infection is given by Rishbeth (1983).

2. GROWTH RATE.

- Maintain an even growth rate (plan thinning and understorey removal to minimise sudden changes in ring width).
- Avoid very slow growth from overstocking and competition (narrow ring widths due to dry but fertile sites may be acceptable).

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APPENDICES

SOURCE	CHARACTERISTIC QUALITY OR PROPERTIES OF OAK
AS RECORDED BY LASLETT (1894)	
Britain	Strong, tough, hard. Good for shipbuilding. Light brown colour.
N.W. France	Similar to Britain.
Italy	Hard, tough, strong. Less elastic but more heavy than British oak. Splits in seasoning, but not prone to shakes (exception is Sicilian oak).
Poland "Dantzic"	Form straight. Moderate hardness and strength. Porous. Bright distinct rays. Good for planking and steam bending. Wears well. Seasons well with little shrinkage.
Russian interior "Riga"	Similar to Polish, but rays more numerous and marked. Very decorative.
Belgium	Straight and mild.
Holland	Not outstanding for ships, nor decorative.
Spain	Not decorative. Porous and mild. Shrinks badly. Very slow grown. Often star shaken.
Turkey (*Q. robur*)	Very good form, but poor quality compared to British.
Turkey (*Q. cerris*)	Not good.
Hungary	Sessile oak. Many types. Quality varies with soil.
America (*Q. alba*)	Very elastic. Low shrinkage. Good strength characteristics, but not equalling British. Reddish brown colour.

APPENDIX 2.1. Usual characteristics of oak timber of different provenances, recorded in the literature.

SOURCE	CHARACTERISTIC QUALITY OR PROPERTIES OF OAK
AS RECORDED BY BEAUVERIE (1910)	
France - Midi	Best for shipbuilding.
France - Vosges and Champagne	Sought after for joinery and furniture.
Holland	Good for joinery and furniture.
Hungary	A notable wood-working timber, lacking defects and fairly mild.
Baltic ports	Less good for shipbuilding.
Spain	Good for shipbuilding.

APPENDIX 2.1. (continued) Usual characteristics of oak timber of different provenances, recorded in the literature.

AUTHOR	TERM FOR DEFECT	DESCRIPTION OF DEFECT
Koehler (1933)	Ring shake	Wood separates within or between rings.
	Rift crack	A radial separation from the pith for a limited distance.
	Star check/shake	Several rift cracks together.
British Standards Institution (1966)	Shakes	Partial or complete separation between adjoining layers of fibres.
	Cross shake	A shake in cross-grained timber.
	Ring/cup shake	A shake following the growth rings.
	Shell shake	Part of ring or cup shake showing in surface of converted timber.
	Heart shake	Shake originating at the heart.
	Star shake	A number of heart shakes more or less in a star.
	Compound shake	A combination of any of the above.
	Felling shakes	Not properly shaken - a tearing of the fibres.
	Thunder shakes	Formed across the grain - properly called 'rupture'.
	Check/split/end split	Terms confused with shakes.
James (1939)	Heart shake	A series of radial cracks, usually widest at the centre of the tree, become narrower as extend outwards, ultimately disappearing at the surface.
	Star shake	Similar to heart shake, but cracks are narrowest at centre and widen outwards.
	Ring shake	Splitting takes place concentrically, following the limit of the annual rings.
	Cup shake	Wide open splits, an advanced stage of ring shake.

Appendix Table 2.2. Terminologies applied to shake and similar defects. (Continued on next page).

AUTHOR	TERM FOR DEFECT	DESCRIPTION OF DEFECT
Corkhill (1948)	Shake	A separation between adjacent layers of fibres - quotes BSI (1938) terms.
Rol (1948)	Shakes	Circular separation of layers of wood following the limits of two annual layers. Due to wind, or else associated with frost crack.
	Star shake / split-cracked-heart.	Radial splits emanating from the heart.
Erteld (1964)	Shakes	Repeats similar list to BSI (1938) and also lists sunchecks, frost checks and felling shakes.
National Hardwood Lumber Association Association USA Grading Rules (1967)	Shake	A separation along the grain, the greater part of which occurs between the rings of annual growth. Rules are detailed for the grading of shaken cypress.
The Forest Dept. Malaya (1968)	Shake	A split, crack or deep check. Specifically: 'round' of 'cup' shake, 'heart' or 'star' shake.
	Shatter shake	Felling damage.
McGinnes (1965)	Ring-shake/loose-heart	Tangential separations in wood.
	Spider/wind shake	Radial separations.

Appendix Table 2.2. (continued.) Terminologies applied to shake and similar defects. (Continued on next page).

AUTHOR	TERM FOR DEFECT	DESCRIPTION OF DEFECT
Garfitt (pers.comm.)	Wind shake	Small, straight line through pith, normally not more than 4" long, even in sound trees.
	Star shake	Cracks radiating from the centre of the tree. Often slightly discoloured and containing sawdust.
	Ring shake	Follows annual ring; often discontinuous. Appears in rings of different ages.
Panshin & deZeeuw (1980)	Shakes	Longitudinal separations of wood in the standing tree.
	Heart shake/rift crack	Radial shake passing through pith.
	Star shake	Numerous radial shakes.
	Ring (also 'cup' & 'round') shake.	Shake in plane of growth increment.

Appendix Table 2.2. (continued.) Terminologies applied to shake and similar defects.

APPENDIX 3.1.

QUESTIONNAIRE ON THE PROBLEM OF SHAKE IN OAK

Part 1 The following questions ask about the association of shake with growing conditions.

1. Is the occurrence of shake related to soil type? e.g. soil texture(e.g. sandy, clay, loam); acidity/alkalinity; etc.

Ring shake YES ☐ NO ☐ Heart (star) shake YES ☐ NO ☐

If 'Yes', please give details:

2. Please list any counties or localities associated with the incidence of shake (high or low) within the U.K.

	Ring shake	Heart (star) shake
Counties or localities with high incidence:		
Counties or localities with low incidence:		

3. Please list any environmental factors associated with incidence (high or low) of shake, e.g. slope; aspect; drainage; altitude; exposure to wind; exposure to frost; pollution; disturbed ground(e.g. by mining); soil depth; etc.

	Ring shake	Heart (star) shake
Factors associated with high incidence:		
Factors associated with low incidence:		

4. Please list any ground vegetation types (e.g. heather, bracken, bramble, etc.) associated with incidence (high or low) of shake.

	Ring shake	Heart (star) shake
Vegetation associated with high incidence:		
Vegetation associated with low incidence:		

5. Please list any other factors associated with incidence (high or low) of shake. e.g. presence of/damage by deer, sheep, climbing plants, fungi, etc.

	Ring shake	Heart (star) shake
a) Animals High incidence of shake:		
Low incidence of shake:		
b) Plants and other High incidence of shake:		
Low incidence of shake:		

6. Please list any silvicultural techniques associated with incidence (high or low) of shake. e.g. origin of stock (planted/coppiced/naturally regenerated); timing or type of thinning; spacing; mixtures; etc.

	Ring shake	Heart (star) shake
High incidence of shake:		
Low incidence of shake:		

Part 2. The following questions ask about the association of shake with th outward characteristics of the tree.

7. Please list any aspects of tree form linked with the incidence (high or low) of shake. e.g. crown size; balance of crown; straightness of bole; etc.

	Ring shake	Heart (star) shake
High incidence of shake:		
Low incidence of shake:		

8. Is it possible to tell from the appearance of a split in the end of a log whether it is a true shake (formed in the standing tree), a crack from felling shock or a drying che
If so, what indications would you look for in each?

APPENDIX 3.1.

9. Please list, in order of importance, any reliable indications (visible <u>before</u> felling) that a tree is internally shaken.

	Ring shake	Heart (star) shake
1.		
2.		
3.		

10. Does shake occur with equal frequency in trees of all diameters? YES NO . If not, please list tree sizes with relatively high and low incidence of shake, (please state whether quarter girth or diameter breast height, and inches or centimetres.)

	Ring shake QG/DBH of trees	Heart (star) shake QG/DBH of trees
High incidence:		
Low incidence:		

Part 3. The following questions ask about the possibility of a genetic influence on susceptibility to shake.

11. Could you please indicate whether, in your experience, variations in the severity of shake <u>within</u> a wood or plantation are greater or less than those <u>between</u> different woods.

Within site variation is:	greater than,	equal to,	less than,	between site variation.
Ring shake	☐	☐	☐	
Heart (star) shake	☐	☐	☐	

12. Considering all the above questions, are there any major differences in these contexts between species of oak (sessile, pedunculate, turkey, etc.)?

Part 4. The following questions ask about the use of shaken timber.

13. What products are made from your logs which are:

a) slightly ring shaken:	
b) slightly heart (star) shaken:	
c) severely ring shaken:	
d) severely heart (star) shaken:	

14. What factors do you take into account when valuing a log containing shake?

15. We need an illustration of the economic importance of shake; please indicate the approximate roadside value of the following grades of log and the value if the same l was shaken.(Here, "severely ring shaken" represents ring shake in over 1/4 of the ring a with two or more rings affected; and "severely heart shaken" represents heart shal extending in several directions from the centre and over 1/3 of the log radius.)

	Shake free £/unit	Ring shake £/unit	Heart shake £/unit
Veneer butts			
Planking butts			
Fencing logs			
Mining timber			
Beam/construction logs.			

APPENDIX 3.2.

FURTHER INFORMATION ON SHAKE: COLLATED FROM CORRESPONDENCE AND INTERVIEWS.

A.3.2.1. REPORTED ASSOCIATIONS OF SITE TYPE AND SHAKE.

Most comments on site and soil type echoed those of the questionnaires. Clay soils were always quoted as giving good quality, sound oak; clay soils cited were in Hertfordshire (London Clay), Lincolnshire (Kimmeridge Clays) Sussex Weald-clays, Oolitic clays, and Culm Measure clays in various counties. London clays produced sound oak as long as patches of gravel drift were avoided. One report described clay-with-flints as growing good, light-coloured oak, with about 10 % of the crop badly shaken but with no staining of the shakes. The Trenchard Clays of the Forest of Dean, on which 85% of the oaks were reputed to be shaken, were an exception to the good reputation of clay soils. Moist, heavy and calcareous soils were all said to produce sound oak. Exceptions were calcareous brash, and water-logged soils.

Thin soils over rock or other un-rootable material were regarded as most likely to produce shaken oak, as were stony (flint or brash) soils or gravel drifts (e.g. "fox-bench" or "cat-grain"). The oaks on thin, poor soils over granite in Devon, the Drybrook Sandstone soils in Forest of Dean, and Upper or Lower Greensands were also regarded as shake-prone.

Sites exposed to wind, those at high altitude and those with steep topography were generally regarded as more shake prone. However, a few people expressed certainty that these factors had no effect. Those associating high altitude with shake said either that this was not a consistent factor, or that high altitude usually coincided with the dry or shallow soils which tend to produce shaken oak.

Oaks on valley sides were considered more shake prone than those on the valley floor, but examples were cited as notable exceptions. In these, the valley-floor soil was always very wet and the oaks were shaken, while oaks on the sides were sound.

Oaks on sites on which bracken grew, were said frequently to be more likely to shake.

The reputation of the different counties for shaken or sound oak was the same as found in the surveys. In addition, Dumfriesshire, Loch Lomond and the West Coast of Scotland were reported to produce shaky oak; sound oak grew on the East Coast of Scotland. Morayshire had both good and bad reports; the soil is sandy but fertile.

In Britain, there were suggestions that shake in sweet chestnut (and oak) is less prevalent on sites in proximity to the sea. The shake-free woodlands said to be examples of this effect were in Kent, Norfolk, parts of Cornwall and Devon (including SE of Exeter), and sites near the Gulf Stream influence. No explanations were proffered; the observed effect could be due to lack of frost, or to coincidental soil-types.

A.3.2.2. REPORTED ASSOCIATIONS OF OAK SILVICULTURE AND SHAKE.

Several interviewees thought that oak singled from coppice stools was highly susceptible to shake. There was thought to be a lower incidence of shake in hedgerow oaks.

Ring shake in oak (also in sweet chestnut and elm) was often associated with a sudden release in growth, such as occurs in a stand after a drastic late-thin or removal of competing long-rotation coppice. The ring shakes were reported to form at the transition from a band of increasingly narrow rings, to a band of much wider rings formed when fast growth resumed after the coppice was cut.

In France also, ring shake was often associated with the change in ring width which occurs at the end of sub-storey rotations in coppice with standard oaks.

In North East France, shake in oak was sometimes termed 'fente de baliveau', 'baliveau' being a drastic first thin of the crop at about thirty years old; the implication was that this shake results from the wind twisting and bending tall, thin, newly exposed trees.

A.3.2.3. REPORTED ASSOCIATIONS OF TREE CONDITION AND SHAKE.

Shakes are rarely reported in trees of less than 30 - 40 cm dbh, but above that size, age of tree was not considered to be associated with incidence or severity of shake.

Trees with wound damage in the trunk, such as sustained during thinning in a stand, were said to be associated with high incidence of shake - particularly ring shake. Ribs, splits or grooves running up the bole were often used as warnings that an oak might be shaken, but these external signs were not considered reliable, mainly because their absence did not guarantee a sound tree (Plates 3.13 - 3.16).

Severe ring shakes were said to follow the same ring not only throughout its length in the bole of the tree, but also in the simultaneously formed ring in the branches. Where shakes are suspected to be far reaching, some woodmen inspect the branch stubs before cross-cutting the bole, in order to maximise the length of clean timber.

Equal numbers of reports stated that oaks with thin bark were more, or less, likely to contain shake. Similarly, thin bark was associated with mild timber by some and hard timber by others.

A.3.2.4 REPORTED ASSOCIATIONS OF TIMBER CHARACTERISTICS AND SHAKE.

The wood of shaken oaks was said to be wetter than that of sound; the wood was described as heavy and slow to dry. Pink coloured ash timber was described similarly - though ash has never been reported as shaken.

Tree fellers described a large quantity of pungent, clear brown liquid which is released when certain shaken oaks are felled; the shakes in these trees are dark stained, the wood is wet, and the phenomenon is characteristic of particular sites. Such descriptions are similar to the symptoms of bacterially caused 'wet-wood' in oak (Sections 2.2.2.3 and 2.3.3.4), but there were no reports of shaky oak being difficult to season, apart from the opening of the shake splits. This may have been because the degrade due to shake was so great that checking and honey-comb after drying were relatively insignificant.

The characteristic white staining of shakes in oaks was reported frequently, with implications of regional variation in its presence in shaken timber. It was seen more often in oaks grown in Western counties and Wales than in Eastern and Northern counties.

A few people noted that shake was rare in 'brown oak' (trees infected with the fungus Fistulina hepatica).

The term mineral stain was used to describe dark grey or black bands, seen in the log cross section and undulating within or between the annual rings of oak on certain sites

(Plates 3.11 and 3.12). The cause seems to be the presence of layers of gelatinous fibres which are apparently unrelated to lean or form of the tree. Mineral stain was said to cause no difficulties in seasoning, but it reduces value of joinery or veneer timber because it is visually unacceptable. Mineral stain was reported to be bad in Devon, except on the clays, and one timber merchant said that it is more prevalent in British oak than in any European oak of the same species. The oaks of the Weald and the sessile oak of Savernake were said to produce light coloured heart wood free of mineral stain. The only two reports making any association between its presence and shake, said that oaks with mineral stain were less likely to be shaken, but this was not supported by observations during field surveys; the difference in observations may have been due to the fact that mineral stain was less noticeable in stained, shaken trees than in clean, defect-free timber of pale colour.

APPENDIX 3.3.

Site survey results: means per site of tree and site factors.

SITE	%SHAKEN	INDEX	%PSHAKEN	%ROTTEN	MEANDBH	SAPW TH	BARK TH
1	5	*	*	*	*	*	*
2	42	35	0	3	53	4.0	*
3	45	6	25	0	97	3.6	2.0
4	0	*	0	0	40	*	*
5	3	25	3	0	75	2.5	2.5
6	0	*	0	0	50	3.0	2.0
7	41	13	37	7	95	3.0	2.1
8	43	57	22	10	67	4.0	2.0
9	78	29	57	33	56	3.0	2.0
10	12	22	4	0	67	3.0	2.0
11	48	22	16	0	*	3.0	*
12	47	15	30	*	72	4.0	*
13	30	*	*	*	*	*	*
14	54	27	29	30	69	3.0	*
15	69	42	54	46	95	*	*
16	56	30	35	6	75	3.0	1.8
17	21	24	21	*	73	*	*
18	12	30	2	20	78	2.5	1.0
19	27	13	5	1	94	2.0	2.0
20	44	30	21	2	70	3.0	*
21	40	39	16	8	78	4.0	2.0
22	45	23	45	70	66	3.0	2.0
23	69	20	47	11	62	5.0	1.5
24	20	30	0	0	90	*	*
25	0	*	0	0	*	3.0	1.5
26	25	20	10	0	59	2.5	1.0
27	20	1	0	0	83	4.0	2.6
28	50	27	33	0	46	3.0	1.6
29	63	20	42	13	54	3.5	1.7
30	81	6	44	19	52	3.0	1.4
31	51	8	30	12	58	*	*
32	30	9	0	20	69	4.5	2.0
33	65	13	29	10	57	*	*
34	56	24	12	*	*	*	*
35	44	29	23	9	71	4.0	1.5
36	35	25	30	5	70	*	*
37	39	8	10	14	34	4.3	1.2
38	53	29	40	5	48	4.0	1.2
39	50	15	25	*	*	*	*
40	55	14	2	*	42	*	*
41	76	16	27	0	38	*	*
42	57	17	36	15	57	*	*

Mean dbh = cm; SAPW TH/BARK TH = sapwood and bark thicknesses (cm)

Site survey results: means per site of site and tree factors.

Site	WR FREQ	% W TW	ALTITUDE	CLAY%	SAND%	PH H2O	PH CACL2
1	*	*	25	2	64	*	2.91
2	5.0	*	130	17	26	*	3.31
3	5.0	10	10	3	85	4.10	3.01
4	*	*	41	34	46	7.52	6.73
5	5.0	10	75	20	47	4.23	3.39
6	5.0	0	55	12	63	7.55	6.96
7	4.0	78	60	10	30	3.50	2.67
8	4.0	75	210	3	60	4.08	2.85
9	5.0	89	95	6	35	3.73	2.96
10	4.0	60	120	10	42	3.74	2.70
11	*	22	120	8	32	3.88	3.31
12	5.0	*	95	17	31	3.80	3.26
13	*	*	150	28	23	3.88	3.15
14	2.0	80	95	3	52	4.00	3.05
15	*	0	150	9	64	5.02	2.85
16	4.0	*	165	16	65	3.74	3.91
17	*	*	230	52	35	3.53	2.90
18	4.0	60	60	5	67	4.01	3.38
19	5.0	*	40	16	19	4.02	3.07
20	4.0	*	135	11	67	*	3.09
21	4.0	42	80	4	87	4.00	2.76
22	4.0	*	20	16	68	4.04	3.05
23	*	*	20	10	55	4.08	3.44
24	*	*	20	12	56	4.62	3.50
25	*	*	15	23	39	3.80	2.75
26	4.0	70	160	66	21	3.66	3.13
27	4.0	80	120	8	52	3.94	2.69
28	5.0	50	140	15	40	3.95	3.34
29	4.0	36	240	18	40	3.90	*
30	*	36	10	2	50	3.90	*
31	*	*	150	16	41	4.00	*
32	4.7	0	*	13	32	5.60	*
33	*	*	190	9	52	4.20	*
34	*	*	190	10	43	4.60	*
35	*	46	178	3	62	5.10	*
36	*	*	120	12	63	4.80	3.60
37	4.6	*	100	20	33	4.20	3.70
38	4.0	60	120	7	47	4.20	3.10
39	*	*	*	*	*	*	*
40	*	*	120	*	*	*	*
41	*	*	60	*	*	*	*
42	*	*	180	*	*	*	*

WR FREQ = number of wide rays per 1 cm tangent; altitude = m;
% W TW = percentage of oaks with abundant grey banding;
pH H2O = pH measured in water; pH CACL2 = pH measured in $CaCl_2$ solution.

Site survey results: means per site of site and tree factors.

Site	%STONE	%MOISTUR	%LOI	K	MG	CALCIUM	SODIUM	MANGAN
1	46.6	30.4	14.8	0.26	0.67	1.80	0.09	0.65
2	31.7	14.5	2.8	0.44	0.08	0.10	0.09	0.00
3	2.7	13.4	4.8	0.19	0.31	1.10	0.09	0.05
4	4.3	16.7	2.9	0.31	0.67	61.50	0.17	0.00
5	2.0	31.3	3.6	1.05	1.00	7.10	0.09	0.36
6	6.1	21.9	5.4	0.74	0.75	64.80	0.19	0.01
7	3.4	21.8	7.8	0.20	0.17	0.52	0.13	0.04
8	24.2	14.0	2.6	0.26	0.12	0.35	0.09	0.02
9	2.3	18.0	4.5	0.23	0.08	0.17	0.11	0.12
10	1.2	28.3	13.1	0.46	0.17	0.75	0.09	0.11
11	30.4	19.7	4.0	0.30	0.08	0.28	0.09	0.18
12	4.1	15.5	2.2	0.31	0.08	0.12	0.02	0.09
13	1.3	24.1	7.0	0.41	0.25	1.00	0.09	0.14
14	0.0	34.6	6.2	0.10	0.17	0.50	0.09	0.07
15	5.4	11.5	3.3	0.41	0.08	0.30	0.04	0.04
16	52.6	14.1	2.4	0.20	0.08	0.22	0.16	0.00
17	40.9	13.6	4.1	0.31	0.08	0.20	0.09	0.11
18	3.7	17.7	2.7	0.18	0.08	0.40	0.04	0.04
19	46.9	14.8	3.6	0.13	0.17	1.05	0.17	0.07
20	33.0	12.2	2.4	0.13	0.08	0.27	0.07	0.04
21	75.4	5.6	2.2	0.20	0.12	0.45	0.09	0.04
22	3.6	16.2	2.3	0.16	0.06	0.10	0.06	0.02
23	26.7	11.3	1.9	0.22	0.03	0.02	0.09	0.01
24	0.7	9.8	1.3	0.10	0.67	1.10	0.09	0.01
25	1.3	26.4	1.6	0.31	0.17	0.50	0.09	0.07
26	58.2	27.8	5.6	0.46	0.25	1.05	0.17	0.14
27	11.0	*	3.0	0.10	0.08	0.40	0.13	0.14
28	20.5	14.0	2.1	0.33	0.08	0.05	0.04	0.04
29	34.0	*	*	0.40	0.20	0.60	0.30	0.05
30	25.0	*	10.6	0.40	0.60	0.60	0.40	0.20
31	12.0	*	2.5	0.30	0.30	0.90	0.20	0.20
32	6.0	*	9.6	0.70	1.60	4.80	0.20	0.40
33	17.0	*	10.2	0.40	0.20	1.30	0.10	0.10
34	3.0	*	4.8	0.20	0.10	0.70	0.10	0.10
35	6.0	*	7.9	0.40	0.60	4.20	0.20	0.40
36	4.0	*	2.0	0.20	0.00	0.40	0.00	0.10
37	1.0	29.0	8.7	0.20	0.10	0.30	0.02	0.30
38	12.0	16.0	4.0	0.05	0.00	0.22	0.02	0.07
39	*	*	*	*	*	*	*	*
40	*	*	*	*	*	*	*	*
41	*	*	*	*	*	*	*	*
42	*	*	*	*	*	*	*	*

%MOISTUR = moisture content; %LOI = organic matter;

Exchangeable cations (potassium, magnesium, calcium, sodium and manganese) are expressed as me/100 g.

Site survey results: means per site of site and tree factors.

Site	IRON	AL	CA:FE	CA:AL	%SILT	SPECIES	RINGWIDT
1	39.0	8.6	0.24	1.06	34	*	*
2	47.0	13.3	0.01	0.03	57	1	*
3	8.0	2.3	0.35	4.23	11	2	0.31
4	3.6	1.0	35.40	307.40	20	2	*
5	20.8	5.4	1.70	6.56	32	2	0.29
6	5.3	5.3	61.10	202.50	25	*	0.16
7	16.5	2.6	0.50	1.02	50	2	0.25
8	11.8	0.6	0.14	2.75	32	3	0.24
9	16.0	22.0	0.07	0.04	59	2	0.19
10	39.0	2.2	0.10	1.68	48	1	0.25
11	19.5	8.0	0.08	0.19	60	*	*
12	12.0	3.1	0.02	0.04	52	3	0.31
13	15.0	7.6	0.34	0.67	49	*	*
14	7.2	9.8	0.33	0.24	45	2	0.25
15	49.0	8.4	0.03	0.19	27	2	0.18
16	39.0	12.3	0.05	0.08	19	3	0.19
17	4.5	10.6	0.20	0.08	13	*	0.26
18	18.5	3.4	0.10	0.56	23	3	0.33
19	20.2	9.8	0.26	0.54	66	3	0.33
20	23.6	4.3	0.06	0.30	22	3	0.25
21	15.5	2.7	0.14	1.06	9	3	0.25
22	22.2	6.2	0.03	0.10	16	*	0.23
23	28.0	13.0	0.00	0.00	35	1	0.24
24	20.0	7.4	0.27	0.73	32	2	*
25	24.0	7.8	0.11	0.33	38	1	*
26	4.0	6.8	1.30	0.23	13	2	0.24
27	20.0	5.0	0.10	0.38	40	2	0.26
28	13.9	5.8	0.02	0.04	45	*	0.22
29	60.0	46.8	0.05	0.06	42	2	0.24
30	44.0	10.0	0.06	0.26	48	1	0.21
31	8.5	10.0	0.60	0.50	43	3	*
32	24.0	4.0	1.00	6.00	50	3	0.31
33	27.0	7.0	0.20	0.90	40	*	*
34	15.0	6.0	0.20	0.60	42	*	*
35	24.0	11.0	0.90	1.90	35	1	0.26
36	7.0	2.0	0.30	1.20	20	1	0.24
37	17.0	7.0	0.10	0.20	42	3	0.21
38	8.0	1.0	0.14	1.10	46	2	0.23
39	*	*	*	*	*	1	*
40	*	*	*	*	*	*	*
41	*	*	*	*	*	*	0.14
42	*	*	*	*	*	2	0.19

Iron, aluminium and ratios of calcium to iron and aluminium are expressed in parts per million. Ring width = cm.
Species: 1 = sessile oak; 2 = pedunculate oak; 3 = hybrid oak.

APPENDIX 3.4

Data from site-surveys of shake incidence and severity (Chapter 3). This summary table lists those regressions which had a significance higher than P = 0.050. For list of all variables tested, see Section 3.2.2.7 part II.

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P
Percentage shaken	+percentage of trees with rot	9.1	.044
"	-percentage of clay in soil	8.5	.042
"	-percentage moisture in soil	14.4	.024
"	-Mg in soil	14.1	.012
"	-Ca "	17.1	.006
"	+Al "	8.6	.041
"	-Ca:Fe "	14.4	.011
"	-Ca:Al "	14.2	.011
"	-mean ring width	16.2	.016
"	-Ca +Fe	15.7	.019
"	-clay -moisture	17.5	.031
"	-moisture -pH	27.8	.006
"	-moisture -Ca	33.7	.002
"	-moisture -Mg	46.1	<.001
"	-Ca -ringwidth	42.3	<.001
"	-Mg -ringwidth	14.2	.056
"	-moisture -ringwidth -Ca +Fe	56.0	.001
"	-moisture -ringwidth -Ca:Fe	54.5	.001
"	-moisture -ringwidth -Ca:Al	54.5	.001
"	-moisture -ringwidth -Ca +Al	60.9	<.001
"	-moisture -ringwidth -Ca +Al +rot	66.7	.001
"	-ringwidth -moisture	21.0	.041
"	-moisture +rot +Al -Mg	54.8	<.001

APPENDIX 3.4 (continued)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P
Percentage shaken	-moisture -ringwidth +Al -Mg +rot	56.8	.004
"	-moisture -Ca -ringwidth	56.3	<.001
"	-moisture -Ca:Fe -ringwidth -Mg	55.1	.001
"	-moisture -ringwidth +Al	31.8	.019
"	-moisture -Mg +Al	52.6	<.001
"	-moisture -Mg +Al -ringwidth	50.9	.002
"	-moisture -clay +Al -ringwidth	37.5	.016
"	-moisture -ringwidth -Ca +rot	61.4	.001
"	-moisture -ringwidth -Mg +rot	48.0	.007
"	+rot -ringwidth -Mg +Al	24.3	.042
"	-ringwidth -Mg +Al	20.1	.039
"	-moisture -ringwidth +Al -Mg +rot -Ca:Fe	65.6	.002
"	-moisture -ringwidth +Al -Ca:Fe	59.1	.001
"	-moisture +rot +Al -Ca	47.6	.002
"	-moisture -Ca +Al	40.5	.001
"	-ringwidth -Ca +Al	45.2	.001
Percentage ring shaken	+rot	26.9	.001
"	-Mg	13.0	.017
"	-Ca	8.2	.050
"	+Al	10.3	.031
"	-mean ring width	17.3	.013
"	+rot -pH	33.6	.003
"	-Mg +Al	21.3	.007
"	+rot -ringwidth	37.5	.001
"	+rot -ringwidth -Mg	44.0	.001

APPENDIX 3.4 (continued)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P
Percentage ring shaken	+rot -ringwidth -Ca	56.0	<.001
"	+rot -ringwidth -Ca:Fe	55.1	<.001
"	+rot -moisture	34.8	.003
"	+rot -Mg +Al	42.2	<.001
"	+rot -Ca +Al	35.1	.001
"	+rot -ringwidth -Ca +Al	59.1	<.001
"	+rot -moisture -Ca	37.3	.005
"	-Ca -moisture +Al -ringwidth +rot	61.8	.002
"	-moisture -ringwidth +rot -Ca:Al	58.6	.001
"	+rot -moisture -ringwidth	43.0	.007
"	-Ca -moisture +Al -ringwidth	54.8	.001
"	+rot -moisture -K	33.5	.009
"	+rot -moisture -Mg	40.9	.003
"	+rot -ringwidth +Al	42.2	.002
"	+rot -ringwidth -Mg +Al	49.1	.001
"	+rot -Ca	30.9	.001
"	+rot -ringwidth -moisture -Mg	45.9	.009
"	+rot -ringwidth -moisture +Al	48.5	.006
"	+rot -ringwidth -moisture -Mg +Al	50.8	.008
"	-ringwidth -Mg +Al	35.2	.004
"	-moisture -Mg +Al	26.3	.018
"	+rot -moisture -Ca:Al	37.0	.005
"	-moisture -Mg +Al	26.3	.018
"	+rot -ringwidth -moisture -pH	60.1	.001
"	-ringwidth -Ca:Fe	43.9	<.001
"	-Ca -moisture +rot -ringwidth	59.0	.001

APPENDIX 3.4 (continued)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P
Mean index of shake	+altitude	9.4	.041
("	-moisture	10.7	.066)
"	-organic matter	11.7	.031
("	-Na	8.4	.056)
"	-Mn	10.9	.034
"	+sand	5.5	.101
"	+sand -Mn	12.6	.050
"	-Mn +altitude -moisture	31.5	.014
"	-moisture +altitude	33.7	.005
"	+altitude -moisture +sand	40.4	.004
"	+altitude -sodium	18.5	.020
"	+altitude +sand	19.5	.016
"	+altitude -Mn	18.8	.019
"	+altitude -organic matter -Mn	23.7	.016
"	+altitude -organic matter +sand	24.9	.013
"	+altitude -organic matter	21.1	.014

APPENDIX 3.4 (continued)

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P
Calcium in soil	+ Magnesium in soil	13.2	.014
Potassium in soil	+Magnesium in soil	39.3	$<.001$
Potassium in soil	+Calcium in soil	9.0	.038
Moisture in soil	+organic matter in soil	45.8	$<.001$
pH of soil	+Calcium in soil	90.0	$<.001$
pH of soil	+Magnesium in soil	23.0	.004
%age with mineral stain	-K	36.3	.003
"	-Mg	30.8	.007

APPENDIX 3.5

SITE SURVEY DATA:

REGRESSION CALCULATIONS AND ANALYSES OF VARIANCE.

Regression equation:

Percentage of shaken oaks =
106.0 - 0.9 moisture - 0.9 Ca + 1.1 Al - 214.0 r.width

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	105.9	20.8	5.08	0.000
%moisture	-0.9	0.4	-2.34	0.032
calcium	-0.9	0.2	-3.79	0.001
aluminium	1.1	0.6	1.77	0.095
ring width	-214.0	72.3	-2.95	0.009

s = 13.3 r^2 = 60.9%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	4	6473.6	1618.4	9.2
Residual	17	3001.0	176.5	
Total	21	9474.6		

Regression equation:

Percentage of shaken oaks =
104.0 - 0.9 moisture - 0.9 Ca + 1.2 Al - 214.0 r.width + 0.1 rot

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	104.0	22.0	4.75	0.000
%moisture	-0.9	0.4	-2.31	0.037
calcium	-0.9	0.2	-3.78	0.002
aluminium	1.2	0.6	1.85	0.085
ring width	-214.0	77.2	-2.77	0.015
% with rot	0.1	0.2	0.49	0.629

s = 12.6 r^2 = 66.7%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	5	6835.0	1367.0	8.6
Residual	14	2218.8	158.5	
Total	19	9053.7		

APPENDIX 3.5 continued.

Regression equation:

Percentage of shaken oaks =
46.8 - 0.7 moisture + 1.4 Al - 42.9 Mg + 0.2 rot

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	46.8	10.0	4.68	0.000
% moisture	-0.7	0.4	-1.49	0.153
aluminium	1.4	0.7	2.05	0.053
magnesium	-42.9	13.4	-3.19	0.005
% with rot	0.2	0.2	1.23	0.234

s = 15.4 r^2 = 54.8%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	4	7792.6	1948.2	8.26
Residual	20	4715.4	235.8	
Total	24	12508.0		

Regression equation:

Percentage of oaks with ring shake =
80.7 + 0.3 rot - 248.0 r.width - 0.7 Ca + 0.5 Al

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	80.7	17.5	4.61	0.000
% with rot	0.3	0.2	1.96	0.063
ring width	-248.0	64.5	-3.84	0.001
calcium	-0.7	0.2	-3.17	0.005
aluminium	0.5	0.3	1.62	0.119

s = 12.2 r^2 = 59.1%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	4	5957.5	1489.4	10.03
Residual	21	3119.1	148.5	
Total	25	9076.6		

Regression equation:

Percentage of oaks with ring shake =
76.6 - 0.6 Ca - 0.7 moisture + 0.9 Al - 185.0 r.width + 0.3 rot

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	76.7	20.8	3.68	0.002
calcium	-0.6	0.2	-2.50	0.025
% moisture	-0.7	0.4	-1.91	0.077
aluminium	0.9	0.6	1.46	0.167
ring width	-185.0	73.4	-2.52	0.024
% with rot	0.3	0.2	1.70	0.110

s = 12.0 r^2 = 61.8%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	5	5127.6	1025.5	7.15
Residual	14	2007.0	143.4	
Total	19	7134.5		

APPENDIX 3.5 continued.

Regression equation:

Percentage of oaks with ring shake =
125.0 + 0.3 rot - 234.0 r.width - 0.7 moisture - 10.2 pH

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	125.0	27.0	4.63	0.000
% with rot	0.3	0.2	1.86	0.082
ring width	-234.0	73.1	-3.20	0.006
% moisture	-0.7	0.4	-1.82	0.088
pH	-10.2	3.7	-2.80	0.013

s = 12.2 r^2 = 60.1%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	4	4886.2	1221.6	8.15
Residual	15	2248.3	149.9	
Total	19	7134.6		

Regression equation:

Mean index of shake severity =
11.8 + 0.1 altitude - 0.5 moisture + 0.2 sand

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	11.8	10.7	1.11	0.282
altitude	0.1	0.03	3.45	0.003
% moisture	-0.5	0.3	-1.52	0.144
% sand	0.2	0.1	1.83	0.082

s = 9.6 r^2 = 40.4

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	3	1718.2	572.7	6.19
Residual	20	1851.1	92.6	
Total	23	3569.3		

Regression equation:

Mean index of shake severity =
27.5 - 0.7 moisture + 0.1 altitude

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	27.5	6.7	4.10	0.001
% moisture	-0.7	0.3	-2.27	0.034
altitude	0.1	0.03	2.94	0.008

s = 10.2 r^2 = 33.7%

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	2	1407.9	704.0	6.84
Residual	21	2161.4	102.9	
Total	23	3569.3		

APPENDIX 3.5 continued.

Regression equation:

Mean index of severity =
8.9 + 0.1 altitude - 1.0 organic matter + 0.2 sand

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	8.9	9.6	0.92	0.365
altitude	0.1	0.03	2.66	0.013
% organic matter	-1.0	0.7	-1.39	0.176
% sand	0.2	0.1	1.55	0.131

$s = 11.0$ $r^2 = 24.9\%$

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	3	1572.4	524.1	4.31
Residual	27	3279.8	121.5	
Total	30	4852.2		

Regression equation:

Percentage of oaks with mineral stain =
70.4 - 53.1 K - 18.9 Mg

Indep. variable	Coeff.	St. dev.	t-ratio	P
Constant	70.4	10.0	7.03	0.000
Potassium	-53.1	34.9	-1.52	0.146
magnesium	-18.9	21.3	-0.89	0.387

$s = 24.0$ $r^2 = 35.5\%$

VARIATION DUE TO	DF	SUM OF SQUARES	MEAN SQUARE	F
Regression	2	7157.3	3578.6	6.23
Residual	17	9767.9	574.6	
Total	19	16925.2		

APPENDIX 3.6

Character	t	df	P	mean sessile	mean pedunc
% shaken on site	0.50	12	0.63	47.9	41.4
% ring shaken on site	-0.52	16	0.61	21.6	26.4
mean index	0.09	14	0.93	22.0	21.6
sapwood thickness (cm)	1.13	8	0.29	3.7	3.2
bark thickness (cm)	1.35	10	0.21	1.6	1.9
wide ray frequency (n/cm)	0.66	1	0.63	4.5	4.1
% trees with rot in butt	-0.81	17	0.43	7.4	11.5
mean ring width (cm)	-0.06	13	0.95	0.24	0.24
mean diameter (cm)	-1.13	16	0.28	63.0	69.8
% trees w mineral stain	0.31	10	0.76	47.3	51.3
altitude of site (m)	-0.43	10	0.67	92	107
% clay in soil	-0.91	15	0.38	11.0	16.3
% sand in soil	0.12	14	0.91	48.9	48.0
% silt in soil	0.69	15	0.50	40.1	35.7
% stone in soil	0.30	15	0.77	13.9	11.8
% moisture in soil	-0.09	5	0.93	20.1	20.6
Soil organic matter (%LOI)	0.48	7	0.64	5.7	4.8
pH of soil	-0.59	13	0.56	3.16	3.39

Survey results: summary of differences between means of data from sessile oak sites and pedunculate oak sites.

Sites with sessile oak = 8; sites with pedunculate oak = 13

continued ...

APPENDIX 3.6. (continued)

Character	t	df	P	mean sessile	mean pedunc
Ca:Fe in soil (ppm)	-1.04	11	0.32	0.2	7.6
Ca:Al in soil (ppm)	-1.02	11	0.33	0.8	26.8
Ca in soil (me/100 g)	-1.04	11	0.32	0.94	6.20
K in soil (me/100 g)	0.53	15	0.60	0.35	0.30
Mg in soil (me/100 g)	-0.54	14	0.60	0.24	0.31
Na in soil (me/100 g)	0.34	8	0.74	0.14	0.12
Mn in soil (me/100 g)	0.61	9	0.55	0.13	0.09
Fe in soil (ppm)	1.50	15	0.15	30.4	19.4
Al in soil (ppm)	-0.32	15	0.75	8.5	9.9

Survey results: summary of differences between means of data from sessile oak sites and pedunculate oak sites.

Sites with sessile oak = 8; sites with pedunculate oak = 13

APPENDIX 3.7.

SPECIES DIFFERENCES IN SHAKE ASSOCIATIONS WITH SITE OR TREE CHARACTERISTICS.

No significant differences had been found between sessile oak sites and pedunculate oak sites, for site factors, tree characteristics or incidence and severity of shake. However, there is a possibility of species difference in response to site factors. Therefore, the single regression analyses carried out on data for all 42 sites, were repeated separately for the thirteen pedunculate oak sites and for the eight sessile oak sites; a few of the multiple regressions were also repeated. Regression analyses of data from single-species sites are summarised in Appendix 3.8.

SESSILE OAK. There were too few sites to base firm conclusions on the results of these regressions, but it seemed that there was a positive association between the percentage of oaks with rot, and a) the percentage of shaken oaks in a site (r^2 = 53.7%), and b) the percentage of oaks containing ring shake (r^2 = 51.6%); the regression equations were significant at $P < 0.050$. There was a strong positive association between site altitude and the severity of shake (r^2 = 72.7%). These results confirmed or strengthened those from analyses of all 42 sites together.

continued ....

APPENDIX 3.7. (continued)

PEDUNCULATE OAK. There was a positive association between the percentage of oaks with rot, and a) the percentage of shaken oaks (r^2 = 50.8%), b) the percentage of oaks with ring shake (r^2 = 55.5%), and c) the mean severity of shake in oaks (r^2 = 35.8%); the regressions were significant at $P < 0.010$ for incidence of shake, and $P < 0.050$ for severity. There were negative associations between a) the amount of magnesium in the soil, and b) mean ring width, and the percentages of shaken oaks and oaks with ring shake.

There was no link between the severity of shake in pedunculate oaks, and the altitude of site, or percentage of soil moisture. This contrasted with the results of regressions using data from sessile sites and from all sites, despite the fact that the pedunculate sites occurred over the whole range of altitude.

APPENDIX 3.8

Data from site-surveys of shake incidence and severity (Chapter 3). Summary lists of those regressions which had a significance higher than P = 0.050. For list of all variables tested, see Section 3.2.2.7 part II.

DEPENDENT VARIABLE	INDEPENDENT VARIABLES	ADJUSTED R^2 (%)	P	TOTAL DF
RESULTS FROM SESSILE OAK SITES.				
Percentage of shaken oaks on site	+rot	53.7	.037	6
"	-pH	91.1	.007	4
"	-moisture	84.4	.053	5
Percentage of oaks with ring shake	+rot	51.6	.042	6
Mean index	+altitude	71.8	.021	5
RESULTS FROM PEDUNCULATE OAK SITES.				
Percentage of shaken oaks on site	+rot	50.8	.004	12
"	-Mg	53.6	.004	11
"	-ring width	39.1	.023	10
"	-Mg +rot	71.4	.001	11
Percentage of oaks with ring shake	+rot	55.5	.002	12
"	-Mg	37.8	.020	11
"	-ring width	42.9	.017	10
Mean index	+rot	33.6	.028	11

APPENDIX 3.9

Soil component	t	df	P	mean below sound	mean below shaken
moisture (%)	0.93	8	0.38	19.1	13.1
pH (in $CaCl_2$)	0.20	9	0.84	3.38	3.31
stone (%)	-1.17	13	0.26	23.7	39.3
organic matter (% LOI)	1.10	11	0.30	2.74	2.25
clay (%)	1.06	13	0.31	12.1	9.2
sand (%)	-0.57	13	0.58	53.9	59.4
potassium (me/100 g)	0.69	7	0.51	0.48	0.27
magnesium (me/100 g)	-0.70	8	0.50	0.12	0.20
calcium (me/100 g)	0.21	13	0.84	1.70	1.32
iron (ppm)	-0.80	10	0.44	15.4	22.1
aluminium (ppm)	-1.02	10	0.33	4.8	7.4
Ca:Fe (ppm)	0.79	7	0.46	3.1	0.7
Ca:Al (ppm)	0.88	7	0.41	9.8	1.8

Survey results: differences between means of soil factors for soils beneath individual shaken and sound oaks.

Two soil samples (one from under sound oak, one from under shaken oak) taken from each of eight sites; site numbers 8, 11, 14, 16, 20, 21, 23 and 46.

APPENDIX4.1.1.MEANS PER TREE OF WOOD STRUCTURE CHARACTERISTICS IN BLOCK A (ANNUAL RINGS 1955 - 1964).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SHAKEN OAKS IN SHAKE-PRONE WOODLANDS															
LL3	1	0.59	0.28	0.30	54.4	1	20	11.8	11.8	5.5	0.22	259	225	47722	0.88
G1295	3	1.19	0.43	0.76	40.1	1	13	9.4	8.8	5.2	0.30	278	319	71849	1.16
G1232	5	1.73	0.78	0.95	49.0	2	15	14.7	14.1	5.4	0.26	235	311	59100	1.33
LL6	7	1.44	0.49	0.95	35.4	1	-	10.6	9.0	7.2	0.13	-	-	-	-
G1248	9	2.94	0.97	1.97	35.2	2	-	10.0	8.6	4.4	0.19	-	-	-	-
PHu	11	3.02	0.63	2.39	23.3	2	-	14.2	13.6	6.1	0.23	-	-	-	-
SOUND OAKS IN SHAKE-PRONE WOODLANDS															
LL4	1	2.09	0.68	1.41	34.6	2	19	12.6	11.3	5.5	0.21	258	324	67676	1.26
G1243	3	1.85	0.72	1.13	41.6	2	13	10.4	9.6	3.0	0.32	236	285	53929	1.22
G1225	5	4.71	1.53	3.18	34.4	4	18	9.4	8.7	5.4	0.16	235	365	71596	1.56
LL2	7	0.97	0.27	0.69	29.8	1	-	14.7	14.2	4.5	0.32	-	-	-	-
G1218	9	0.54	0.22	0.32	42.1	1	-	16.2	16.2	6.7	0.22	-	-	-	-
PHq	11	4.24	0.78	3.66	23.6	2	-	6.8	5.7	5.0	0.11	-	-	-	-

†In Appendix Tables 4.1 - 4.2, quantified wood structure characteristics are means of values from a number of rings per tree. Variation between rings within a tree was often high (earlywood percentage of ring ranged from 20 - 100% in some cases); consequently, mean EW% figures do not equal the percentages which can be calculated from the means of ring width and earlywood width in these tables. The note on page 201 is relevant to means of tree-values given in Appendix Table 4.3.

APPENDIX 4.1.1. continued: MEANS PER TREE OF WOOD STRUCTURE CHARACTERISTICS IN BLOCK A (1955 - 1964).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SHAKEN OAKS IN SOUND WOODLANDS															
B19	2	1.38	0.34	1.04	24.9	1	18	7.8	6.8	5.0	0.13	244	249	48139	1.04
W3	4	0.68	0.34	0.34	57.2	2	16	17.0	16.0	7.0	0.24	179	202	28976	1.14
B18	6	1.56	0.34	1.22	22.7	1	18	7.3	6.2	3.9	0.15	265	264	55473	1.02
WIII	8	0.56	0.26	0.30	45.1	1	-	16.4	15.4	7.8	0.20	-	-	-	-
B2	10	0.96	0.31	0.65	33.4	1	-	0.9	0.8	0.4	0.21	-	-	-	-
InV A only	12	1.30	0.39	0.91	30.7	1	-	4.8	4.1	2.5	0.17	-	-	-	-
SOUND OAKS IN SOUND WOODLANDS															
B15	2	0.89	0.31	0.58	36.5	1	12	4.2	3.5	2.3	0.16	270	256	54992	0.96
WIV	4	2.08	0.62	1.46	34.4	2	19	10.0	9.3	5.0	0.19	228	276	51141	1.22
B16	6	1.51	0.61	0.90	42.2	2	15	7.4	6.4	4.6	0.14	287	325	74160	1.15
WII	8	0.45	0.17	0.29	47.8	1	-	5.8	5.3	3.9	0.12	-	-	-	-
B4	10	0.68	0.31	0.37	47.6	1	-	4.1	3.9	3.6	0.10	-	-	-	-
InIII	12	0.29	0.29	0.0	100.0	1	-	7.3	7.3	2.9	0.24	-	-	-	

† See note, p.371

APPENDIX4.1.2.MEANS PER TREE OF WOOD STRUCTURE CHARACTERISTICS IN BLOCK B (ANNUAL RINGS 1935 - 1944).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SHAKEN OAKS IN SHAKE-PRONE WOODLANDS															
LL3	1	1.30	0.32	0.98	25.8	1	18	11.2	10.5	5.5	0.20	256	256	53071	1.02
G1295	3	1.94	0.55	0.82	46.7	1	14	3.6	3.4	1.8	0.15	294	357	84690	1.22
G1232	5	3.30	1.03	2.27	34.1	3	14	13.6	12.3	4.7	0.26	237	329	63845	1.40
LL6	7	1.66	0.62	1.04	38.2	2	-	8.4	7.1	5.0	0.16	-	-	-	-
G1248	9	4.51	1.21	3.29	30.3	3	-	8.0	7.1	3.8	0.14	-	-	-	-
PHu	11	3.21	0.85	2.36	33.8	2	-	14.0	13.0	10.5	0.25	-	-	-	-
SOUND OAKS IN SHAKE-PRONE WOODLANDS															
LL4	1	1.68	0.65	1.03	40.0	2	17	13.0	12.4	6.0	0.21	278	328	72908	1.19
G1243	3	1.40	0.60	0.80	45.9	2	15	7.8	7.2	3.1	0.24	223	273	48926	1.23
G1225	5	7.54	1.73	5.73	23.9	4	20	6.8	6.6	3.0	0.22	232	356	68573	1.54
LL2	7	2.02	0.57	1.45	29.2	2	-	10.1	8.8	2.7	0.32	-	-	-	-
G1218	9	0.53	0.26	0.27	51.4	1	-	14.5	14.5	6.2	0.24	-	-	-	-
PHq	11	-	-	-	-	-	-	-	-	-	-	-	-	-	-

† See note, p.371

APPENDIX 4.1.2 continued: MEANS PER TREE OF WOOD STRUCTURE CHARACTERISTICS IN BLOCK B (1935 - 1944).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
							SHAKEN OAKS IN SOUND WOODLANDS								
B19	2	1.12	0.28	0.84	27.0	1	22	7.4	7.6	4.7	0.16	219	211	36807	0.98
W3	4	3.81	1.10	2.71	31.3	4	21	21.6	19.4	8.8	0.21	201	279	46164	1.40
B18	6	1.95	0.47	1.48	26.1	2	18	7.4	6.4	4.6	0.14	256	284	58020	1.13
WIII	8	3.78	1.09	2.69	31.9	4	-	21.9	18.0	7.5	0.23	-	-	-	-
B2	10	1.15	0.30	0.86	26.0	1	-	1.3	1.0	0.8	0.13	-	-	-	-
InV	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-
							SOUND OAKS IN SOUND WOODLANDS								
B15	2	1.43	0.38	1.05	26.7	1	20	4.3	3.5	3.1	0.11	255	265	53645	1.05
WIV	4	2.07	0.71	1.36	37.1	2	20	10.0	8.7	6.0	0.14	231	298	55594	1.30
B16	6	1.90	0.71	1.19	38.1	2	16	5.3	4.7	4.6	0.10	269	317	68100	1.19
WII	8	1.82	0.46	1.36	27.9	2	-	16.5	13.8	6.2	0.22	-	-	-	-
B4	10	1.16	0.41	0.75	36.3	1	-	6.0	5.2	4.5	0.18	-	-	-	-
InIII	12	0.64	0.28	0.36	45.1	1	-	6.9	6.6	2.6	0.25	-	-	-	-

† See note, p.371

APPENDIX4.1.3.MEANS PER TREE OF WOOD STRUCTURE CHARACTERISTICS IN BLOCK C (ANNUAL RINGS 1901 - 1910).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SHAKEN OAKS IN SHAKE-PRONE WOODLANDS															
LL3	1	2.04	0.40	1.64	19.3	1	-	14.4	10.2	6.0	0.18	-	-	-	-
G1295	3	2.09	0.60	1.49	32.0	1	-	13.6	12.3	4.2	0.30	-	-	-	-
G1232	5	3.50	0.95	2.55	32.5	3	-	13.8	10.7	5.7	0.20	-	-	-	-
LL6	7	1.85	0.70	1.15	38.0	2	-	9.1	7.5	7.0	0.11	-	-	-	-
G1248	9	5.08	1.43	3.66	28.4	4	-	9.5	8.5	4.6	0.19	-	-	-	-
PHu	11	3.78	0.71	3.07	24.6	2	-	12.9	10.5	5.6	0.18	-	-	-	-
SOUND OAKS IN SHAKE-PRONE WOODLANDS															
LL4	1	2.72	0.83	1.89	32.2	2	-	8.8	7.5	5.5	0.14	-	-	-	-
G1243	3	2.35	0.72	1.63	32.3	2	-	10.9	9.5	5.0	0.37	-	-	-	-
LL2	7	1.24	0.29	0.95	24.0	1	-	6.0	5.3	2.0	0.28	-	-	-	-
G1218	9	2.80	0.78	2.02	31.0	2	-	12.6	11.0	5.9	0.19	-	-	-	-

No data for G1225 and PHq.

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SOUND OAKS IN SOUND WOODLANDS (data for one site only)															
InIII	12	0.91	0.33	0.58	35.6	1		5.1	4.7	2.5	0.18	-	-	-	-

† See note, p. 371

APPENDIX 4.2. MEANS PER TREE, OF WOOD STRUCTURE CHARACTERISTICS IN BLOCKS A + B (ANNUAL RINGS 1955 - 1964, AND 1935 - 1944).

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
SHAKEN OAKS IN SHAKE-PRONE WOODLANDS															
LL3	1	0.94	0.30	0.64	40.1	1	19	11.5	11.2	5.4	0.21	257	241	50396	0.95
G1295	3	1.18	0.49	0.75	46.1	1	13	6.5	6.1	2.4	0.25	286	338	78270	1.19
G1232	5	2.51	0.90	1.61	41.5	2	14	14.2	13.2	5.1	0.26	236	320	61558	1.37
LL6	7	1.55	0.56	0.99	36.8	1	-	9.6	8.0	6.4	0.13	-	-	-	-
G1248	9	3.72	1.09	2.63	32.7	3	-	9.0	7.8	4.7	0.17	-	-	-	-
PHu	11	3.10	0.74	2.38	28.5	2	-	14.1	13.3	1.4	0.24	-	-	-	-
SOUND OAKS IN SHAKE-PRONE WOODLANDS															
LL4	1	1.89	0.67	1.22	37.3	2	18	12.8	11.9	5.7	0.13	268	326	70292	1.23
G1243	3	1.63	0.66	0.97	42.6	2	14	9.1	8.4	3.0	0.28	229	279	51428	1.22
G1225	5	6.05	1.62	4.43	29.4	4	19	8.1	7.7	4.2	0.18	233	360	70084	1.55
LL2	7	1.49	0.42	1.07	29.5	1	-	12.4	11.6	3.6	0.32	-	-	-	-
G1218	9	0.54	0.24	0.30	46.8	1	-	15.4	15.4	6.2	0.25	-	-	-	-
PHq A only	11	4.24	0.78	3.66	23.6	2	-	6.8	5.7	5.0	0.11	-	-	-	-

† See note, p.371

APPENDIX 4.2. continued: MEANS OF WOOD STRUCTURE CHARACTERISTICS IN BLOCKS A + B (ANNUAL RINGS 1955 - 1964, AND 1935 - 1944) FOR EACH TREE.

Tree	Pair No.	Ring width mm	Early wood width mm	Late wood width mm	Early wood %†	EWV row no.	EWV freq	Wide ray % in EW	Wide ray % in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
							SHAKEN OAKS IN SOUND WOODLANDS								
B19	2	1.25	0.31	0.94	26.0	1	20	7.6	7.2	4.8	0.15	231	230	42473	1.01
W3	4	2.25	0.72	1.52	44.3	2	18	19.3	17.7	7.8	0.22	190	240	37570	1.27
B18	6	1.75	0.40	1.35	24.4	1	18	7.3	6.2	4.2	0.14	260	275	56847	1.07
WIII	8	2.17	0.67	1.50	41.5	2	-	19.1	16.7	7.7	0.22	-	-	-	-
B2	10	1.06	0.30	0.75	29.7	1	-	1.1	0.9	0.6	0.16	-	-	-	-
InV A only	12	1.30	0.39	0.91	30.7	1	-	4.8	4.1	2.5	0.17	-	-	-	-
							SOUND OAKS IN SOUND WOODLANDS								
B15	2	1.16	0.34	0.82	31.6	1	16	4.2	3.5	2.7	0.13	262	260	54318	1.00
WIV	4	2.08	0.66	1.41	36.4	2	20	10.0	9.0	5.3	0.17	230	287	53367	1.26
B16	6	1.70	0.66	1.04	40.2	2	16	6.3	5.5	4.6	0.12	278	321	71130	1.17
WII	8	1.06	0.30	0.77	39.7	1	-	9.4	8.1	5.2	0.18	-	-	-	-
B4	10	0.92	0.36	0.56	42.0	1	-	5.0	4.4	4.1	0.11	-	-	-	-
InIII	12	0.46	0.29	0.18	72.6	1	-	7.0	6.8	2.8	0.24	-	-	-	-

† See note, p. 371

		Ring width mm	Early wood width mm	Late wood width mm	Early wood % †	EWV row no.	EWV freq	Wide ray% in EW	Wide ray% in LW	WR freq	WR size in LW mm	EWV tan diam um	EWV rad diam um	EWV area um²	EWV shape
MEANS OF OAKS FROM SHAKE-PRONE WOODLANDS															
Shaken trees	$\bar{x}$	2.2	0.68	1.50	37.6	2		10.8	9.9	4.2	0.21	260	300	63408	1.17
	s.d.	1.1	0.29	0.85	6.3	1		3.1	3.0	1.9	0.05	25	52	14029	0.21
Sound trees	$\bar{x}$	2.6	0.73	1.94	34.9	2		10.8	10.1	4.6	0.21	243	322	63935	1.33
	s.d.	2.1	0.48	1.68	8.9	1		3.3	3.5	1.2	0.08	22	41	10832	0.19
	n	6	6	6	6	6		6	6	6	6	3	3	3	3
	t														-2.248
	P	ns	ns	ns	ns	ns		ns	ns	ns	ns	ns	ns	ns	0.154
MEANS OF OAKS FROM SOUND WOODLANDS															
Shaken trees	$\bar{x}$	1.63	0.46	1.16	32.8	1		9.9	8.8	4.6	0.18	227	248	45630	1.12
	s.d.	0.50	0.18	0.34	8.2	0		7.6	6.7	2.8	0.04	35	24	10019	0.14
Sound trees	$\bar{x}$	1.23	0.44	0.80	43.8	1		6.8	6.2	4.1	0.16	257	289	59605	1.14
	s.d.	0.58	0.18	0.42	14.6	0		2.4	2.1	1.1	0.05	24	31	9992	0.13
	n	6	6	6	6	6		6	6	6	6	3	3	3	3
	t	2.152 +		3.066 *	-1.538			1.236	1.182			-4.646 *	-7.444 *	-12.140 **	
	P	0.083	ns	0.028	0.183	ns		0.271	0.291	ns	ns	0.040	0.014	0.005	ns

APPENDIX 4.3. DIFFERENCES IN WOOD STRUCTURE (= ANNUAL RINGS) BETWEEN SHAKEN AND SOUND TREES WITHIN SHAKEN AND SOUND WOODLANDS. Differences between the means tested with t-tests of paired samples.

† See note, p.371

APPENDIX 4.4.

COMPARISONS OF MEAN STRUCTURE CHARACTERISTICS IN WOOD OF SHAKEN AND SOUND OAKS FORMED IN THE SAME CALENDAR YEARS.

RESULTS OF t-TESTS OF PAIRED SAMPLES:

Degrees of freedom = 5 for earlywood vessel parameters (except row number); df = 11 for all other characteristics.

Wood structure characteristic	t-ratio	Student's t at P = 0.10
Ring width	0.154	1.796
Earlywood width	0.290	"
Latewood width	0.107	"
Earlywood percentage of ring	0.960	"
Earlywood vessel row number	0.572	"
Earlywood vessel frequency	0.131	2.015
Wide ray percentage of earlywood	0.920	1.796
Wide ray percentage of latewood	0.760	"
Wide ray frequency	0.078	"
Wide ray size	0.330	"
Earlywood vessel tangential diameter	0.470	2.015
Earlywood vessel radial diameter	-1.600	"
Cross-sectional area of EWVs	1.037	"
Earlywood vessel shape	1.979	"

APPENDIX 4.5.

COMPARISONS OF MEAN STRUCTURE CHARACTERISTICS IN WOOD OF SHAKEN AND SOUND OAKS FORMED AT EQUIVALENT CAMBIAL AGES.

RESULTS OF t-TESTS OF PAIRED SAMPLES:

Degrees of freedom = 9 for all characteristics.

Wood structure characteristic	t-ratio	P
Ring width	0.797	0.549
Earlywood width	0.175	0.859
Latewood width	1.005	0.343
Earlywood percentage of ring	-1.233	0.248
Wide ray percentage of earlywood	1.620	0.137
Wide ray percentage of latewood	1.374	0.201
Wide ray frequency	0.951	0.631
Wide ray size	-0.190	0.847

APPENDIX 4.6.

COMPARISONS OF MEAN WOOD STRUCTURE CHARACTERISTICS IN OAKS FROM SHAKE-PRONE AND SOUND WOODLANDS (WOOD FORMED IN SAME CALENDAR YEARS).

RESULTS OF t-TESTS:

Degrees of freedom = 22. L = data transformed to log base 10 prior to calculation of t-test, because variances not equal.

Wood structure characteristic	t-ratio	P
Ring width	L 1.674	0.105
Earlywood width	L 2.079	0.047
Latewood width	L 1.505	0.143
Earlywood percentage of ring	L -0.316	0.753
Earlywood vessel row number	1.548	0.132
Earlywood vessel frequency	-1.360	0.203
Wide ray percentage of earlywood	1.300	0.210
Wide ray percentage of latewood	1.471	0.152
Wide ray frequency	0.089	0.927
Wide ray size	1.910	0.066
Earlywood vessel tangential diameter	0.608	0.562
Earlywood vessel radial diameter	1.879	0.087
Cross-sectional area of EWVs	1.665	0.124
Earlywood vessel shape	1.277	0.229

APPENDIX 4.7.

COMPARISONS OF MEAN WOOD STRUCTURE CHARACTERISTICS IN OAKS FROM SHAKE-PRONE AND SOUND WOODLANDS (WOOD FORMED AT EQUIVALENT CAMBIAL AGES).

RESULTS OF t-TESTS:

Degrees of freedom = 20. L = data transformed to log base 10 prior to calculation of t-test, because variances not equal.

Wood structure characteristic	t-ratio	P
Ring width	L 4.816	0.0001
Earlywood width	L 4.186	0.0005
Latewood width	L 4.707	0.0002
Earlywood percentage of ring	-2.297	0.046
Earlywood vessel row number	L 2.514	0.020
Wide ray percentage of earlywood	1.99	0.057
Wide ray percentage of latewood	1.503	0.165
Wide ray frequency	1.429	0.165
Wide ray size	L 1.479	0.151

SEED ORIGIN		VARIABLES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
A	$\bar{x}$	13.2	2.6	6.5	11.0	59.4	13.0	19.5	9.7	7.1	11.4	56.7	14.4	21.5	10.0	7.1	49.3	27.4	11.3	18.4	4.3
	sd	0.9	0.7	3.5	5.5	7.1	1.9	4.3	4.1	3.3	4.5	5.8	3.6	4.5	4.5	3.3	7.3	7.4	4.0	5.1	2.8
B	$\bar{x}$	14.0	3.3	6.9	4.6	64.7	13.4	20.3	10.1	7.8	6.8	60.6	14.1	21.9	10.4	8.0	40.2	35.4	13.3	21.2	2.8
	sd	1.0	1.4	3.2	3.1	6.8	2.3	4.3	4.8	3.5	2.7	4.0	2.9	3.8	2.9	3.6	9.2	8.6	3.5	4.3	3.2
C	$\bar{x}$	13.4	3.0	6.4	6.0	67.2	12.5	18.8	8.0	6.7	5.9	61.3	16.4	23.9	9.8	7.0	43.9	33.2	12.2	19.2	3.8
	sd	1.3	0.9	2.3	2.2	3.3	2.4	2.4	2.4	1.6	2.5	3.6	3.5	4.0	3.4	1.7	7.7	6.0	3.0	2.3	2.6
D	$\bar{x}$	15.1	3.2	4.6	6.3	66.4	14.1	17.0	7.8	5.5	8.7	56.4	16.2	21.6	12.5	5.4	49.4	29.6	13.2	18.5	2.4
	sd	1.2	0.7	1.8	4.7	6.9	3.1	3.0	3.3	1.7	3.1	3.9	2.7	3.3	3.8	1.9	8.0	5.9	3.9	4.6	1.8
E	$\bar{x}$	12.8	3.1	4.5	7.7	65.8	13.4	18.0	8.5	5.8	4.6	62.1	13.6	19.4	13.9	5.4	44.6	33.4	13.3	18.7	3.2
	sd	1.3	0.9	2.0	4.5	7.1	2.4	2.4	4.1	2.7	3.8	6.6	2.8	4.3	5.6	2.2	6.8	5.0	4.2	3.6	2.7
F	$\bar{x}$	13.6	2.8	5.3	6.2	67.1	12.8	17.4	8.5	6.2	9.6	59.8	15.2	22.4	9.1	6.2	45.5	34.2	12.1	18.3	2.0
	sd	1.6	1.0	2.0	2.9	4.9	3.2	3.0	4.0	2.5	5.3	4.3	4.3	7.1	3.8	2.5	10.1	9.9	3.1	3.9	2.1

Appendix 5.1.1. Means and standard deviations of tissue proportions measured in the 1971 ring in 11 oak seed origins (n=12)
Key to variable numbers given at end of table.

(....continued overleaf)

SEED ORIGIN		VARIABLES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
G	$\bar{x}$	14.1	3.2	8.1	7.4	60.1	12.9	21.0	11.4	9.0	12.1	55.8	13.0	22.0	10.0	9.8	46.7	28.9	10.0	19.8	4.2
	sd	2.0	1.0	2.6	4.3	7.8	2.3	4.3	4.2	2.6	4.0	7.0	2.9	4.1	3.8	2.9	9.2	7.9	3.8	5.7	2.4
H	$\bar{x}$	13.8	2.8	6.4	7.6	65.2	12.2	18.7	8.0	8.0	9.7	59.8	12.6	20.3	9.6	7.8	46.2	32.3	10.7	18.4	3.0
	sd	1.4	0.6	2.0	4.1	6.3	3.2	3.4	3.2	2.1	4.6	6.3	3.0	2.9	3.5	2.5	7.6	6.0	4.0	4.0	2.2
J	$\bar{x}$	12.5	3.4	4.8	5.5	66.3	12.1	16.9	11.0	5.6	7.2	59.3	15.5	21.0	12.1	5.7	50.4	24.7	13.7	19.3	5.3
	sd	0.9	1.0	2.4	2.2	5.3	3.6	5.2	4.7	2.8	3.7	3.3	3.3	4.6	4.2	2.7	8.6	7.3	3.6	3.6	4.0
K	$\bar{x}$	12.2	3.0	4.3	6.6	63.3	14.9	18.5	11.0	5.2	8.8	60.3	13.8	19.9	11.8	5.1	47.4	31.3	13.1	19.0	3.1
	sd	1.7	1.0	2.5	3.3	5.9	2.5	2.9	3.5	2.8	3.3	4.2	3.0	6.3	3.3	2.9	11.9	8.7	4.4	5.6	2.3
L	$\bar{x}$	12.1	3.3	5.6	6.5	64.5	14.2	19.8	9.6	6.6	9.1	56.1	15.6	22.2	12.1	7.1	41.4	36.3	11.6	18.7	2.7
	sd	1.4	0.7	2.5	4.0	6.2	2.9	3.5	3.7	2.6	4.4	4.6	2.6	4.2	2.9	2.7	9.5	9.4	2.8	3.6	1.1

Appendix 5.1.1. Means and standard deviations of tissue proportions measured in the 1971 ring in 11 oak seed origins (n=12)

Key to variable numbers: 1- dbh; 2- 1971 ring width; 3- LateWood Zone 1 Wide Ray; 4- LWZ1 Vessel; 5- LWZ1 Fibre; 6- LWZ1 Narrow Ray; 7- LWZ1 Total Ray; 8- LWZ1 Parenchyma; 9- LateWood Zone 2 WR; 10- LWZ2V; 11- LWZ2F; 12- LWZ2NR; 13- LWZ2TR; 14- LWZ2P; 15- EarlyWood WR; 16- EWV; 17- EWF; 18- EWNR; 19- EWTR; 20- EWP.

APPENDIX 5.1.2. MEANS AND STANDARD DEVIATIONS OF EARLYWOOD VESSEL CHARACTERISTICS IN ELEVEN SEED ORIGINS OF OAK.

SEED ORIGIN		FREQUENCY n/cm	TAN. DIAM(um)	RAD. (DIAM)um	AREA um^2	SHAPE r:t diam.
A	$\bar{x}$	19.7	195	226	35823	1.18
	sd	2.6	18	19	5849	0.07
B	$\bar{x}$	19.1	195	227	35805	1.18
	sd	3.0	14	26	6334	0.12
C	$\bar{x}$	21.6	194	231	36084	1.22
	sd	3.7	19	14	4831	0.09
D	$\bar{x}$	20.0	209	254	42889	1.23
	sd	4.1	16	26	7084	0.09
E	$\bar{x}$	22.6	186	220	32944	1.20
	sd	3.6	13	20	5003	0.06
F	$\bar{x}$	23.2	168	226	31002	1.38
	sd	5.3	9	13	2965	0.08
G	$\bar{x}$	23.8	186	239	36347	1.30
	sd	3.3	15	35	8164	0.13
H	$\bar{x}$	20.5	201	222	36127	1.12
	sd	3.2	22	30	8391	0.06
J	$\bar{x}$	22.4	196	233	36842	1.20
	sd	2.6	12	18	4740	0.04
K	$\bar{x}$	19.6	192	255	40108	1.35
	sd	2.4	14	28	7135	0.08
L	$\bar{x}$	20.3	180	233	34016	1.32
	sd	4.3	14	15	3754	0.12

SEED ORIGIN		VARIABLES 1	2	3	4	5	6	7
A	$\bar{x}$	41.1	56.8	13.7	25.3	0.753	0.745	-
	sd	5.6	7.0	2.1	5.3	0.016	0.054	
						4	4	
B	$\bar{x}$	45.4	59.1	13.2	26.1	0.895	0.868	-
	sd	77.2	8.1	1.8	5.7	0.034	0.045	
						4	4	
C	$\bar{x}$	43.9	53.0	13.1	28.9	0.876	0.886	9.50
	sd	6.8	8.8	2.2	7.0	0.045	0.027	0.36
						4	4	3
D	$\bar{x}$	50.7	63.4	12.2	24.3	0.795	0.796	-
	sd	7.8	8.2	1.9	6.6	0.074	0.045	
						5	5	
E	$\bar{x}$	51.0	57.6	11.2	25.9	0.850	0.832	8.60
	sd	10.4	8.6	2.6	6.0	0.067	0.048	3.96
						10	10	2
F	$\bar{x}$	44.8	50.1	13.4	28.3	0.853	0.847	7.50
	sd	12.3	18.7	2.8	6.1	0.061	0.028	5.64
						7	7	3

Appendix 5.1.3. Means and standard deviations of heartwood and sapwood proportions and wood properties in oaks of 11 different seed origins. Key to variable numbers overleaf.

SEED ORIGIN		VARIABLES 1	2	3	4	5	6	7
G	$\bar{x}$	45.8	57.2	13.2	26.6	0.786	0.771	-
	sd	9.1	10.9	2.2	7.5	0.034	0.041	
						10	10	
H	$\bar{x}$	61.5	46.7	12.8	22.3	0.822	0.813	9.80
	sd	10.1	10.1	2.1	5.7	0.066	0.055	1.12
						6	6	11
J	$\bar{x}$	45.3	55.8	12.8	24.3	0.878	0.816	10.28
	sd	11.0	16.2	1.9	9.3	0.062	0.045	1.73
						10	10	12
K	$\bar{x}$	42.9	58.4	13.9	21.2	0.785	0.780	10.00
	sd	8.6	12.8	1.6	5.6	0.043	0.046	1.05
						8	8	12
L	$\bar{x}$	47.6	62.0	12.7	20.4	0.802	0.790	9.32
	sd	11.4	11.5	2.4	5.0	0.063	0.063	0.80
						10	10	11

Appendix 5.1.3. Means and standard deviations of heartwood and sapwood proportions and wood properties in oaks of 11 different seed origins.

Key to variable numbers: 1- Heartwood rings as percentage of total ring number; 2- Heartwood diameter as percentage of disc diameter; 3- Sapwood ring number; 4- Sapwood width (cm); 5- density of 1971 ring (g/cm^3); 6- mean density of disc at 0.5 m (g/cm^3); 7- splitting strength in radial longitudinal plane (N/mm^2).

N.B. n = 12 unless otherwise stated (figures in third row per seed origin).

RING WIDTH (mm)

T- t. of Significance f r A INGW using UNIQUE sums of squares

Source of Variation	SS	DF	MS	F	Sig of F
RESIDUAL	31.08	38	.82		
PLOT	4.67	10	.47	.57	.827
SEEDOR	13.43	10	1.34	1.64	.132
TREE W SEEDOR BY PLO	58.52	66	.89	1.08	.401

EWV TANGENTIAL DIAMETER (μm)

T. t. of Signif ca e f F1 P using UNIQUE sums f squares

Source of Variation	SS	DF	MS	F	Sig of F
RESIDUAL	7687.81	38	202.31		
PLOT	3250.67	10	325.07	1.61	.142
SEEDOR	11315.11	10	1131.51	5.59	.000
TREE W SEEDOR BY PLO	1[illegible]79.04	66	240.59	1.19	.285

EWV RADIAL DIAMETER (μm)

ARAD

Tests of Significance for [redacted] using UNIQUE sums of squares

Source of Variation	SS	DF	MS	F	Sig of F
RESIDUAL	1[illegible]1[illegible].61	38	558.33		
PLOT	6453.[illegible]	10	645.38	1.16	.349
[redacted] SEEDOR	1[illegible]254.4[illegible]	10	1225.44	2.19	[redacted] .040
TREE W SEEDOR BY PLO	397[illegible].86	66	513.29	.92	.6[illegible]

Appendix 5.2. Multivariate analyses of variance of ring width and earlywood vessels in diameter class II trees from the Penyard oak seed origin trial.

EWV AREA (μm^2)

Tests of Significance for [redacted] A AREA using UNI

Source of Variation	SS	DF	MS	F	Sig of F
RESIDUAL	1302406560	38	34273_57		
PLOT	505578794.7	10	5_55 8 4	1.48	.1_7
[redacted] SEEDOR	952_ 85 5.0	10	9522 8_1	_.78	[redacted] .011
TREE W SEEDOR BY PLO	2347424_19	66	3_56 0_4	1.04	.459

EWV SHAPE (R:T DIAM)

Tests of Significance for [redacted] ASHAPE using UNIQUE sums of squares

Source of Variation	SS	DF	MS	F	Sig of F
RESIDUAL	.34	38	.01		
PLOT	.04	10	.00	.43	.920
[redacted] SEEDOR	.64	10	.06	7.13	[redacted] .000
TREE W SEEDOR BY PLO	.52	66	.01	.87	.698

Appendix 5.2. (continued).
Multivariate analyses of variance of ring width and earlywood vessels in diameter class II trees from the Penyard oak seed origin trial.

APPENDIX 5.3.

INTENSIVE SAMPLING OF FOUR SEED ORIGINS: SUMMARY OF ANALYSES OF VARIANCE.

The following notes and summary table give further details of the results reported in section 5.7.1.7. for differences between the means of seed origins A, B, D and H in variables measured over five diameter classes (n = 58).

Heartwood proportions of H were significantly different from the other three origins, with the highest percentage of rings but the lowest percentage of disc diameter, as in the diameter class II (DCII) samples.

Ranks of means of sapwood ring number and sapwood width of A, D and H were in the same order as when DCII samples were compared, but both ring number and width means of origin B were much greater when measured over all diameter classes. Seed origin A was significantly different from B, D and H when measured over all diameter classes.

Wide ray proportions in all three zones of the ring were similar whether measured in DCII trees or averaged over all diameter classes, but in the latter samples, D differed significantly from B as well as from H.

Means of vessel proportions in latewood zone 1 of A, B, D and H were ranked in the same order as for the DCII samples, but the significance of the differences between A and D, and H and B was greater.

Seed origin A had a significantly smaller proportion of fibres in latewood zone 1, than B, D or H.

Means of vessel proportions in latewood zone 2 of A, B, D and H were ranked in the same order as for comparisons of DCII trees, but the differences were significant when trees of all diameter classes were averaged: A was significantly greater than B and D, H was greater than B.

Narrow ray proportion in latewood zone 2 was significantly greater in D than in H, although no means were significantly different when DCII trees were compared. Axial parenchyma in the same zone was significantly greater in H than in D.

Ranks of means of earlywood vessel proportions were in the same order as when DCII samples were compared, but the differences between origin B (lower EWV percentage) and A and D were significant.

Means of earlywood fibre proportions of A, B, D and H were ranked in the same order as for the DCII samples. B was significantly greater than A and H.

Earlywood narrow ray proportions were not significantly different between seed origins when trees of DCII were compared, but when measurements over all diameter classes were compared, H had significantly lower proportions than D, B and A.

Ranks of ring density and disc density means were in the same order as for DCII samples. Significances of differences between means were the same also, with the exception of more significant differences from the low density seed origin A.

VARIABLE		SEED ORIGIN A	H	D	B	Sig. of F	CR
DBH (cm)	x̄	11.7	12.3	13.1	12.5	ns	
	sd	3.0	3.2	3.6	2.9		
RING WIDTH (cm)	x̄	2.6	2.7	2.9	2.9	ns	
	sd	0.9	1.2	1.1	1.1		
HEARTWOOD % OF RINGS	x̄	30.3	54.9	43.1	43.4	***	7.6
	sd	17.5	17.2	15.8	13.2		
		H B D	**A D B**	**H A**	**A H**		
HEARTWOOD % OF DIAMETER	x̄	43.3	39.6	54.7	57.4	***	8.7
	sd	23.8	14.9	18.0	14.8		
		B D	**B D**	**H A**	**H A**		
							SED
SAPWOOD RING NUMBER	x̄	15.1	13.9	13.2	13.1	***	0.55
	sd	0.4	0.3	0.3	0.3		
		B D H	A	**A**	**A**		
SAPWOOD WIDTH (cm)	x̄	2.71	2.25	2.43	2.26	***	0.14
	sd	0.88	0.80	0.75	0.68		
		H B D	**A**	A	**A**		

Appendix 5.3.2 Differences in oak wood structure between means of seed origins A, B, D and H; measured across trees of all diameter classes.

n = 59 trees per seed origin for heartwood and tissue proportions (12 trees were sampled from each of five diameter classes). Differences between pairs of origins were tested with Tukey's HSD test and the critical range for pairs of means is given for significance at P < 0.05; seed origins which differ from each other at P < 0.01 are in bold print.

n = 6 - 10 trees per seed origin for density variables. Differences between pairs of means therefore tested with t-ratio (standard errors of difference calculated as described in section 5.4; approximate SED listed in this table). (Continues overleaf).

VARIABLE		SEED ORIGIN A	H	D	B	Sig. of F	CR
WIDE RAY % in LWZ1	x̄	5.6	6.2	4.7	6.3	**	1.3
	sd	2.8	2.4	2.4	2.9		
			D	B H	D		
VESSEL % in LWZ1	x̄	9.8	8.4	6.6	6.1	***	1.9
	sd	4.0	4.9	3.6	3.6		
		B D	B	A	A H		
FIBRE % in LWZ1	x̄	61.9	65.0	66.2	65.3	***	3.0
	sd	6.4	6.2	6.0	6.3		
		D B H	A	A	A		
WIDE RAY % in LWZ2	x̄	6.4	7.1	5.5	7.2	**	1.4
	sd	3.0	2.6	2.7	3.2		
			D	B H	D		
VESSEL % in LWZ2	x̄	10.4	9.3	7.8	6.7	***	2.0
	sd	4.3	5.0	4.1	3.2		
		B D	B	A	A H		
NARROW RAY % in LWZ2	x̄	13.4	12.9	14.7	14.0	*	1.5
	sd	3.2	3.1	3.5	3.1		
			D	H			
AXIAL PARENCHYMA % in LWZ2	x̄	10.6	9.5	12.4	11.4	***	2.0
	sd	4.6	3.9	4.5	3.1		
			D	H			

Appendix 5.3.2 cont. Differences in oak wood structure between means of seed origins A, B, D and H; measured across trees of all diameter classes. Continues overleaf.

VARIABLE		SEED ORIGIN A	H	D	B	Sig. of F	CR
WIDE RAY % in EW	x̄	6.5	7.4	5.4	7.4	***	1.4
	sd	3.0	2.9	2.6	3.2		
			D	H B	D		
VESSEL % in EW	x̄	47.0	45.0	46.7	41.8	**	4.1
	sd	8.6	9.6	7.8	8.4		
		B		B	A D		
FIBRE % in EW	x̄	30.7	34.7	31.6	35.1	**	3.7
	sd	8.2	8.3	6.9	7.8		
		B H	A		A		
NARROW RAY % in EW	x̄	11.9	10.2	13.0	12.3	***	1.6
	sd	3.5	3.7	3.3	2.8		
		H	D B A	H	H		
TOTAL RAY % in EW	x̄	18.3	17.6	18.4	19.7	+	2.0
	sd	4.2	4.6	4.3	3.6		
			B		H		
							SED
1971 RING DENSITY (g/cm³)	x̄	0.754	0.828	0.795	0.869	**	0.31
	sd	0.056	0.071	0.063	0.059		
		B H	A	B	A D		
DISC DENSITY (g/cm³)	x̄	0.757	0.820	0.784	0.857	**	0.22
	sd	0.050	0.058	0.035	0.054		
		B H	A	B	A D		

Appendix 5.3.2.(continued). Differences in wood structure and properties between means of seed origins A, B, D and H; measured across trees of all diameter classes.

APPENDIX 5.4.

Correlations of growth rate variables with wood structure and property variables in the four intensively-sampled seed origins. **(Notes overleaf).**

VARIABLE CORREL. WITH RING WIDTH	CORRELATION COEFFICIENT				
SEED ORIGIN	A	B	D	H	A+B+D+H
EARLYWOOD					
WR	0.135	0.154	*** 0.470	0.192	** 0.221
NR	* 0.277	0.221	* 0.285	** 0.390	*** 0.291
TR	* 0.323	* 0.306	*** 0.502	** 0.427	*** 0.392
V	* 0.315	0.157	0.128	0.053	0.131
F	** -0.378	* -0.271	*** -0.453	-0.216	*** -0.288
P	** -0.357	-0.143	-0.035	-0.192	** -0.186
LATEWOOD Z1					
WR	0.104	0.162	*** 0.487	0.165	** 0.217
NR	** 0.433	* 0.328	*** 0.461	* 0.324	*** 0.379
TR	** 0.405	* 0.328	*** 0.541	* 0.337	*** 0.395
V	* 0.348	-0.032	0.014	0.253	0.102
F	** -0.397	-0.146	** -0.437	-0.258	** -0.259
P	-0.103	-0.075	-0.018	* -0.303	-0.129
LATEWOOD Z2					
WR	0.150	0.180	*** 0.528	0.117	** 0.233
NR	0.084	* 0.323	*** 0.503	* 0.371	*** 0.338
TR	0.170	** 0.394	*** 0.618	** 0.440	*** 0.415
V	-0.265	-0.074	-0.219	-0.135	** -0.191
F	-0.183	-0.116	(*) -0.273	-0.138	* -0.160
P	** -0.362	-0.214	-0.162	0.013	0.007
EARLYWOOD Vs					
SIZE (AREA)					* 0.313
SHAPE					*** 0.530
RAD.DIAM.					** 0.441
TAN.DIAM.					0.060

APPENDIX 5.4. continued.

Correlations of growth rate variables with wood structure and property variables in the four intensively-sampled seed origins.

VARIABLE CORREL. WITH DIAM. B.H.	CORRELATION COEFFICIENT				
SEED ORIGIN	A	B	D	H	A+B+D+H
LATEWOOD Z1					
WIDE RAY	** 0.414	* 0.322	*** 0.553	* 0.287	*** 0.360
HEARTWOOD					
% OF RINGS	*** 0.533	*** 0.553	*** 0.685	*** 0.451	*** 0.513
% OF DIAM.	*** 0.495	* 0.347	*** 0.643	*** 0.578	*** 0.502
SAPWOOD					
WIDTH					*** 0.257
RING NUMBER					*** -0.383

NOTES:

All variables: n = 58 or 59, for single seed origins.

All variables except earlywood vessel dimensions: n = 229 for combined seed origins.

Earlywood vessel dimensions: n = 44 for combined seed origins.

WR = wide ray %; NR = narrow ray %; TR = total ray%; V = vessel%;
F = fibre%; P = axial parenchyma%.

Correlations significant at: * P < 0.050

** P < 0.010

*** P < 0.001