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A Literature Review

R. Worrell
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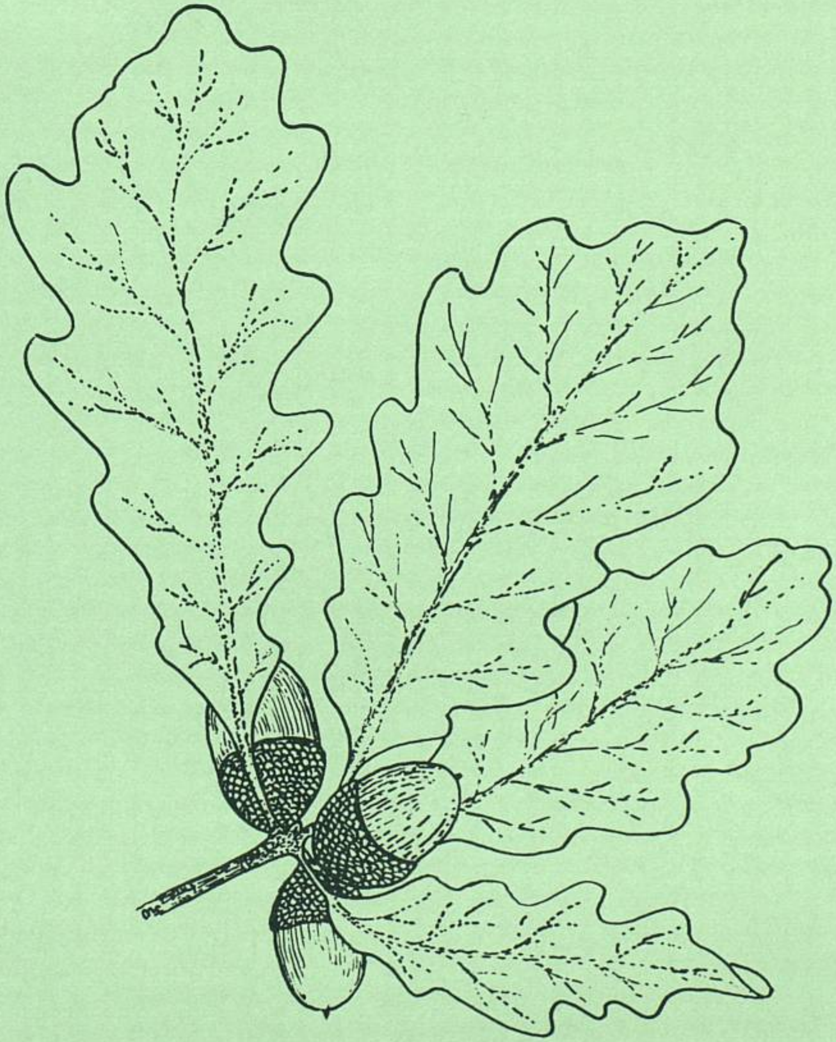

FORESTRY COMMISSION OCCASIONAL PAPER 31

Factors Affecting the Natural Regeneration of Oak in Upland Britain

A Literature Review

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Chapter 1
Introduction

Concern over an apparent lack of regeneration in many of Britain's native broadleaved woodlands has given rise to several initiatives aimed at regenerating and extending such woods. The progress of such initiatives in upland areas is limited by a lack of detailed information on several aspects of natural regeneration including:

a. the influence of site and crop factors on the distribution and numbers of seedlings and saplings and the timing of their establishment;

b. the outcome of management intervention aimed at encouraging regeneration.

Substantial difficulties have been encountered in attempting to regenerate oakwoods. This is particularly important in Wales where 44% of the broadleaved woodland area is oak. This review collates information on the natural regeneration of oak *(Quercus petraea* and *Quercus robur)* in upland Britain and the factors which influence it.

Lack of regeneration

Several surveys have shown that regeneration is sparse or lacking in the majority of upland broadleaved woodlands, including Wales (Woods, 1985), northern England (Lake District Planning Board, 1987) and Scotland (MacKenzie, 1987). For example in the Lake District, regeneration was recorded in only 9% of the sample woodlands and generally consisted of species other than those of the main crop. A survey of woodlands in the Brecon Beacons (Brecon Beacons National Park, 1984) showed that in 20% of woodlands there was no natural regeneration; 36% showed poor regeneration, with very few seedlings or saplings; and a further 36% only 'moderate regeneration' with occasional seedlings or saplings. In Argyll, Scotland the Nature Conservancy Council estimated that 63% of the native woods were in danger of dying out because of the lack of saplings (MacKenzie, 1987).

In the case of oakwoods, an apparent lack of regeneration has been a particular cause of concern amongst both foresters and ecologists and the difficulties of regenerating oak have been a recurrent topic both in Britain and abroad (Haugh, 1907; Watt, 1919; Moore, 1933; Wyllie Fenton, 1945; Shaw, 1974; Rackham, 1980; Newbold and Goldsmith, 1980; Evans, 1988). Ecologists have expressed concern over the even-aged structure of woodlands which they consider to be of lower conservation value than woodlands with a multiple age structure. Foresters have been concerned that the lack of regeneration may lead to the degeneration of certain woods and the loss of a valuable timber resource. Problems with regeneration appear to be largely restricted to areas within existing woods; several authors report oak successfully invading open areas adjoining oakwoods (Mellanby, 1968; Barkham, 1978; Rackham, 1980).

Rackham (1980) reported that in only 7% of the woods in eastern England is oak regeneration adequate to ensure normal replacement. Several authors record abundant seedlings after good seed years but then report that seedlings gradually die off over about a 5 year period (Ovington and Murray, 1964; Shaw, 1968a; Linhart and Whelan, 1980; Bondarenko, 1987). Shaw (1968a) showed that 2-year-old seedlings were the most frequent age class recorded in woods in north Wales but that few survived beyond 4 years of age. A similar pattern was shown by Wyllie Fenton (1945) in woods in south-east Scotland. In Argyll, while oak seedlings were recorded in many of the woods, saplings were present only in 12% of them (MacKenzie, 1987). Linhart and Whelan (1980) found only 5-50 seedlings/saplings per hectare in a mixed oak forest in Wales which had been fenced for 19 years.

In contrast, several authors have reported the existence of adequate levels of regeneration in certain woods, either with the exclusion of browsing by fencing (Pigott, 1983) or without it (Haggett and Small, 1971; Barkham, 1978; Woods, 1985). Some authors, whilst recording only low numbers of oak seedlings and saplings, have suggested that regeneration may nevertheless be adequate to replace the woodland over a long time period (Shaw, 1974; Barkham, 1978).

Note: For the purpose of this publication 'oakwoods' are loosely defined as woodlands containing a significant proportion of oak of natural or planted origin.

History of oak regeneration

Oak has been a component of vegetation in Britain since the Boreal period and several pollen analyses show oak increasing relative to other species well into the historical period (Rackham, 1980). Rackham states that there can be no doubt that oak regenerated more freely in the past than it does now and suggests that oak reproduction is a problem of the last hundred years (Rackham, 1974 and 1980).

From the earliest historical times, many rural activities and industries were dependent on a steady supply of small or medium diameter oak and there is little historical evidence that difficulties were encountered in raising such trees (Anderson, 1967; Rackham, 1980). In Scotland the native woodlands were also a valuable source of shelter and winter pasture for domestic animals (black cattle) and throughout Britain oakwoods were valued for pannage.

During the 18th century pressure to exploit the upland oakwoods increased as they became an important source of timber and bark for a growing urban population and of fuel wood for the early iron smelting industry. By 1800 oak coppices managed on a 20-30 year rotation for bark for tanning existed in many parts of upland Britain (Tittensor, 1970; Lindsay, 1975; Rackham, 1980). While a large proportion of recruitment would be from coppice stools, Rackham believes that regeneration from seed was also frequent and attributes this in part to the presence of a succession of regeneration sites provided by coppice cutting.

After about 1750 sheep were introduced and eventually replaced cattle over a large part of Scotland. These were usually run without proper enclosure of woodlands and have been a powerful influence in restricting regeneration. Similar pressures arose with the rise of the sporting estates in the Victorian era, which led to a dramatic increase in grazing by deer and hares which has continued to the present.

Many of our present oakwoods originate from the period 1780-1910 and a proportion of these are obviously derived from neglected coppice (Rackham, 1980). These woods are now characterised by a lack of trees in the age class 2 to 50 or more years of age (Rackham, 1980). Because such woods appeared to be able to regenerate themselves in the past, the lack of regeneration has become regarded as an anomaly. This phenomenon was first noted and studied by Watt (1919). Other authors, whilst accepting that problems are encountered in regenerating oak, remain unconvinced that the situation now is fundamentally different from earlier times (Shaw, 1974).

Postulated causes for the lack of regeneration

Studies have offered a wide variety of interpretations of, and explanations for, the lack of regeneration which characterise many of Britain's upland oakwoods. Changed land-use patterns which have led to excessive grazing by both domestic and wild (sporting) animals in unenclosed woods or to the cessation of cutting of suitable regeneration sites are often cited (e.g. Rackham, 1980; Mackenzie, 1987). Some authors have suggested that recent disturbance of ecosystems has led to excessive predation of acorns (Ashby, 1959) or unfavourable environmental conditions for regeneration (Ovington and Murray, 1964). Recent studies have concentrated on physiological limitations to the growth of seedlings through their apparent inability to tolerate shading (e.g. Jarvis, 1964a). The effects of defoliating caterpillars dropping from overstorey trees and of the oak mildew *(Microsphaera alphitoides)* have also received attention (Shaw, 1968b and 1974; Rackham, 1980).

The following review collates information on the environmental factors which influence successive stages of the regeneration process in oak, i.e. acorn production, acorn survival, dispersal, germination and seedling establishment.

Chapter 2
Acorn production

Seed years

Seed years in oak occur at rather irregular intervals (Table 1). Heavy seed years in Britain are recorded at 6-7 year intervals, with intermediate moderate years occurring every 3-4 years (Matthews, 1963; Jones, 1950). Aldhous (1972) gives interval between 'good' seed years as 2-4 years for *Quercus robur* and 3-5 years for *Quercus petraea;* the corresponding figures according to Evans (1988) are 3-6 *(Quercus robur)* and 2-5 *(Quercus petraea).* There is obviously some difficulty in defining a 'good' seed year.

On the Continent the frequency of heavy seed years varies from 3-4 years in favourable areas of

Table 1 The occurrence of good seed years in oak in Britain

Year	*Seeding*	*Location*
1955	Heavy	Yorkshire
1959	Heavy	Yorkshire, Midlands, East Anglia
1960	700 000 per ha	Devon
1961	None	Devon
1962	400 000 per ha	Devon
	Good	New Forest
1963	No records	
1964	413 000 per ha	Wales
	Good	New Forest
1965	98 000 per ha	Wales
1966	None	Wales
1967	None	Wales
1968	16 000-654 000 per ha	Wales
	Good	New Forest
1969	25 000-83 000 per ha	Wales
1970	26 000-601 000 per ha	Wales
1971	28 000-655 000 per ha	Wales
	Good	New Forest
1972	300-119 000 per ha	Wales
1976	Heavy	New Forest, Windsor
1977	None	
1978	Good	
1979	None	
1980	Very good	South-east England
1981	None	
1982	Fairly good	South-west England
1983	None	
1984	Very good	New Forest and south-west England
1985	Some seed	
1986	None	
1987	None	Lake District
	Very good	Southern Britain
1988	None	Lake District
1989	Very good	Dean and Hereford

Sources: Yorkshire — Pigott (1983); Devon — Ovington and Murray (1964); Wales — Shaw (1974); New Forest — Small (1982); Lake District — Mitchell (personal communication) and Waddell (personal communication).

France, to 6-11 years on montane and dry sites (Jones, 1959; Alent́ev, 1980; Everard, 1987).

It is widely accepted that the frequency of seeding is influenced by climate, decreasing with increasing latitude, elevation and oceanicity (Jones, 1959; Matthews, 1963).

In intervening years there may be no acorn production over wide areas. However, even in poor years individual trees and woods will produce some seed. Similarly, in good years, certain woods may fail to produce seed (Jones, 1959).

In any particular year seed production varies from wood to wood (Shaw, 1968a and 1974), though within a region a trend towards a particular level of seed production is usually discernible. Ovington and Murray (1964) reported that in a single wood spanning a wide range of ecological conditions, similar annual trends in acorn production were recorded on the different site types (Table 2).

Acorn quantities

Individual trees

In good seed years individual 120 to 140-year-old trees in Bagley Wood, Oxfordshire produced an average of 50 000 acorns, with individuals producing up to 90 000. Mean density of acorns on the ground below the tree crowns was 50-70 per m^2, with up to 120-170 per m^2 below prolific trees and a single observation of 800 per m^2 (Jones, 1959).

Woods

Acorn trapping studies in Devon and north Wales have shown that in good seed years mean densities of up to 50-80 acorns per m^2 occur over whole woods (Ovington and Murray, 1964; Shaw, 1968a and 1974), which is equivalent to up to 500 000 to 800 000 per hectare (see Table 2). In morderate seed years values of 50 000 to 200 000 acorns per hectare were recorded in these woods. In certain poor years absolutely no acorn production occurred.

Table 2 Acorn production in Yarner Wood, Devon

Elevation (m)	237	136	130
Number of oak trees per hectare	1000	373	160
Average height (m)	11.8	20.8	23.4
1960			
Number of acorns (10^3 per ha)	653	732	770
Dry weight (kg per ha)	418	380	645
Average dry weight (g)	0.64	0.52	0.84
% apparently viable	91	64	72
1961			
Number of acorns (10^3 per ha)	0	0	0
1962			
Number of acorns (10^3 per ha)	488	621	683
Dry weight (kg per ha)	166	328	328
Average dry weight (g)	0.34	0.41	0.48
% apparently viable	68	50	78

After Ovington and Murray, 1964.

Means of assessing acorn fall

Acorn traps provide the most reliable means of estimating acorn fall (Ovington and Murray, 1964; Shaw, 1968a). Ground counts underestimate acorn fall because of predation by mammals (Ashby, 1959) and the difficulties of locating acorns under luxuriant vegetation. Peak ground densities of acorns are recorded in mid-November and normally correspond to about 30% of the actual fall (Figure 1). One of the best means of estimating total acorn fall is by counting acorn cups, acorn numbers equating to about 85% of total cup count (Shaw, 1968a).

Acorn weight and size

Acorn size varies from year to year, good seed years being characterised by larger and heavier acorns. Acorn sizes are usually greater on lowland and southern sites as opposed to upland and northern sites (Jones, 1959).

Jarvis (1963b) quotes acorn sizes as being between 0.5 and 1.0 cm^3 for *Quercus petraea* in Yorkshire. The fresh weights of acorns in Bagley Wood, Oxfordshire varied between 1.2 and 6.9 g, with a mean of 2.5 g for *Quercus petraea;* and between 1.6 and 8.5 g with an average of 3.5 g for *Quercus robur.* Ovington and MacRae (1960) recorded fresh weights of between 1 and 12 g for *Quercus petraea,* with the majority being between 3 and 7 g.

Acorn weights are usually quoted as dry weights. According to Jones (1959) dry weights are about 50% of fresh weights. Mean dry weights in upland woods vary between 0.2 and 1.5 g (0.4-0.6 being most frequent), with individual acorns weighing up to 3.0 g (Jarvis, 1963b; Ovington and Murray, 1964; Shaw, 1968a). Total dry weight production of acorns in a good seed year may be about 300-400 kg per ha (Table 2).

Ovington and Murray (1964) recorded variations in average acorn weight according to crop and site characteristics, with the greatest weights being recorded on sites at lower elevation and with lower stocking density (see Table 2).

Tree age

The age of first fruiting usually occurs at about 40-50 years but earlier in coppice (20-25 years). Jones (1959) believes there to be no difference between the two species but Shaw (1974) records that *Quercus petraea* begins to flower at an earlier age than *Quercus robur.* Maximum acorn production usually occurs between 80 and 140 years and seeding may continue beyond age 200 (Newbold and Goldsmith, 1980; Evans, 1988).

Timing

Acorn fall usually begins in late September or early October, with the main fall occurring in the third week of October in southern and lowland areas and during early November in upland and northern areas (Jones, 1959; Ovington and Murray, 1964; Shaw, 1968a). Limited numbers of acorns may fall in December and even into January in certain years (Ovington and Murray, 1964). The timing of acorn fall varies from year to year, presumably in response to summer warmth (Ovington and Murray, 1964).

Distribution

Experiments with seed traps have failed to show any obvious patterns of acorn distribution on the ground, in relation to, for example, distance from trunks (Ovington and Murray, 1964). Relative numbers of acorn in specific traps varied from year to year and the average size of acorns in specific traps was not related to trap location.

Acorns falling on sloping ground tend to occur in bands along the contour (Shaw, 1968a).

The influence of climate

Heavy seeding requires summer warmth both in the year of seeding and the year preceding it (Jones, 1959; Matthews, 1963), though no studies have attempted to correlate seeding with specific climatic factors. Summer warmth allows the build up of the necessary photosynthetic reserves and, it is claimed, a warm late summer/autumn in the year previous to seeding allows adequate flowering buds to be laid down.

The other main influence of climate on acorn production is through killing of the flowers by spring frosts or their destruction by high winds or hail (Jones, 1959). Shaw (1968a) recorded a high incidence of failed flower peduncles in most years including poor seed years and states that this may be due to failure of pollination, fertilisation, or, most importantly, failed late embryo development.

In particularly cold summers acorns may fail to grow and mature.

Site characteristics

With the exception of the results of Ovington and Murray (1964) shown in Table 2, no work has been done to investigate possible correlations between site characteristics and acorn production.

Biotic influences

Defoliating caterpillars, particularly *Tortrix viridana* and *Operophtera brumata* have been observed to cause loss of flowers and subsequent failure of seeding and evidence suggests that insects may contribute to the irregularity of acorn crops (Jones, 1959; Bonnet-Masimbert, 1973). Crawley (1985) showed that control of insects increased acorn crops but attributed this to the effects of release from the normal levels of defoliation, rather than from predation of flowers or young acorns. Infestation of acorns by knopper galls can also be locally significant. Gurnell (1987) reported that up to 40% of acorns were commonly infested during a 13 year study of an oak wood at Alice Holt Forest in Surrey.

Crop characteristics

Acorn production is greatest on open-grown trees in sunny positions (Jones, 1959) and seeding fellings to increase crown size and light penetration is a standard treatment in encouraging seed production on the Continent (Everard, 1987). However, Szappanos (1984) reported that the seed crop per tree in thinned stands with crown cover between 32% and 56% was not significantly related to crown cover. He also failed to reveal any differences in acorn production between the different compass aspects of tree crowns.

Ovington and Murray (1964) recorded acorn fall in three parts of Yarnley Wood, Devon with different crop and site characteristics and found that acorn numbers and average acorn size were greatest in areas with the lowest stocking density (this was confounded with elevation; see Table 3). Despite these differences they expressed surprise that acorn production was not more variable in view of the variation in crop and site (stocking 160-1000 stems per ha; elevation 130-237 m). Similarly Shaw (1968a) recorded high acorn production in "rather stunted small crowned trees (10 m high and 100 years old)" in Coed Camlyn.

The effect of canopy structure on acorn production appears to have been inadequately studied.

Summary

- Although there are difficulties in defining good seed production levels, heavy seeding in oak occurs irregularly with anything from 2-7 year periods between mast year.

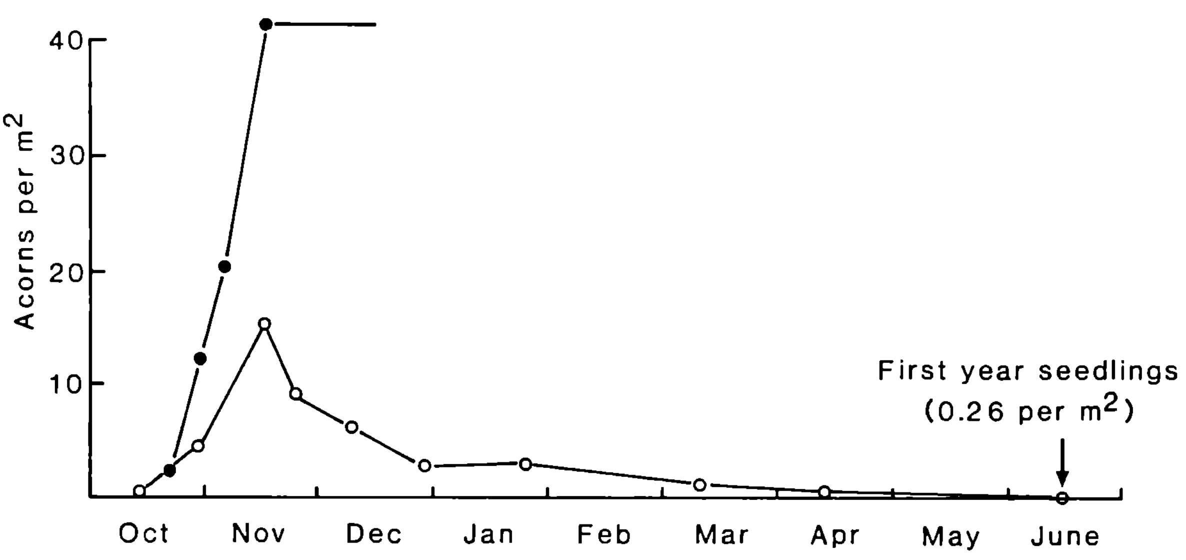

Figure 1 Acorn fall and ground density of acorns at Coed Cymerau, 1964-65. (After Shaw 1968a.) ● = acorn fall (cumulative); o = acorn ground density.

- In good seed years, up to 800 000 acorns per hectare have been recorded beneath oak woods. Open-grown or heavily thinned trees have been shown to produce larger amounts of seed.

- The size and weight of acorns varies from year to year, being larger and heavier in good seed years. Acorn sizes on upland sites are usually smaller than those found in lowland woods. Sizes in the range 0.5 to 1.0 cm^3, and weights of between 1 and 12 g have been recorded.

- Age of first fruiting in oak occurs at or around 40-50 years of age. Maximum production occurs between 80-140 years although seeding may continue beyond 200 years.

- Acorn fall begins in late September or early October, with peak ground densities occurring around mid November. No obvious spatial pattern of acorn distribution in relation to tree stems has been recorded, although acorns falling on to sloping ground tend to occur in bands along the contour.

- Very little work has been done linking site characteristics and acorn production.

- Seed production can be seriously affected by a number of biotic agents, particularly defoliation by *Tortrix* and *Operophtera* caterpillars and infestation by knopper galls. In one study, as many as 40% of the total acorns produced were found to be infested with knopper galls.

Chapter 3
Acorn survival

It is clear that acorns are produced in considerable profusion, even in upland woods. However, acorn losses are also high. Indeed Shaw (1974) points out that such losses are "a positive necessity if man is not to be eliminated by oak trees!"

Conversion rates

Shaw (1968a) coined the term 'conversion rate' to describe the ratio of the number of first year seedlings recorded relative to the number of acorns produced. He recorded figures of between 0.5% and 1.5% for both natural acorn fall and planted (unprotected) acorns (the latter figure being based on a very small number of seedlings in a poor seed year). So, for example, an acorn fall of 400 000 per hectare resulted in a seedling density recorded the following summer of 2600 per ha. Ovington and Murray (1964) recorded conversion rates of about 0.1% in the upper part of Yarnley Wood, as compared with 0.5% in the lower part.

The main cause of failure to produce 1 year seedlings is due to acorn predation (80-90%), the remainder being accounted for by failure to germinate. Caging of areas to protect from birds and mammals generally results in greatly increased seedling production compared with unprotected areas (Shaw, 1968b — see below).

Ground numbers

Numbers of acorns recorded on the ground peak at about 30% of the total produced, and then immediately begin to drop rapidly as the result of predation (Figure 1). For example, Shaw (1968a) recorded a ground density of 154 000 per ha (37% of total fall) in November, which then fell to 29 400 by end of December (6 weeks). This corresponds to loss of about 120 000 acorns per ha or 60 kg dry weight per ha in 6 weeks. Total losses of 200 kg per ha were recorded by the following spring, though only small losses were observed during January and February.

Rates of loss due to predation are lower in years in which acorn fall is less (Shaw, 1968a). For example losses due to predation of 25 000 per ha in 7 weeks were recorded in the same wood following acorn fall of 98 000 acorns per ha.

Losses from trees

Values for acorn losses from trees are derived from the differences between estimates of acorn fall and estimates of cup fall (as recorded in acorn traps). Estimates of losses from trees vary widely. The most reliable estimates were made by Shaw (1968a) who concluded that losses averaged 15% of total acorn production in Wales. Ovington and Murray (1964) recorded 8.4% in Devon, whilst Tanton (1965) estimated that 92% were lost from trees at Monks Wood nature reserve in Lincolnshire. No explanations are forthcoming for the latter high figure.

Losses from trees are attributed mainly to pigeons and squirrels.

Predation

Predation constitutes the major cause of loss of acorns and studies have revealed the effectiveness of various predators (see below). Several authors point out the necessity of the activities of predators for the dispersal of oak seed.

Wood pigeons

Pigeons, which swallow large quantities of acorns whole, are the single most important predator of acorns (Jones, 1959; Shaw, 1968b; Tanton, 1965) and may account for up to 60% of acorn losses (Shaw 1968b). Flocks in Coed Cymerau fed initially in crowns then, after acorn fall in November and December, they began to feed on the floor (flocks up to 200 were observed and total numbers feeding were higher). During this period pigeons may feed exclusively on acorns, having 8-70 acorns in their crops at any one time (Jones, 1959; Shaw 1968b). Shaw (1968b) equates this with a consumption of 50 g per bird per day.

Moore (1933) reported that, in an experiment in south-west England, 51% acorn losses were due to birds, of which pigeons were the most important.

Corvidae

Crows, jays, jackdaws and magpies all feed on acorns and will fly away and bury them for later consumption. Their relative contribution to acorn losses is unknown.

Mice and voles

Mice and voles, particularly the wood mouse *Apodemus sylvaticus* and the bank vole *Clethrionomys glareolus* are known to be important predators of acorns (Ashby, 1959) and prefer acorns to other types of tree seed (Miles, 1972). Shaw (1968b) considered them to be the most important predators after wood pigeons and attributed 44% of acorn losses to mice and voles in Wales. In one experiment he recorded losses of 17 kg of acorns per ha in 8 months. Mice and voles also removed 80-90% of planted acorns (320 acorns; equivalent to 170 g dry weight) in 24 hours, these being taken away and stored (see Chapter 4). Activity was greatest in December and again in the spring but was low during January and February, presumably because stored acorns are consumed during this period. Moore (1933) reported that all unprotected acorns sown in an experiment in south-west England were removed within one month, mainly by mice and voles.

Only one study runs against the main evidence, that of Tanton (1965) in which only small losses were recorded from caged areas which were accessible to small rodents, but not to birds or squirrels. Vincent (1977) reported that there was a positive correlation between size and breeding success of rodent populations and seed crops, though seed crop success or failure in any one year had no permanent effect on rodent populations.

Squirrels

Predation by squirrels may cause significant losses (Jones, 1959; Tanton, 1965), but no studies have been carried out to quantify their contribution to acorn predation.

Rabbits

Rabbits may contribute to acorn losses locally (Wyllie Fenton, 1945) and may scratch up buried seed (Miles, 1972).

Insects

Insect infestation of acorns is very variable and does not always lead to death. The most important agents are *Curculio venosus* and *C. glandium* (Jones, 1959; Ovington and Murray, 1964). Jones (1959) found 8 and 30% infestation on adjacent *Quercus robur* trees; the corresponding figures for *Quercus petraea* being 11 and 50%. Shaw (1968a) recorded virtually no parasitism at Coed Cymerau in one specific year when levels of about 10% were observed at other oak woods in north Wales. In Yugoslavia, Maksimović *et al.* (1982) reported that insect predation caused a total yield reduction of acorns of 25-56%.

Fungi and bacteria

Fungi are the main agents causing deterioration of acorns and preventing germination. The main agents are *Altenaria* spp., *Ceratocystis* spp., *Fusarium* spp. and *Phomopsis* spp. (Hangyal-Balul, 1986). Fungicidal treatment has been shown to have no effect on seedling production (Hangyal-Balul, 1986).

Climate

Climatic injury to acorns may occur due to desiccation or freezing. Temperatures below -6°C to -9°C were found to be lethal by Jones (1959).

Acorns of *Quercus petraea* are also susceptible to immersion in water whereas *Quercus robur* acorns survive well in non-stagnant water.

The influence of site conditions on acorn survival

Litter

Litter derived from oak leaf-fall provides an important source of protection for fallen acorns, particularly against injury due to drying and frost (Jones, 1959; Jarvis, 1963a; Shaw, 1968a). Litter may also confer some protection against predation, particularly by birds. Leaf-fall occurs at the same time or a little after acorn fall and subsequently litter forms drifts. A high proportion of surviving acorns are found in areas of litter accumulation (Shaw, 1968b). Wyllie Fenton (1945) reported that young oak trees occurred "almost without exception" where there was leaf litter on the forest floor.

Vegetation type

The main influence of vegetation type on acorn survival appears to be as the result of its indirect effect on litter retention. Heavily grazed areas with a short sward result in poor retention of litter and it is therefore assumed that acorn survival will be correspondingly reduced (Shaw, 1974).

One study in Germany reported that predation of acorns was more severe in heavily grazed areas than in areas with an abundant herb layer (Wolf, 1982). However, Shaw (1974) observed increased mammal activity under bracken and speculated that this may lead to increased acorn predation.

Summary

- The term 'conversion rate' has been coined to describe the ratio of the number of first year seedlings relative to the number of acorns produced. Figures of between 0.1% and 1.5% have been recorded.
- The main reason for the low success rate is acorn predation, the remainder being accounted for by a failure to germinate. Estimates of acorn losses from trees vary widely but are most often attributed to pigeons and squirrels. Many studies cite pigeons as the single most important predator of acorns accounting, in some cases, for up to 60% of losses.
- Mice and voles are also known to be important predators and to prefer acorns to other tree seed. They have been observed removing 80-90% of directly sown acorns and have also been quoted as responsible for up to 40% of total losses in other cases.
- Litter derived from oak leaf-fall provides an important source of protection for fallen acorns, particularly against desiccation and frost. Large proportions of surviving acorns are often found in areas of litter accumulation.

Chapter 4
Dispersal

Oak is largely dependent on mammals and birds for seed dispersal. The only abiotic dispersal method which is reported is flooding (Knight, 1985).

The majority of seed is carried a few tens of metres from the parent trees usually by rodents (Jensen and Nielson, 1986). However acorns may be carried quite large distances by birds, up to 4-5 km having been observed (Jones, 1959).

Mice and voles carry away and bury seed some of which is left in suitable positions for germination. Caches of 3-8 acorns may be found close to the surface but many acorns are thought to be placed too deep underground to germinate. Jensen and Nielsen (1986) recorded autumn population densities of mice and voles of up to 50 individuals per ha on a heath in Denmark and recorded a mean dispersal distance of acorns of 15 m (maximum 43 m). The historical colonisation rate of the wood was 300 m in 100 years.

Squirrels carry and bury seed usually within 10 m of trees but distances of up to 80 m have been observed (Jones, 1959).

Jays, rooks and ravens carry seed away and bury it in turves often in shelter of bushes or under dead leaves (Jones, 1959; Bossema, 1979). Pigeons may contribute to dispersal by disgorging acorns at considerable distances from parent trees (Mellanby, 1968). Shaw (1968a) observed that the activity of birds results in significant uphill spread of seedlings.

Chapter 5
Germination

Viability

Acorn viability is generally about 80% (Aldhous, 1972; Shaw, 1968a). Shaw recorded slightly lower figures in October (60-70%) but found that viability then rose quickly to 80-90+%. There is some evidence that viability drops again in late spring (Shaw, 1968a).

Shaw (1968a) found viability to be dependent on acorn weight, being 50% for acorns of 0.5 g or less (dry weight) and rising to 90% above 1.5 g. No such clear relationship was found by Ovington and MacRae (1960) though they did note that the smallest and largest acorns tended to have lower viability percentages. Jones (1959) notes that acorns of 0.5 g fresh weight (0.25 dry) are the smallest which will germinate.

Viability is lower in field conditions than in laboratory tests (Shaw, 1968b). A loss of viability of about 10% occurs if acorns are collected and stored for any length of time (Shaw, 1968b; Aldhous, 1972).

The effect of seedbed conditions

Litter

Acorns covered by a thin cover of litter show the highest germination rates in natural (i.e. unprotected) conditions (Shaw, 1968b; Jones, 1959). Jarvis (1963a) attributes this to higher moisture content of litter-covered acorns though litter also affords some protection from frost (Shaw, 1968a).

Removal of vegetation

Moore (1933) reported higher germination rates of protected acorns when surface vegetation was removed leaving exposed mineral soil (109% of laboratory viability test values), than when acorns were left on the undisturbed forest floor (86%).

Burying

Burying of acorns has long been recognised as a means of increasing germination success and this has been achieved in Continental practice by cultivation or pannage with pigs. Acorns lying unprotected on the soil surface rarely if ever survive to produce seedlings (Shaw, 1968b), either due to predation or, on dry sites, as the result of desiccation (Watt, 1919).

Somewhat surprisingly Shaw (1968b) found that, when protected from predators, acorns lying on the surface germinated well and in some experiments produced more seedlings than buried acorns. This he attributed to the high moisture status of upland sites in Wales providing sufficient moisture to surface acorns but causing buried acorns to become waterlogged. However, when unprotected, buried acorns produced 50% more seedlings than unburied acorns, this being largely due to their escaping predation. Similarly Ovington and MacRae (1960) recorded that only 1% of acorns germinated on soil surface whereas 80% of acorns buried below 1 inch produced seedlings. Saparnov (1983) showed that seedling yield decreased if acorns were buried too deeply.

Mellanby (1968) reported that rotavation of meadows greatly increased seedling establishment and attributed this to acorns being more easily buried.

Vegetation type

The germination success of acorns lying on the surface seems to be generally unaffected by surface vegetation, though bryophyte cover seems to be particularly favourable (Shaw, 1974).

Germination may be inhibited by *Deschampsia flexuosa* litter and humus (Jarvis, 1964b).

Other site factors

Neither slope position nor light were significantly related to germination success (Shaw, 1968b).

Summary

- Acorn viability has been shown to vary both with acorn weight and the time of year. Recorded viability figures are in the order of 60-80%. It has also been noted that both small and large acorns tend to have lower viabilities.
- Acorns covered by a thin litter layer have been shown to have the highest germination rates and this has been attributed to the higher moisture content of litter covered acorns.

- The burying of acorns is recognised as a means of increasing regeneration success by protecting them from predators and desiccation. There is, however, some evidence to suggest that on sites which experience high rainfall, buried acorns may be prone to waterlogging.
- The type of surface vegetation present seems to have little influence on the germination process, though bryophyte cover appears the most favourable.

Chapter 6
Seedling establishment, survival and early growth

The influence of acorn size

First-year seedling height and weight are strongly correlated with acorn size and weight, which in turn are correlated with cotyledon weight and nutrient reserves (Figure 2). Jarvis (1963b) believes these differences continue to be influential for many years. Larger seedling size provides an advantage in competing both with other oak seedlings and with ground vegetation.

The large reserves of nutrients which are available to oak seedlings confer a considerable advantage over smaller seeded trees in competing with ground vegetation.

Seedling number and distribution

Shaw (1968a) recorded first-year seedling densities of 2600 per ha after a good seed year (1964) and 1500 per ha after a moderate seed year (1965). The density of seedlings of age 2 or more years in the period 1965-67 were in the range 2200-3800 per ha. These were recorded under 'reasonably homogenous' tree cover of 120 to 140-year-old oaks (stocking 390 per ha) in Coed Cymerau. Shaw (1968b) also provides data on the distribution of seedling age (see Figure 3), showing that the most frequent age class was 2-year-old seedlings (30%). Few seedlings apparently survived beyond year 4. A few seedlings of up to 8 years in age were recorded but where these occurred under the canopy, there was often dieback.

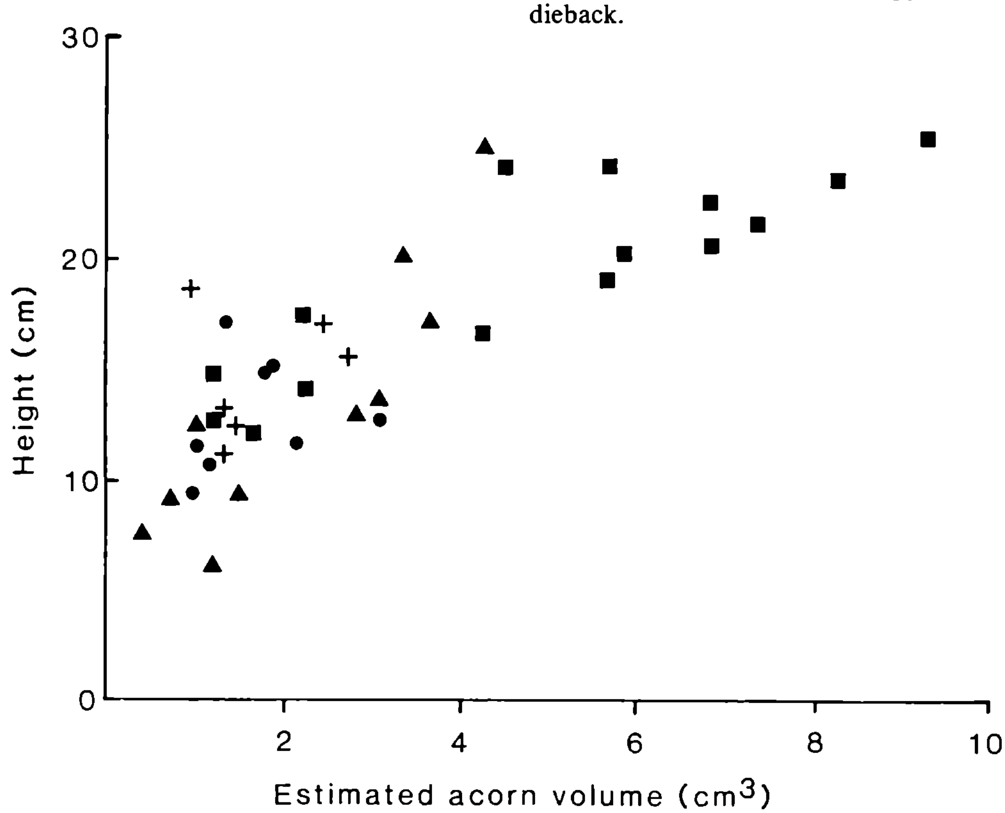

Figure 2 The relation between acorn volume (estimated from pericarp remains) and stem height of seedlings after the first season's growth; seedlings from Padley Wood ▲; seedlings from Blackbrook Wood: *Deschampsia* humus +, *Holcus* leaf humus ●, with roots penetrating into the A/C horizon ■. (After Jarvis 1963b.)

Rackham (1980) described a "shimmering carpet of countless oaklings" in southern England after the mast year of 1976 and estimated that in one wood in Hertfordshire 70 000 seedlings per ha survived into 1978.

Pigott (1983) observed that regeneration occurred both under crown and in gaps in the canopy in a fenced enclosure in Yarncliffe Wood, Yorkshire, but that survival and growth were best in gaps. In five 100 m^2 plots *centred on gaps* seedling densities after 17 years averaged 1000 per ha but in 1981 observations in a larger area revealed a seedling density of 290 per ha. Pigott (1983) recorded that intermittent recruitment had occurred since 1960 (following a good seed year in 1959). This was in contrast to birch, which had failed to regenerate in any except the first year after enclosure due to the extension and development of the grass sward *(Deschampsia flexuosa)*.

Linhart and Whelan (1980) found only 5-50 seedlings/saplings per ha in a mixed oak forest in Wales (Coed Gorswen) which had been fenced for 19 years. This was despite considerable acorn production (e.g. 601 000 acorns per ha in 1970 — Shaw, 1968a). The lack of regeneration was attributed to shading by brambles which invaded gaps in the canopy and to the lack of ground disturbance.

In mixed woods containing oak, the densities of oak seedlings are often reported to be lower than those of other species. For example Mitchell (personal communication) reported that in a wood in which 15% of the overstorey was oak, only 0.6% of the seedlings were of oak.

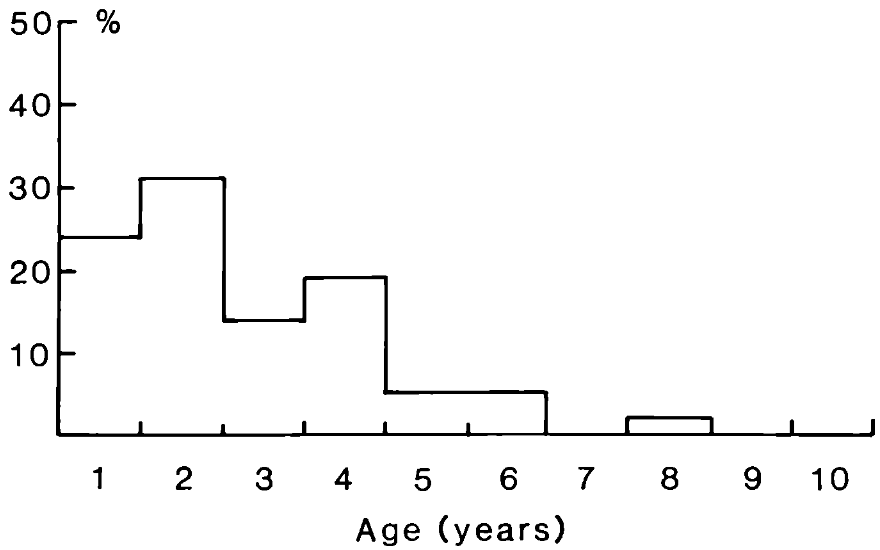

Figure 3 Age distribution of a sample of 42 oak seedlings in Coed Cymerau, July 1966. (After Shaw 1968a.)

Growth rates

Jones (1959) gives details about the early growth patterns of seedlings. Height growth occurs mainly in May to June, with a proportion of seedlings showing renewed growth later in the summer. Ovington and MacRae (1960) recorded that 30% of seedlings renewed growth in July and increased their height by an average of 38%.

The height of first-year seedlings in Yarncliffe Wood ranged from 8 to 25 cm (Jarvis, 1963b). The mean height of seedlings growing in outdoor pot experiments ranged from 12 to 17 cm after year 1, 17 to 28 cm after year 2 and 21 to 38 cm after year 3; the variation in height being the result of different shading treatments (Ovington and MacRae, 1960).

Pigott (1983) recorded that the tallest saplings at Yarncliffe Wood in North Yorkshire after 26 years of enclosure averaged 3.6 m, equating to a mean annual growth rate of 13.3 cm per year. These were all located in gaps in the canopy.

The effect of light conditions

Field observations unanimously report that regeneration is most successful in gaps in the canopy (Ovington and Murray, 1964; Shaw, 1968b and 1974; Barkham, 1978; Pigott, 1983). Authors concerned with classical regeneration methods report that natural regeneration will only survive for 2 to 3 years before thinning of the canopy is required (Haugh, 1907; Bonderenko, 1987). Only one paper records oak regeneration being able to persist for considerable periods under the canopy (Belostokov, 1974).

There remains considerable disagreement and misunderstanding over the degree to which oak should be regarded as shade tolerant. For example Harley (1982) states that "the over-riding silvicultural characteristic of oak is its light demanding nature" whereas Jarvis (1964a) concludes that "oak seedlings can be conveniently classified as shade plants".

Table 3 The effect of light on the survival and growth of oak seedlings (after Shaw, 1974)

Percentage daylight	*Survival %*	*8-year mean height (cm)*	*Maximum height (cm)*
85%	72	35	150
43%	42	20	32
31%	16	26	41
19%	32	18	31
15%	18	18	22

Table 4 Relative light intensities at Padley Wood. (Jarvis, 1964)

	Relative light intensity
Clearings 8 m by 10 m canopy to canopy	40-65%
Beneath normal canopy	12-28%
Beneath very low branches	7-10%
In dense bracken	0.9-4.2%

The apparent inability of oak to be able to regenerate under its own canopy has led to considerable research on the response of oak seedlings to light conditions (Jarvis, 1964a; Ovington and MacRae, 1960).

The main findings of this work are as follows.

1. Reduced light results in increased height, leaf area, leaf area ratio and chlorophyll content in 1-year-old seedlings; but in decreased root weight, root:stem ratio and net assimilation rate. Stem weight is unaffected.

2. Laboratory experiments on 1-year-old seedlings have shown that adequate growth may occur at light levels (relative to full daylight) of 10% (heavy canopy). Maximum growth rates of seedling (height) are thought to occur in 20-40% relative light intensity which is equivalent to open canopied woodland or small clearings. However field observations indicate higher, light intensities are more favourable (i.e. > 50%) and Shaw (1968a and 1974) recorded the best survival and growth in high light intensities (85%) (see Table 3).

3. Oak seedlings may be considered as shade plants. Compensation point (i.e. at which carbon assimilation due to photosynthesis equals losses due to respiration) is 2-6% of full daylight but 8% if the effects of mildew are taken into account. *Quercus petraea* casts and tolerates heavier shade than *Quercus robur*. Oak endures the same levels of shade as *Vaccinium* (Jones, 1959; Shaw, 1974).

The ability of oak seedlings to tolerate shade has long been appreciated (Haugh, 1907) and is confirmed by the results above. However, the longer-term growth and survival of oak seedlings is impaired by shading, as is well known and shown quantitatively from the results of work by Shaw (1974) in Tables 3 and 4.

If one accepts that young oak is tolerant of shade, the action of another agent is implicated in the inability of oak to regenerate under its own canopy (Shaw, 1974). Early research suggested that this lack of regeneration may be due to environmental conditions (Watt, 1919; Ovington and Murray, 1964). However Shaw (1968b and 1974) believes that the poor survival and growth of seedlings under the canopy is due to defoliation caused by caterpillars falling from the canopy. Rackham (1980) believes that shade is an important factor which makes seedlings less able to recover from unfavourable influences such as defoliation, browsing or fungal attack.

Defoliation

Seedlings growing under mature oak trees are susceptible to severe defoliation by caterpillars falling from the canopy (Shaw, 1968b and 1974). Seedlings placed in various positions under the canopy experienced defoliation levels of 39-84% during one summer, whereas defoliation was negligible (**ca.** 3%) on seedlings placed just 10 m from the canopy edge.

The main agents of defoliation are thought to be *Tortix viridana, Operophtera brumata* (winter moth) and *Erranis defoliaria.* These cause defoliation in May and June, which may be followed by a new flushing of leaves and renewed growth ('growth spurts'). Hilton *et al.* (1987) studied the effects of artificial defoliation of 2-year-old *Quercus robur* seedlings and concluded that defoliation causes:

1. earlier production of 'growth spurts' (which are normal in underfoliated trees) and the formation of more lateral branches which are susceptible to winter frost damage;

2. the production of more abundant smaller leaves;

3. reduced growth rates.

Hilton *et al.* suggest that substantial natural defoliation could cause failure of regeneration, though in unshaded plots leaf loss would result in retarded growth rather than death.

The presence of defoliated seedlings is difficult to detect because they appear as small sticks indistinguishable from other elements of the field layer. This may have led to this problem being overlooked in previous studies.

Grazing and browsing

Heavy grazing by domestic animals or high populations of wild animals can eliminate regeneration and this is thought by many to be the most important single factor limiting regeneration in many woods (Wyllie Fenton, 1945; Rackham, 1980; Smith, 1983; Woods, 1985; Shaw, 1974; Evans, 1988; Bunce, 1989). In ancient woodlands the presence of cohorts of regeneration has been linked to periods of reduced grazing intensity. Using such methods Tubbs (1986) determined a maximum grazing level under which regeneration might still be expected to occur in the New Forest.

Various workers mention the deleterious effects of different animals, including mice, voles, rabbits, hares, deer, sheep and cattle, but very little quantitative information is available. Each may be important according to local conditions.

Browsing causes seedlings to take on a bush-like structure with large roots. Extremely high root to shoot ratios have been recorded with up to 90% of weight being in swollen tap roots (Shaw, 1974). The storage of nutrients which can be accommodated in the tap root confers considerable resistance to browsing. Plants under 50 cm high have turned out to be 25 years old and protection of such plants often results in fast resumption of growth which soon places the sapling out of danger of further damage (Shaw, 1974). However, according to Mellanby (1968), oak seedlings subject to more than 4 or 5 mowings in meadows eventually die.

The relatively high tolerance of oak to browsing means that some regeneration can take place in the presence of a certain level of browsing (Woods, 1985; Mitchell, personal communication).

Total exclusion of grazing over a long period tends to encourage invasion by grass and may eliminate certain plants leading to a reduction in nature conservation value of certain woodlands (Shaw, 1974). Small mammals will often thrive in vigorous grass cover and this may lead to damage to seedlings (Ashby, 1959). These factors have lead some authors to investigate the effects of controlled grazing regimes (Mitchell, personal communication). In a study of regeneration of species other than oak (mainly rowan) in a mixed oakwood, Mitchell (personal communication) reported that summer grazing at low intensities can encourage seedling establishment; winter grazing is least harmful to the subsequent survival of seedlings but that winter grazing causes the greatest decrease in growth rates. Grazing during the winter was also recorded by Barkham (1978) as being the most harmful to the growth of oak regeneration.

The effect of vegetation type

Oak is better at establishing itself in competition with other vegetation than are many other tree species (Jones, 1959; Pigott, 1983). However, in common with other species, survival and growth rates are diminished by the presence of competing vegetation (Evans, 1988). This is often due to shading but root competition for moisture is also important.

Only limited studies have been carried out which quantify the effects of vegetation type on seedling establishment. Wyllie Fenton (1945) gives a list of 9 vegetation types in which he recorded no oak regeneration in south-east Scotland and stated that the presence of seedlings was almost always in areas of leaf litter or where there was sparse coverage of ferns.

Oak seedlings compete successfully with other shrubs and trees and they establish well in patches of thorn or gorse (Wyllie Fenton, 1945; Shaw, 1974; Evans, 1988). *Vaccinium* also seems to be associated with successful regeneration conditions (Watt, 1919; Shaw, 1974) and oak seems to be able to establish itself in *Calluna* swards (Wyllie Fenton, 1945).

Bracken

Bracken cover may provide some protection from browsing (Barkham, 1978), but it poses a number of problems and though oak seedlings may be frequent, they often slowly disappear. This may be due to excessive shading; surviving seedlings becoming etiolated and susceptible to layering (Shaw, 1974).

Brambles

Brambles are often associated with regeneration being poor or absent due to the heavy shade they cast (Everard, 1987; Linhart and Whelan, 1980), though Evans (1988) states that oak may grow up through brambles because they afford some protection from browsing.

Grasses

Grazing may cause an increase in the abundance and vigour of *Deschampsia flexuosa*, the humus of which may inhibit seedling growth (Shaw, 1974; Jarvis, 1964b). *Holcus mollis* may also be a strong competitor (Shaw, 1974; Jarvis, 1964b).

On a gleyed site in France *Molinia coerulea* and *Carex brizoides* were shown to be effective at restricting seedling establishment of both *Quercus petraea* and *Quercus robur* (Becker and Levy, 1983).

Trees and shrubs

Oak is able to grow up through areas of scrub and successful regeneration has been reported in the presence of gorse, thorn bushes and birch (Wyllie Fenton, 1945; Shaw, 1974; Peterken, 1981). Reduction of grazing pressure in upland woods often initially leads to regeneration of birch but this may be followed by successive recruitment of oak saplings which grow up amongst the birch and may eventually become dominant (Peterken, 1981).

The effects of climatic factors

Frost

Spring frost is a common cause of damage (Haugh, 1907; Jones, 1959), young shoots being damaged by frosts of below -12°C in March, -6°C to -7°C in April and -4°C to -5°C in May. There are no apparent differences in susceptibility to frost between the two species. Low winter temperature may cause damage to 1-year seedlings (Aussenac, 1975), particularly if combined with dry winds (Jones, 1959). Frost heave on heavy soils may also lead to the death of seedlings (Evans, 1988).

Water status

Little is known about the effects of moisture, though Jarvis (1963a) concluded that in dry years water stress may develop in seedlings growing under mature trees or in competition with their roots. He also reported greater water stress in surface layers of the soil outside as opposed to inside woods.

Becker and Levy (1983) reported that drainage did not improve acorn germination and seedling survival on a gleyed site in France. They concluded that the influence of soil water status on the longer-term survival and growth of seedlings is site-dependent and appears to act to a large extent via the indirect effects of water status on competing vegetation.

Soil conditions

Soil conditions are not thought to be important for the early establishment of seedlings (Ovington and MacRae, 1960; Jarvis, 1963b), though addition of Ca and N to soils of very low fertility caused increased growth in pot experiments (Jarvis, 1963a).

Barkham (1978) reported that regeneration in a wood near Dartmoor was most frequent in areas of block scree.

Root competition

It is likely that root competition may be a significant factor influencing the growth of seedlings (Shaw, 1974) but its effects have not been studied in detail (Shaw, 1974; Jarvis, 1963a).

Fungal attack

Mildew *(Microsphaera alphitoides)* is a serious problem for seedlings under heavy shade (Haugh, 1907; Jones, 1959; Shaw, 1974), though no detailed studies of its effects in field conditions are available.

Summary

- The height and weight of first year seedlings has been shown to be strongly correlated with acorn size and weight. Larger seedlings have an advantage in competing with other ground vegetation.
- Seedling numbers of up to 70 000 per ha have been recorded, although in mixed species woodland the majority of seedlings are often of species other than oak.
- The height growth of oak seedlings occurs mainly during May and June with further growth possible in July.
- Although much debated, it is generally accepted that young oak seedlings are tolerant of shade. However, their subsequent growth and survival is impaired by shading, leading to the concentration of older seedlings beneath gaps in the canopy.
- Oak is commonly reported to be incapable of regenerating beneath its own canopy. Some observers believe that this is mainly due to the defoliation of seedlings by caterpillars falling from the canopy. The most significant damage is caused by *Tortrix, Operophtera* and *Erronis* species.
- Heavy grazing by domestic and/or wild animals is thought by many to be the single most important factor limiting regeneration in many woods. However, the relatively high tolerance of oak to browsing means that some regeneration can still succeed in the presence of moderate browsing levels. Indeed, the total exclusion of grazing can encourage vigorous grass invasion which may hinder regeneration.
- One of the most significant climatic factors affecting the growth of seedlings is frost. The frost heave of some soils may also lead to the death of young plants.

Chapter 7
Silvicultural methods

Evans (1988) notes that as a formal management system natural regeneration has been surprisingly little used in Britain, and contrasts this with its extensive use on the Continent. In Britain, natural regeneration has been the subject of conflicting advice, and the degree of success has been variable. Amongst the successes with oak, Evans (1988) lists experience from the 1930s at Salisbury Trench, South Bentley and Brick Kiln in the New Forest and Grizedale in the Lake District.

Intervention to increase regeneration

To increase seedling numbers Shaw (1974) suggests:

1. reducing acorn predators;
2. excluding grazing animals to increase surface vegetation and therefore litter retention;
3. carrying out disturbance of soil to cover acorns.

However he states that the numbers of seedlings produced without intervention would usually be adequate for normal replacement if more of them survived beyond year 2.

Fencing

Fencing is thought to be the single most effective way of stimulating regeneration (Woods, 1985; Rackham, 1980). Pigott (1983) reported that fencing at Yarncliffe Wood in Yorkshire resulted in the successive recruitment of oak saplings and after 26 years of enclosure the tallest saplings were 4-5 m high. Pigott (1983) also noted that fencing resulted in the immediate establishment of birch on disturbed areas but subsequent birch regeneration was prevented as the result of competition with ground vegetation *(Deschampsia flexuosa).*

However, Linhart and Whelan (1980) found that fencing of a mixed wood at Coed Gorswen, initially stimulated the survival of tree saplings of species other than oak, and had very little effect on oak regeneration. This they attributed to shading by brambles which invaded gaps in the canopy and to the lack of ground disturbance.

Treeshelters

Treeshelters are one of the most useful means of protecting regeneration from both small and large mammals and birds and their use may result in considerable gains in height growth (see Table 5).

Table 5 Height development of matched pairs of oak plants/shoots in an Exmoor woodland, showing the effect of individual protection by treeshelter. Number of pairs compared for each plant type in brackets. (Evans, 1988)

	Mean height (cm)			
Plant type	*Initial*	*Year 1*	*Year 2*	*Year 3*
Natural regeneration (15)				
Treeshelter	14	27	54	76
No treeshelter	14	16	21	34*
Transplants (1+1s) (15)				
Treeshelter	32	52	94	123
No treeshelter	32	32	31	43*
Oak coppice shoots (10)				
Treeshelter	32	132	178	200
No treeshelter	29	32	44	43*

*Trees heavily browsed by red deer. In fact even better growth would have been achieved in this instance by using 1.8 m treeshelters.

(Evans, 1988). However, instances have been reported of natural regeneration of oak being killed as the result of shelters being placed over them, this being attributed to reduced light levels especially when used in conditions of partial shade, i.e. under the canopy (Mitchell, personal communication). Evans (1988) suggests that treeshelters be put over seedlings during September of their first year to maximise the chances of survival.

Direct sowing

This was a classical treatment on the Continent, with acorns being sown (with or without burying) at high densities under shelterwood to achieve high initial seedling stockings where natural seeding fell short. Large quantities of acorns are needed due to predation.

Cultivation

Cultivation in the form of pannage by pigs has long been practised and discing is often carried out in conjunction with use of the uniform shelterwood system on the Continent (Everard, 1987; Price, 1990). Mellanby (1968) noted that rotavation greatly increased seedling establishment and reported rapid establishment in an arable field near an oakwood (242 oak trees per ha after 6 years). Pryor and Savill (1986) concluded that the failure of natural regeneration in Britain could often be ascribed to insufficient ground preparation and recommended more thorough ground cultivation following good seed years.

Weed control

Simazine applied at the time of direct sowing of acorns has been shown to reduce weed invasion but no effect on acorn germination, seedling survival or growth was recorded (Kramarev, 1973). Evans (1988) states that uniform application of weeding is not necessary but that careful selective treatment of established seedlings may be beneficial. Hand weeding or the use of a weed wipe is recommended during the first year, subsequent weeding requirements being similar to those of plantations. Lanier (1988) suggests that even where regeneration is dense the control of bramble and large herbaceous plants (purple moor grass, sedges, ferns) is necessary to ensure the survival of seedlings. Where regeneration is of low density it is necessary to clear vegetation from around the isolated trees.

Silvicultural systems

The most frequent silvicultural systems used in conjunction with natural regeneration of oak are the shelterwood system, group selection and strip regeneration (Orlov, 1980; Evans, 1988; Galoux, 1976; Small, 1982; Savill, 1988).

The shelterwood system is used extensively on the Continent but has been much less widely applied in Britain. Pryor and Savill (1986) suggest that ecological factors inhibiting regeneration may not be entirely to blame for the limited use of this system due to the fact that British foresters have never gained the experience and skill needed to manage such crops. Small (1982) regards the shelterwood system with protection from deer as the best method of stimulating natural regeneration in the New Forest.

The group selection system is the most frequently used form of irregular forestry in Britain (Savill, 1988) and has been used for the regeneration of oak in the New Forest, despite being associated with a number of problems (Small, 1982; Voysey, 1982). Smith (1983) considers group regeneration to be well suited for use in upland oakwoods. Strip regeneration, i.e. cutting in narrow strips with or without some retention of overstorey trees, is practised particularly in Eastern Europe.

Attempts to apply the group selection system to oak-dominated woodlands in Grizedale were largely a failure due to browsing pressure by deer, with regeneration being virtually absent after 30 years of management (Voysey, 1982).

Shelterwood systems

Shelterwood systems are widely used on the Continent (Everard, 1987) and have been used successfully in the New Forest (Small, 1982). Price (1990) describes the uniform shelterwood system used in the Bellême State Forest in France. A floating periodic block system is used which identifies three types of stand.

1. 'Groupe de Régénération' — stands to be regenerated.

2. 'Groupe de Préparation' — stands to be regenerated during the next 25 year period.

3. 'Groupe d'Amélioration' — stands where cleaning and thinning operations are to be carried out.

In 'Groupe de Régénération' seeding fellings are carried out to reduce stocking to about 200 stems per ha and to allow the crown to build up and so to promote seeding. Any understorey species are removed and in some forests the forest floor is disced prior to seed fall in the first good seed year. After successful establishment (seedling cover at least 3 per m^2), the first secondary felling is carried out which removes 40% of the standing trees. Three or more secondary fellings and a final felling are then carried out before the end of the 25 year period to remove all trees and free the natural regeneration. It is recognised that seedlings "need light", but too rapid removal of overstorey makes them susceptible to spring frosts and hot summer sun, as well as removing the seed source should regeneration fail. Planting of up to 20% is carried out where regeneration fails. Initial seedling stocking is 'many' thousands per hectare. When seedlings are 1-2 m high the areas are racked and cleaned. Subsequent cleaning operations lead to thinning after about 30 years.

Less elaborate methods have been developed for weed-prone sites involving only one seedling felling and a final felling, separated by 1 or 2 years (Everard, 1987). Pryor and Savill (1986) observed that in many cases in Britain the incompleteness of the crop arising from the initial seed fall has tempted managers to retain the overstorey too long. This has only served to inhibit the growth of the regeneration and allow rank weed growth in unstocked areas.

Irregular shelterwood systems may also have potential for use in Britain but Poore (1989) considers their application to be limited to more shade tolerant and regularly seeding species.

Group selection system

In the group selection system, thinning, felling and regeneration are carried out in groups of different ages within a stand. The group size will vary according to species, being larger for light demanders. The diameter of groups is thought to have to exceed 1.5 to 3 times mature tree height and the optimum size of coupe is thought to be about 0.5 ha (Garfitt, 1984; Poore, 1988). Matthews (1989) recommends smaller group sizes and relates them to the intended final number of trees (Table 6).

Small (1982) describes experiments with the group selection system (group size not greater than 0.2 ha) in conjunction with planting in the New Forest (Pondhead Enclosure). Survival of planted trees was poor due to lack of light and deer damage and regeneration was limited to beech and birch. Voysey (1982) also reported that regeneration (including transplants) in groups in Grizedale was severely limited by browsing by deer.

Summary

Silvicultural operations

- Natural regeneration has been surprisingly little used in Britain as a formal management system. There has been a lack of clear advice on its use and only low levels of success have been achieved in practice. However, interest in utilising regeneration is increasing.

Table 6 Group selection of oak related to final stocking. (Matthews, 1989)

Diameter of group (m)	*Area (ha)*	*Number of plants at 2 m spacing*	*Number of trees of 'final size'*
11-13	0.01	25-35	1
33-36	0.10	215-255	5
48-49	0.18	450-470	10

- Fencing is thought to be the single most effective way of stimulating regeneration through its effect in controlling browsing. Although treeshelters are also a useful means of protecting regeneration, instances of seedlings dying in shelters have been recorded. This has been attributed to low light levels within the shelters, particularly where they are placed over seedlings beneath an existing tree canopy.

- Cultivation of the ground surface has also been highlighted as having an important effect on seedling establishment. It has been suggested that a failure to cultivate many regeneration sites when good mast years occur has been a contributory factor in the low levels of success obtained in many woodlands.

- Although vegetation type has little effect on acorn germination, rank and tall weeds can seriously hinder the subsequent growth of seedlings. Even where regeneration is dense, the control of bramble and large herbaceous plants may be necessary. This can be achieved by selective use of herbicides or by hand weeding.

Silvicultural systems

- The most commonly used silvicultural systems for the natural regeneration of stands are the shelterwood, group selection and strip regeneration systems.

- Shelterwood systems are widely used on the continent and often involve quite intensive stand management. Less elaborate systems have been developed in Britain for weed-prone sites, involving just one seeding felling and a final felling separated by only 1 or 2 years. It has been suggested that a lack of knowledge and skill on the part of British foresters may be contributing to the low success rate often achieved in attempts to promote regeneration, rather than any inherent environmental reasons.

- Irregular shelterwood systems may also have potential for use in Britain but some authors consider their application to be limited to more shade tolerant and regularly seeding tree species.

- The group selection system is the most commonly used form of irregular forestry in Britain and is considered by many to be well suited to oakwoods in upland conditions. This approach involves the thinning, felling and regeneration of groups of different ages within a stand. The diameter of groups is often quoted as having to exceed 1.5-3 times mature tree height for successful regeneration. Others have suggested that 0.5 ha is the optimum size.

Chapter 8

Conclusions

1. Although seeding in oak occurs irregularly, even upland oakwoods produce sufficient acorns over extended periods to allow natural regeneration to take place. In good seed years acorn fall of up to 700 000 acorns per hectare occurs.

2. Approximately 0.5% of acorns survive to produce first year seedlings. The majority of acorn loss is due to predation.

3. Failure to regenerate can be ascribed mainly to the death of seedlings between the ages of 1 and 4 years. This is frequently due to browsing. Oak also appears to fail to regenerate under its own canopy and while the reason for this is not certain, the influence of low light levels on the growth of seedlings, acting over several years, together with defoliation by caterpillars falling from the canopy, are likely to be important. Regeneration is most successful in canopy gaps and at the edges of woods.

4. The most influential site factor is vegetation type, through its effect on litter retention, shading and competition. There is some disagreement over the ability of oak to regenerate in competition with vigorous growth of bracken and brambles.

5. Soil and climatic conditions do not appear to impose significant restrictions on regeneration.

6. Fencing, soil cultivation and opening up of the canopy are regarded as the most important silvicultural measures for promoting regeneration. Fencing has been shown to be succesful on upland acid site types because browsing animals are excluded. Fencing alone will seldom be sufficient for good regeneration if canopy gaps do not exist or if vigorous weed competition occurs in any gaps (particularly brambles on base rich sites).

7. In mixed woods, fencing will initially promote more regeneration of species other than oak, particularly ash, sycamore, rowan and birch. On many of these sites however, the proportion of oak regeneration will eventually increase.

8. Where woodland management is carried out with timber production as the primary objective, management intervention will be required to produce regeneration in adequate quantities in restricted time periods (e.g. to comply with the requirements of grant schemes). This will consist of fencing and opening parts of the canopy, with maybe some form of ground preparation and/or weeding. Information on the success of these measures is currently very poor.

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