

**The population ecology of acorn weevils and their influence on natural
regeneration of oak.**

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The population ecology of acorn weevils and their influence on natural regeneration of oak

The aim of the thesis is to investigate the population biology of the acorn weevil *Curculio glandium* and to determine the impact of acorn mortality on recruitment by the host tree, *Quercus robur*. The study involves a combination of observational studies, field experimentation and theoretical modelling. Observations were made of weevil numbers and acorn production over a 4 year period to supplement and extend an existing long-term data set on the reproductive performance of English oak. Acorn numbers fluctuated 10 fold and weevil numbers 60 fold over the period 1986-1989. Field experiments were carried out on weevil mortalities during the larval stage, varying weevil density and location. These experiments demonstrated that the minimal larval duration was 2 years, with several weevils entering protracted larval development. Experiments were also carried out on the production of acorns, and on the relationship between acorn attributes (identity of parent tree, acorn size, infestation by weevil larvae) and seedling recruitment. It was discovered that weevil infestation was not inevitably lethal to an acorn, but that infested acorns produced less competitive seedlings. The impact of weevil infestation was felt most severely by the smallest acorns. Adult weevils avoided the largest acorns, however, perhaps because they were unable to obtain a firm footing during oviposition. The experiments demonstrated the importance of acorn burial, with 100% seed mortality of surface-placed seed, compared with only 30% mortality of buried seed. The theoretical work involves an analysis of the life history of *Curculio glandium* and addresses the general question of why such protracted delayed reproduction might be adaptive (the larvae take 2 or more years to develop despite the fact that some members of the genus are capable of full development within one year). The explanation for the behaviour may lie in the fruiting behaviour of the host tree. Over an 11 year period, *Q. robur* has exhibited alternate bearing in Silwood Park, with only 2 consecutive low acorn crops. It turns out that an individual female weevil would do best to put a fraction p of her offspring into a 3-year life cycle and a fraction $(1-p)$ into a two year life cycle if the probability of two consecutive low acorn crops is p . The impact of feeding by weevils on oak regeneration is likely to be slight in comparison with other acorn feeders like the alien gall wasp *Andricus quercuscalicis*, rabbits, jays and squirrels, but in years when the acorn crop is low, *Curculio glandium* may kill 60% of the acorns that survive attack by the gall wasp. The weevil interacts with other members of the acorn-feeding guild because weevil-infested acorns are less likely to be eaten by seed predators like squirrels and rabbits, and less likely to be dispersed by mice or jays.

1 General Introduction

This thesis addresses a set of interrelated questions about the population biology of the acorn weevil *Curculio glandium* and its host tree the English oak, *Quercus robur*. The aim is to further our understanding of the ecology and evolution of this plant herbivore interaction, with particular reference to the implications for life history evolution of the weevils and the pattern of seed production by the tree. A further objective is to determine the importance, if any, of seed predators in the natural regeneration of *Q. robur*. I begin with an overview of the reproductive behaviour of trees, and then consider the evolution of seed dispersal systems. The introduction concludes with an assessment of natural regeneration by *Q. robur* in present day natural habitats in Great Britain.

1.1 Patterns of Tree Fruiting

Stephenson (1981) reviewed the fruiting behaviour of trees using data from horticulture, forestry, plant physiology and ecology. In this section I shall concentrate on: 1) the occurrence of alternate fruit bearing; 2) the occurrence of the masting habit in iteroparous species; and 3) the occurrence of masting in semelparous perennial species.

1.1.1 Alternate bearing

Although Silvertown (1980) defined mast fruiting on the basis of an inter-seeding period of > 1.5 years, it may be more useful to consider seeding strategies as being divided into alternating species with peaks of seed production in alternate years and true masting species with intervals longer than two years (see below). Alternate bearing cannot be seen as a form of masting in the classic sense of predator satiation, as there is no difficulty (in principle at least, see Hanski 1988) for insect seed predators to delay their reproduction,

so that emergence would coincide with peak fruiting years. I shall show later that a 1 year shift in the alternating pattern of seeding should not create a problem to the life history strategy of a specialist insect feeding on the seed resource.

1.1.2 Masting in iteroparous species

Masting is the synchronous production of large seed crops in one year over large geographical areas, followed by a more or less protracted interval during which there is little or no seed production (Crawley, 1983). True masting in the terms to be used in this thesis occurs where the inter-seeding period is longer than any specialist seed-feeding insect is likely to survive. The seeds of mast fruiting trees are expected either to be distasteful to generalist seed feeders, or to be produced in sufficient abundance to satiate generalist as well as specialist seed predators. The evolution of synchronous reproduction patterns is often attributed to predator satiation (Silvertown, 1980^{and} Janzen, 1976 in plants; Lloyd & Dybas, 1966 in periodical cicadas; and Findlay and Cooke, 1982 in lesser snow geese). An individual breeding out of synchrony would be at a selective disadvantage, since the breeding in the midst of starving predators would mean greatly reduced, if not zero, fitness.

The masting habit has been related to the fact that many late successional trees (e.g. *Quercus*, *Picea* and *Abies*) have high adult survivorship and low population growth rates (Waller 1979). Silvertown (1980) found that the tendency to mast is concentrated in what he calls predator prone species. As pre-dispersal mortality increases there is an increased tendency to show the masting habit. Also, trees with non-fleshy fruits are more likely to display the masting habit than trees bearing fleshy fruits (but see Ogden 1979 for examples of New Zealand fleshy fruited masting species).

1.1.3 Masting in Semelparous Species

Perhaps the best known example of masting in semelparous plants is found in certain species of bamboo (Janzen, 1976). In these monocarpic grasses the inter-mast

periods vary from 3-7 years up to 150 years or more. Janzen hypothesized that the masting habit was a predator satiation mechanism, producing vastly more seeds than could ever be eaten by generalist granivores. He also proposed that a mutant bamboo occurring in the original population and expressing double the inter-seeding period would be at a reproductive advantage because it would have proportionally less of its seeds consumed each time it fruited, thus becoming more prevalent in the population. A succession of these doublings of inter-seeding periods may have occurred through evolutionary time.

1.2 Seed Dispersal and Regeneration in Large Fruited Trees

The effectiveness of seed dispersal is of paramount importance to the fitness of individual trees. Large fruited trees face certain difficulties, because without dispersal agents, the seeds would fall directly beneath the parent tree, and as a consequence, the developing seedlings would suffer intense competition from the established parent plant (Janzen 1970, Connell 1971, Hubbell 1980, Mellanby 1968). Seeds must be transported to suitable microsites for establishment, and the number, size and morphology of fruits will influence the probability of seeds being removed by predators and dispersers.

1.2.1 Passive Dispersal of Seeds

Many species of trees (including *Quercus*, *Fagus*, certain legumes and pines) produce seeds with no obvious means of fruit dispersal, and the seed itself is the reward to the seed-dispersing organisms. There are several cases where the regeneration of tree species appears to require bird dispersal (Clark's nutcracker *Nucifraga columbiana*, and piñon jays *Gymnorhinus cyanocephalus* with piñon pines (Vander Wall & Balda 1977; Ligon 1978), blue jays *Cyanocitta cristata* with *Q. palustris* (Darley-Hill & Johnson 1981), and the European jay *Garrulus glandarius* with *Q. robur* (Chettleborough 1952; Bossema 1979). European jays are also common in stands of *Q. suber* and *Q. macrocarpa* with heavy acorn crops in the Iberian Peninsula (personal observation). All these studies conclude that the birds are beneficial to the fitness of the tree, and two go even further;

Ligon (1979) describes the pinyon jays and pinyon pines as reproductively interdependent, and Bossema (1979) describes the relationship between *Q. robur* and European jays as a symbiosis. Similar studies have also been made on mammalian seed predators (e.g. Fox 1982 on the evolution of oak germination strategies, and Miyaki 1987 working on the dispersal of *Pinus koraiensis* by the red squirrel *Sciurus vulgaris*). Scatter-hoarding by squirrels is extremely important to the regeneration of several tree species (Stebbins 1971; Stapainian & Smith 1984).

1.2.2 Differences in Seed Dispersal Between Individual Trees

Harper (1967) stressed the need to study the performance of individual plants in assessing questions concerned with evolutionary fitness, but very little work has been carried out on the differences in predation and dispersal rates of seeds from different individual trees of the same species. Performance of leaf-feeding herbivores has been studied on oaks with different bud-burst phenologies (Crawley and Akhteruzzaman 1988), and these show highly significant differences in the composition of the herbivore fauna. There are substantial differences between individual *Q. robur* to galling by the cynipid *Andricus quercuscalicis* (Hails and Crawley 1991). Janzen (1969) noted that in some tropical leguminous trees individuals of the same species suffered greatly different rates of seed predation by bruchid beetles. Further studies by Crawley (1985) showed that exclusion of herbivores using insecticide significantly increases seed set in *Q. robur*, and it is clear that insect herbivores can affect the performance of trees in a variety of different ways. The question is whether or not these effects on individual performance translate into any measurable effects on plant populations.

Bossema (1979) noted that jays *Garrulus glandarius* select a narrow range of size classes of acorn, and tend not to remove acorns that have been damaged by weevils or other acorn feeding insects. If acorn traits like size and insect susceptibility were under genetic control, then jays could have a profound effect not only on the dispersal of oaks,

but also on the evolution of seed size and resistance to seed predation. Crawley (personal communication) also has evidence from night-time infra-red video filming, that small mammal species, particularly wood mice *Apodemus sylvaticus* reject weevil infested acorns.

1.2.3 Dispersal in *Quercus robur*

The idea that the nuts of *Quercus* species are dispersed by animal agents is not new. In the U.K. Chettleborough (1952, 1956) was one of the first to quantify the numbers of acorns that jays can remove and the distances that they can carry them. His observations showed that flocks of jays can carry many tens of thousands of acorns up to 1 km. Schuster (1950) found that jays in Germany followed a similar pattern. The most extensive study of jay behaviour in relation to oak dispersal is Bossema's (1979), which concludes by stating that; 'costs to the oak of jays feeding on acorns are far outweighed by the benefits the oak receives. Many acorns are dispersed widely and buried at sites where the prospects for further development into a mature oak are highly favourable' (Bossema, 1979, p. 112).

Mammals also play a role in the dispersal and regeneration of oaks. Jensen & Neilson (1986) studied the dispersal of acorns by wood mice *A. sylvaticus*. The mice cached acorns in their underground runs, and were found to move acorns up to 35m from the edge of a woodland in one year, facilitating the invasion of heathland by the oaks. Miyaki and Kikuzawa (1988) concluded that scatter hoarding by *Apodemus speciosus* and *A. argentatus* was the most important means of storing acorns for the regeneration of *Q. mongolica*. Squirrels may aid the dispersal of *Quercus*, but they tend to be less important in the dispersal of white oaks (like *Q. robur*) than of the red oaks (like *Q. borealis*). In particular, grey squirrels *Sciurus carolinensis* tend to nip out the embryo of white oak species, which kills the seed prior to caching. Red oaks do not germinate until the following spring, and the squirrels do not remove the embryo before hoarding. This allows these red oak acorns to germinate if the cache goes unexploited (e.g. through the death of the squirrel; Fox 1982).

1.2.4 Natural Regeneration in *Quercus* in Great Britain

The study of the regeneration of oak in the British Isles is hampered by the ubiquitous human impact on the environment. Newbold and Goldsmith (1981) concluded that factors determining natural regeneration are probably unique to each individual site and are closely related to the presence or absence of grazing livestock, (see also Griffin 1971 and Piggott 1983). The production of viable acorns appears to exceed the number required to replace the annual mortality in an equilibrium woodland (Jones 1959, Shaw 1968, Griffin 1971, Rackham 1975, Prichard 1980, and Piggott 1983).

After arriving in a suitable microsite, following burial in the ground or beneath a layer of litter (Jones 1959; Shaw 1968; also see Chapter 4), young oaks are subject to a variety of ecological factors which determine their fate. Jones (1959) gives an extensive account of the competitive regimes that may be encountered by seedlings in different plant communities. In the present study I shall focus on the invasion of acid grassland by oaks, with particular reference to relative competitive abilities of healthy and weevil infested acorns (see Chapter 4). The study shows that competition with a dense grass sward consisting of *Anthoxanthum odoratum*, *Festuca rubra*, *Agrostis capillaris* and *Holcus mollis* (Crawley 1990a) has no deleterious effects on the seedling growth or survival of oaks (see also Newbold and Goldsmith 1981; but c.f. Jones 1959 p. 203). *Quercus* seedlings are poor competitors under conditions of deep shade (Jones 1959, but see Piggott 1983) and a combination of deep shade and intense herbivory can completely preclude oak recruitment (e.g. in Nash's Copse and Merten's Acres in Silwood Park; Forrester and Crawley, unpublished results).

Grazing by herbivores, particularly rabbits (Crawley 1990a) and sheep (Piggott 1983) appears to be extremely important in reducing the probability of seedling establishment in *Quercus* species. Shaw (1974) found that much of the failure of oak to regenerate beneath an oak canopy could be attributed to the fall of defoliating caterpillars (chiefly

Tortrix viridana) ^{from the canopy} \. The denser the canopy, the greater the impact of defoliation. Shaw (1974) concluded that there is no general failure of *Quercus* to regenerate except beneath its own canopy. At Silwood Park a substantial cohort of saplings emerged after the myxomatosis epidemic of the mid 1950's, which eradicated 99% of the local rabbit population (see Chapter 6 for a more detailed discussion).

Many studies of oak regeneration have commented on the role of seed feeding weevil larvae in reducing the probability of establishment (Jones 1959; Boucher & Sork 1979; Griffin 1971). Oliver and Chapin (1984) studied the effects of *Curculio fulvus* feeding on the acorns of live oak (*Q. virginiana*) and compared the performance of the emerging seedlings with seedlings that emerged from healthy acorns. The presence of a weevil larva had a significant negative effect on both seedling growth and survivorship. They made no attempt to estimate numbers of seedlings emerging under different regimes of plant competition or grazing.

The next step is to determine whether tree recruitment is limited by seed availability. To test whether recruitment into a plant population is seed limited, requires the simple experiment of planting extra seeds, then determining whether this leads to higher numbers of established seedlings by comparison with control plots (Crawley 1990b). This approach is impractical with long lived organisms like *Q. robur*, but other studies involving experimental planting of acorns have all produced seedling densities higher than those of controls (e.g. Shaw 1968; Griffin 1971; and Oliver & Chapin 1984). It does appear that seedling recruitment in oak is seed limited, at least in areas where there is little competition from mature trees. It is not clear, however, that gap recruitment in a mature *Quercus* forest would be seed-limited, since there may only be enough space for one new tree to replace the individual whose death created the gap, so adding more acorns would only increase seedling competition.

1.3 Overview of the Ecology of Seed Predators

Insect-tree interactions have been reviewed extensively by Janzen (1969, 1970, 1971) and Stephenson (1981). In this section I shall bring together the main themes that are relevant to the present study.

1.3.1 Life History Strategies of Seed Feeding Insects

Seed feeding insects have evolved an array of life history strategies in response to the different environments they inhabit, and from the constraints imposed by exploiting a resource that is variable in quality (e.g. the presence of toxins; Janzen 1969), individual seed size (e.g. the availability of sufficient resource to complete a life cycle of a single larva within one seed; Janzen 1969), and abundance (e.g. some species of trees exhibit the masting habit: (Silvertown 1980; Waller 1979), while in others, fruit production is determined by variable weather conditions).

One important life history strategy that insects employ to solve the problem of temporal variation in seed availability, is to forgo immediate reproduction in favour of subsequent breeding opportunities. This behaviour is described by Hanski (1988, 1989) as extra long diapause, ELD, and is likely to be prevalent in temperate environments where unpredictable year to year variation in resource availability may be superimposed on the predictable seasonal changes in the environment (Hanski 1988). The proportion of individuals entering diapause might be controlled by the density of individuals present or it may be density independent if each individual in the population assesses the same environmental problem independently (Hanski 1988). In the *Curculio-Quercus* system it is plausible that control of ELD is vested in the individual female, and that control of the proportional allocation to long and short diapause is made for each clutch of eggs separately. The mechanism of diapause control is unknown at the present time but is probably endocrine (Richards and Davies 1977).

1.4 Over all aims of the Study

In summary, this study concentrates on the ecology of seed production by *Q. robur* and pre-dispersal seed predation of the acorns of by *C. glandium*. Several independent investigations will be described. Chapter 2 explains the life history of *C. glandium* and outlines a series of experiments and observations that were carried out to determine the factors responsible for regulating *C. glandium* populations at Silwood Park. Chapter 3 examines the fruiting behaviour of *Q. robur* and relates fruit production to weather patterns. Mid-way through the study it was realised that *Q. robur* exhibited alternate bearing, and this forced a re-assessment of the evolutionary implications of oak fruiting patterns for *Curculio* life history evolution. In Chapter 4 the influence of the weevil on the probability of acorn establishment is investigated under different competitive regimes and in the presence and absence of vertebrate herbivores. Chapter 5 presents two complementary models of the life history strategy of the weevil, bringing together theoretical ideas with data from the field studies. The first model involves an analytical approach, while the second uses simulation to investigate the lifetime fitness of contrasting life histories in *Curculio*. Both models agree closely over a realistic range of parameters and serve as a basis for analysing the life cycle of the weevil.

The final chapter provides a synthesis of the seeding strategy of the oak and the life history strategy of the weevil. The limitations of a short term study on a long lived organism are emphasised.

2 The Life Cycle of *Curculio*

Two points about the life cycle of *Curculio* are discussed in detail in this chapter 1) the two year minimum life cycle; and 2) the apparently bet hedging life history strategy.

2.1 The Life Cycle

An unusual feature of the biology of many seed feeding *Curculio* species is the duration of the life cycle. In *C. nucum* feeding in hazelnuts, *Corylus avellana* (Massee 1940, Bovien 1941, Martin 1949, Alkan 1960 and Leska 1973), *C. elephas* in chestnuts, *Castanea sativa* (Popovia 1962), *C. caryae* in pecan nuts (Bissell 1934), and *C. glandium* in acorns of *Q. robur* (Charakov 1957; Komarova 1958) there is always at least one year spent in the ground as a larva and then as a prepupa. The insect can also continue for a further year in the ground before emerging as an adult nearly 3 years after leaving the acorn. *Curculio* species on desert oaks, such as those found in the U.S.A. and Mexico, are also known to have life cycles that can last up to 5 years after emergence from the acorn (Gibson 1969, 1977). Kumpe and Isely (1936) note that one species, *C. rectus*, is capable of passing through its life cycle in one year, although they do not mention which species of *Quercus* this weevil attacks. Other species of *Curculio* in the same study, (*C. pardalis*, *C. baculi*, and another species near *C. parvidens*) all had a minimum two year life cycle, but again no species of *Quercus* were given. *Curculio robustus* from Asia has also been reported to complete their life cycle in 1 year on the acorns of *Q. acutissima* and *Q. varibilis* (Fang 1981).

In the British Isles development of *C. glandium* always takes at least two years and often three (personal observation). During the late summer and early autumn, the female *Curculio* searches out suitable acorns on which to lay her eggs. Using her long rostrum she drills into the developing acorn at the boundary between the cup and the skin of the acorn. She then softens the tissue under the skin of the acorn by repeatedly inserting her rostrum at slightly different angles often up to seven or eight times, thereby forming a

multi-chambered wound. She then lays an egg at the end of one of the chambers by inserting her extendible ovipositor into the cavity made by the rostrum. Usually one egg is laid, but a maximum of seven has been recorded from a single oviposition. In all the female carries about fifty eggs, but dissection may under estimate the total lifetime fecundity, because new eggs are matured as the adult female ages.

About 7-10 days after oviposition the minute larvae hatch and start to feed, initially on the damaged tissue prepared by the female, and then by eating into the reserves stored within the cotyledons.

There are three larval instars (personal observation) lasting 3-4 weeks in total. During this time the larva eats away at the cotyledons to varying degrees, depending on the size of the acorn (Section 4.1). When the larva have finished feeding or the cotyledons have been entirely consumed, the larvae emerges from the acorn by chewing a small circular hole in the skin of the acorn, then buries itself in the ground to a depth of approximately 5 cm.

The larva remains in the ground through out the following summer in an earthen cell (personal observation). During the autumn of the first year in the ground the larva pupates (a process lasting about 10 days) and then emerges as an adult, but it remains underground within the earthen cell throughout the second winter. During the spring of the second year, the adult finally emerges above ground and feeds on oak and other flowers (personal observation) throughout the summer. Not all of the larvae complete their development in the second autumn, however, and a proportion stay as larvae for a further year. They undergo pupation in their second autumn in the ground and emerge as adults two and a half years after the egg was laid in the acorn (see Fig. 2.1). For an excellent summary of the life cycle of these insects see Fabre (1927).

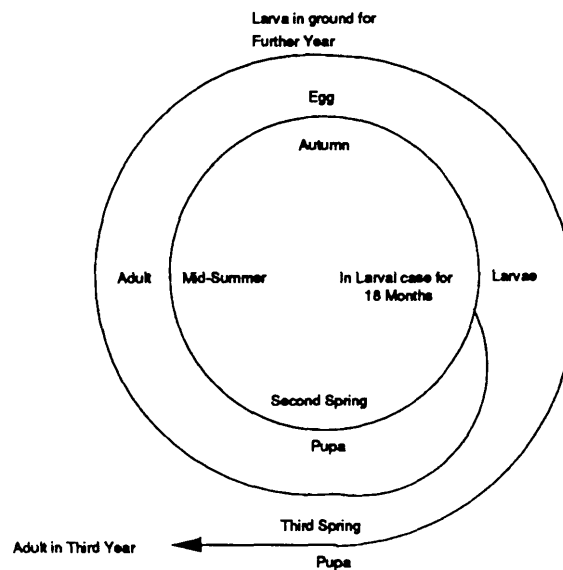


FIG 2.1 The life cycle of *Curculio glandium*. The larva spends at least 18 months in the ground in an earthen cocoon, a proportion emerge as adults in their second summer, while the remainder continue as larvae in the ground for a further year or more.

2.2 Fecundity, Clutch size and Larval Survival in the Acorn

Investigations were carried out into the fecundity, clutch size and larval survival of *C. glandium*. The data were gathered over two years in order to estimate the parameters that will be used later to develop a life history model (see section 5.2).

2.2.1 Methods

During the late summer of the two years of the study, female beetles were gathered using a beating tray in an attempt to measure the fecundity of the adult weevils. Their secretive habits made collection difficult and a total of only 5 fecund females weevils were caught and dissected. Female weevils that had been reared in individual pots emerged around the middle of May and they too, were dissected. These reared females showed no signs of egg production, and it was assumed that a period of feeding is necessary prior to the development of a mature complement of eggs.

In all, 1166 weevil infested acorns were gathered during the autumn of 1987 and reared individually in small plastic pots (3cm diameter) containing a 50:50 mixture of sand and garden peat. It was found that the weevil larvae were able to construct their cells in this medium. Acorn length, breadth and fresh weight were measured. The acorns were then carefully dissected in order to count the numbers of eggs, larvae, or dead larvae they contained. Dead larvae were recognisable as detached head capsules. The acorns were then reassembled by embedding them in the peat in the pots. In the 10 or so cases where this procedure was not sufficient to hold the acorn together, then entomological micro-pins were used. The pots were then placed in an out-door insectary and left for one year. The survival of the emerging larvae to the adult stage and the proportion remaining as larvae were determined. This procedure was repeated in 1988, but with slightly lower replication because of the poorer acorn crop in this year, (a total of 838 acorns were used).

In 1987, 271 weevil larvae that had previously emerged from their acorns were weighed and reared individually in small pots similar to those used in the previous experiment. Their survival to adulthood and the proportion remaining as larva for a further year were recorded. This procedure was repeated in 1988 with reduced numbers (circa 100 larvae). The peat used in the pots appeared to be infested by an entomophagous fungus, and all larvae died.

2.2.2 Results

(i) Fecundity of the weevil

The mean number of eggs per female was 34.6 ± 7.9 . This figure, although derived from a small sample size, will be used later when constructing a model of the life history strategy of the weevil (chapter 5). The quantitative aspects of the model are not greatly affected by the magnitude of the fecundity estimate.

(ii) Distribution of eggs in acorns.

The numbers of eggs in the 233 weevil-infested acorns used in the individual rearings were counted, along with the number of acorns that contained no eggs. Two distributions, the Poisson and the negative binomial, were fitted in an attempt to describe the pattern of oviposition (Fig. 2.2). As with many other biological systems (Hassell 1978) the distribution of eggs within acorns was highly aggregated, the negative binomial distribution providing an excellent fit to the data $k=1.3$.

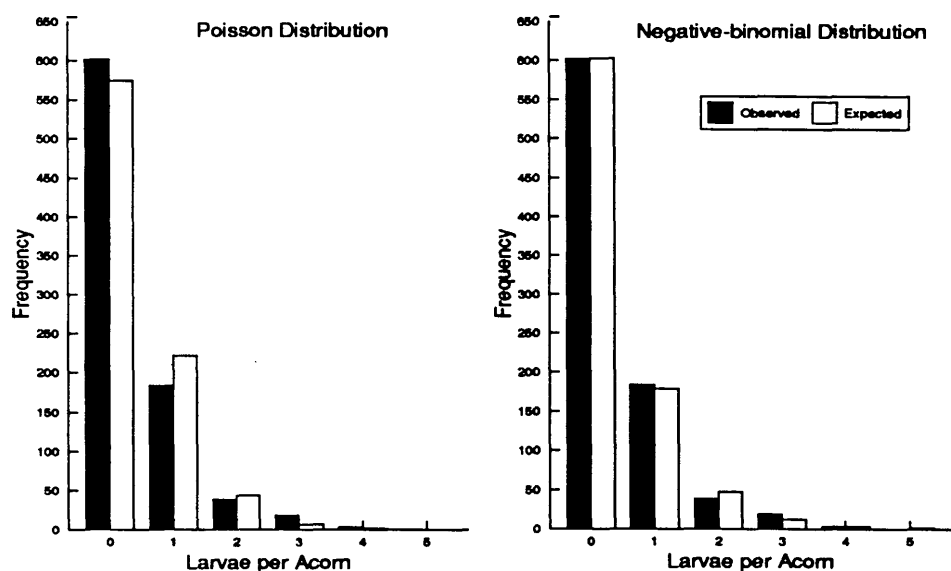


FIG 2.2 Comparison of Poisson and negative binomial distributions of the number of eggs deposited into acorns. The fitted Poisson distribution is significantly different from the observed figures, $\chi^2 = 44.77$, d.f.=2, $p < 0.0001$. The negative binomial distribution with $k=1.3$ provides a close fit to the data, $\chi^2 = 3.699$, d.f.=1, $p=0.054$.

(iii) *The effect of size of acorns on oviposition preferences.*

Acorns were weighed fresh on a flat top balance to an accuracy of 0.01 of a gram, and the presence or absence of a weevil larva was noted. In both 1987 and 1988 the mean size of acorns with weevil eggs was found to be significantly smaller than the mean of acorns without weevil eggs (see Table 2.1 and 2.2 using the t test for samples with unequal variances; Sokal and Rohlf 1981).

i). Preferred size class of acorn 1987

Weevil larva	Acorn weight	n	s ²	F	p
Absent	3.244	488	4.422	2.189	<0.0001
Present	2.049	678	2.02		

Table 2.1 Mean weight of infested and healthy acorns in 1987, (1987, $t=10.9$, d.f.=789, $p<0.00001$,.

ii). Preferred size class of acorn in 1988

Weevil larva	Acorn weight	n	s ²	F	p
Absent	2.506	607	1.698	1.644	<0.0001
Present	1.981	231	1.033		

Table 2.2 Mean weight of infested and healthy acorns in 1988, $t=6.16$, d.f.=529, $p<0.00001$).

In both years the variance in acorn size of the weevil infested acorns was also significantly lower in comparison to healthy acorns, (1987, $F=2.189$, d.f.=488 & 678, $p<0.00001$, and 1988, $F=1.644$, d.f.=607 & 231, $p<0.00001$)

(iii) Competition between larvae within acorns

Analysis of the relationship between the number of eggs laid in an acorn and the number of larvae emerging from the acorn showed no significant density dependence (Fig. 4). However, the proportion of larvae surviving from egg to emergence from the acorn, was influenced by the weight of the acorn; the heavier the acorn, the greater the chance of the full clutch of larvae emerging.

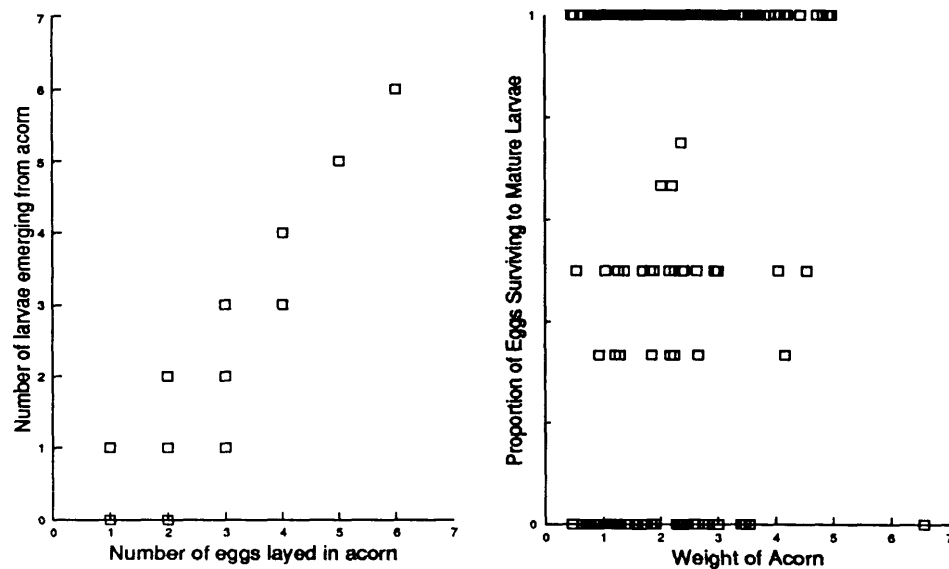


FIG 2.3 a: The number of larvae emerging plotted against the number of eggs deposited in the acorn. There is a 1:1 relationship between these two variables, but when acorn weight is taken into account; **b:** there is a significant effect on the proportion of eggs surviving to produce mature larvae. Larvae that are large enough to make their own way out of the acorn.

Source	Change in Deviance (χ^2)	d.f.	p
Acorn Weight	7.5	1	0.005

TABLE 2.3 Analysis of deviance table of proportion of eggs emerging as a function of acorn weight (Fig 2.3). The analysis was carried out in GLIM using binomial errors. The proportion of the total deviance explained by the model is small, but significant. Error deviance = 311.2 with 231 d.f., total deviance = 318.7 with 232 d.f. (see text for details).

Even though only 2.5 percent of the total deviance in the proportion of the clutch emerging is explained by acorn size in a logistic regression model of proportion of eggs emerging as larvae against the weight of the acorn, the regression is highly significant.

Parameter	Estimate	S.E.	t	p
Slope	0.4056	0.05448	7.445	<0.001

TABLE 2.4 Estimates from the logistic regression of the proportion of weevil larvae emerging against acorn weight: the data are shown in Fig. 2.3b.

The effect of the number of larvae inhabiting each acorn on the final larval body weight also is highly significant (Table 2.5); the higher the number of larvae in an acorn, the lower the final weight of each larva (Fig 2.4).

Source	d.f.	SS	MS	F	p
Larvae/Acorn	5	605.1	121.0	9.49	<0.0001
Error	227	2896	12.76		
Total	232	3501			

TABLE 2.5 ANOVA of between group larval weights against number of larvae developing per acorn.

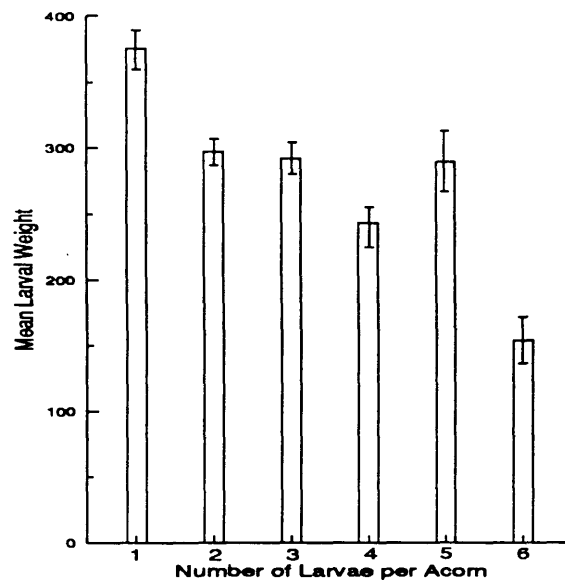


FIG 2.4 Mean larval weights (mg) $\pm$ standard error. All the results for 5 larvae per acorn come from a single relatively large acorn, so the larvae are proportionally heavier. When acorn weight was included as a co-variate, however, it did not explain a significant amount of the variance.

Since fecundity is assumed to be proportional to larval weight in the models that follow (Chapter 5), I carried out a linear regression of final larval weight on initial number of larvae (Fig 2.4).

Parameter	Estimate	S. Error	t	p
Constant	401.87	14.67	27.39	<0.0001
Larvae per Acorn	-38.92	6.26	6.21	<0.0001

TABLE 2.6 Estimates of the linear regression of mean larval weight against larvae per acorn.

The regression of larval weight on number of larvae per acorn is highly significantly negative, and as there^{is} little larval mortality in the acorn, there appears to be scramble competition taking place within the acorn. The resulting larval weight has a strong effect on the survival of larvae over the year they spend in their underground cells.

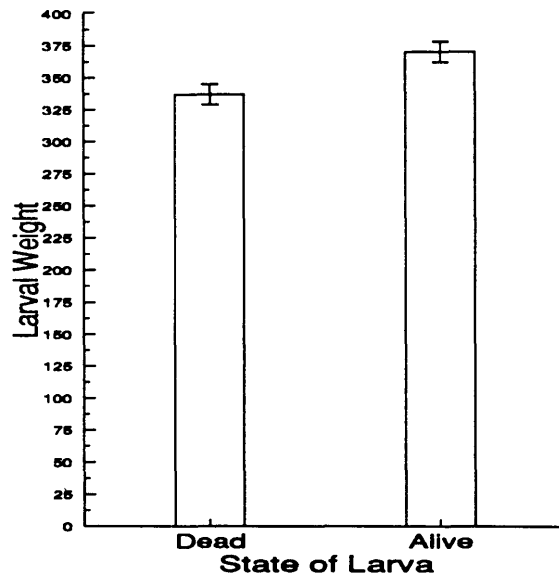


Fig 2.5 Mean weight of surviving weevil larvae $\pm$ standard errors. The difference is highly significant (sample t test $t=3.32$ d.f. = 269, $p=0.0011$).

There is a substantial disadvantage to being a smaller larva, in that there is a reduced chance of surviving two years in the soil. All the very small larvae from acorns that bore 5 or 6 individuals died during the duration of the study. Dead larvae started significantly lighter than surviving larvae (Fig 2.5).

Wild adult female weevils were collected whenever they were seen in the field, and dissected to determine their fecundity. Due to their extremely skulking habits only 5 adults were collected during the 3 years of the study. This is very small sample size, but a regression of fecundity on body size (length of elytra) does shows a clear linear relationship, (Fig 2.6). All the female weevils emerging from the rearing pots were dissected to determine their fecundity, but none contained any eggs.

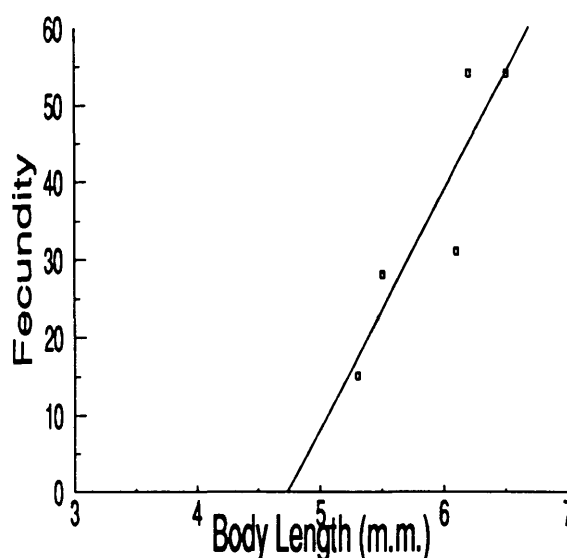


Fig 2.6 Regression of fecundity (total number of eggs determined by dissection) on body size (width across shoulders). Intercept= -145.43, $SE_e=51.58$, $t=2.83$, $p=0.0661$, Slope= 30.741, $SE_b=8.654$, $t=3.55$, $p=0.0381$. N.B. this regression is based on only 5 points.

Of the 271 larvae reared in individual pots 116 survived and of these 95 emerged as adults in their second year, The rest remained as larvae for a further year. (i.e. approximately 18% of the total 1987 cohort).

2.3 Larval Survival in the Ground

The hypothesis that population regulation took place during the larval stage in the ground was tested. It was hypothesised that the larvae would fall prey to soil dwelling carnivores, such as carabid and staphalinid beetles, centipedes and parasites, and that these might act in a spatial density dependent manner.

2.3.1 Methods

Large numbers of weevil larvae were available during the autumn of 1987. Initial investigations showed that weevil larvae placed on the soil surface and confined to a small area using an inverted plastic butter dish, burrowed into the soil. After 3-4 days all the larvae could be recovered at a depth of about 5 cm. There was very little side-ways

movement in the soil. This facilitated an accurate estimation of numbers surviving on recovery. It was therefore assumed that during the duration of the experiment, all surviving larvae could be recovered.

Weevil larvae were placed out at five different densities, (1, 2, 4, 8, and 16 larvae) under inverted butter dishes (10 cm diameter). This gave densities of approximately 88, 176, 353, 707, and 1414 larvae m⁻² respectively. The larvae were placed in four sites around Silwood Park ; three sites were beneath trees and one was in a mesic grassland. The sites were selected to provide a range of conditions where weevils were presumed to overwinter (i.e. beneath trees known to have weevil infested acorns) and an open grassland area to serve as an uninfested comparison.

This gave an experiment with three treatments, each replicated three times. The position of each treatment was randomized and given a unique code. The experimental design was:

- a) Four sites
- b) Five densities of weevil larvae
- c) Four times of retrieval

The groups of larvae were dug up at four different times over the next 15 months. Recovery of the larvae was carried out by digging up approximately twice the diameter of the butter dish to a depth of 20 cm, placing the soil and turf in a plastic bag, and then sorting through the material in a large tray back in the laboratory. The number of weevil larvae that were still alive were recorded. The last sample was taken 15 months after initiation of the experiment, and contained two adult weevils (i.e. all the larvae had either died or become adult during this period).

2.3.2 Results

Due to the destructive sampling required for the recovery of larvae, the time to death of individual larvae could not be calculated. The analysis was therefore carried out on the

proportion of larvae that survived up to different sampling occasions, using GLIM with a fixed binomial denominator (the number of weevil larvae placed on the surface at the beginning of the experiment).

Initially, differences between sites were investigated. Site 4 (The mesic grassland site) showed a small but significantly higher survival rate of larvae ($p < 0.05$). In subsequent analyses, the data are pooled across sites in order to investigate the mortalities of weevil larvae at different population densities. Five survivorship curves were plotted, one for each of the different initial density classes (Fig. 2.8), a regression was carried out for each of the four sampling occasions on the proportion of larvae recovered as a fraction of initial density. A slope of 0 indicates density independent survival, and a slope significantly different from 0 indicates that density dependent mortality is taking place (Table 2.7).

Time in Ground	Slope	S.E.	t	p
3 Months	-0.006506	0.01972	0.3299	N.S.
6 Months	-0.02656	0.02026	1.311	N.S.
9 Months	-0.00894	0.02565	0.3485	N.S.
15 Months	-0.09462	0.04532	2.0878	0.0422

TABLE 2.7 The slopes of the density dependence tests for the larval burial experiment, the effect of elevated density of weevil larvae on larval mortality becoming significant (although only slightly) after 15 months. Note, however that all 4 signs of the regression slopes are negative, suggesting lower proportional survival at higher densities.

There is a very slight response in the proportion dying to the initial density, but this is only detectable after 15 months in the ground (Fig. 2.7). This response of mortality to elevated densities of larvae may not occur at realistic field densities. In Section 2.4 a more realistic estimate of the densities of the weevil larvae will be made, allowing a more legitimate estimate of the impact of density on mortality. Recovered larvae showed no apparent cause of death, no puncturing of the cuticle appeared to have been inflicted by predators, and no signs of infection of fungal pathogens were found.

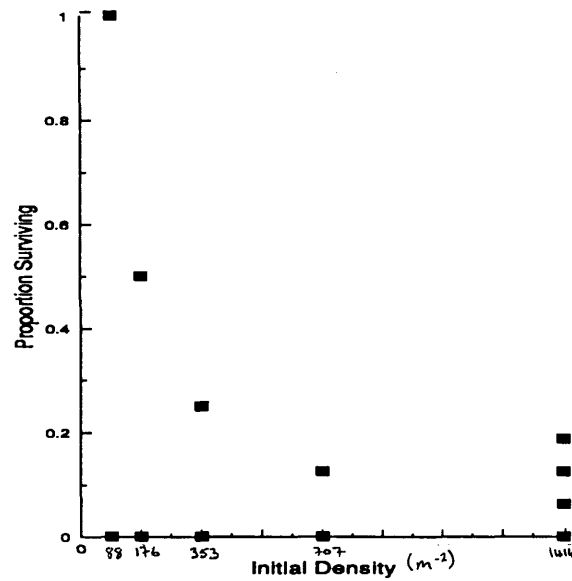


FIG 2.7 Correlation between proportion of weevil larvae surviving and their initial densities, after 15 months in the ground. Data pooled over all 4 blocks. GLIM with binomial errors; Slope, -0.09462, S.E. 0.04532, $t=2.09$, $p=0.0422$

Fig 2.8 shows the survivorship of weevil larvae in the soil at 5 densities. Death rate was, significantly higher during the first three months of burial than subsequently (Fig. 2.8 a-e); this effect was consistent at all initial densities.

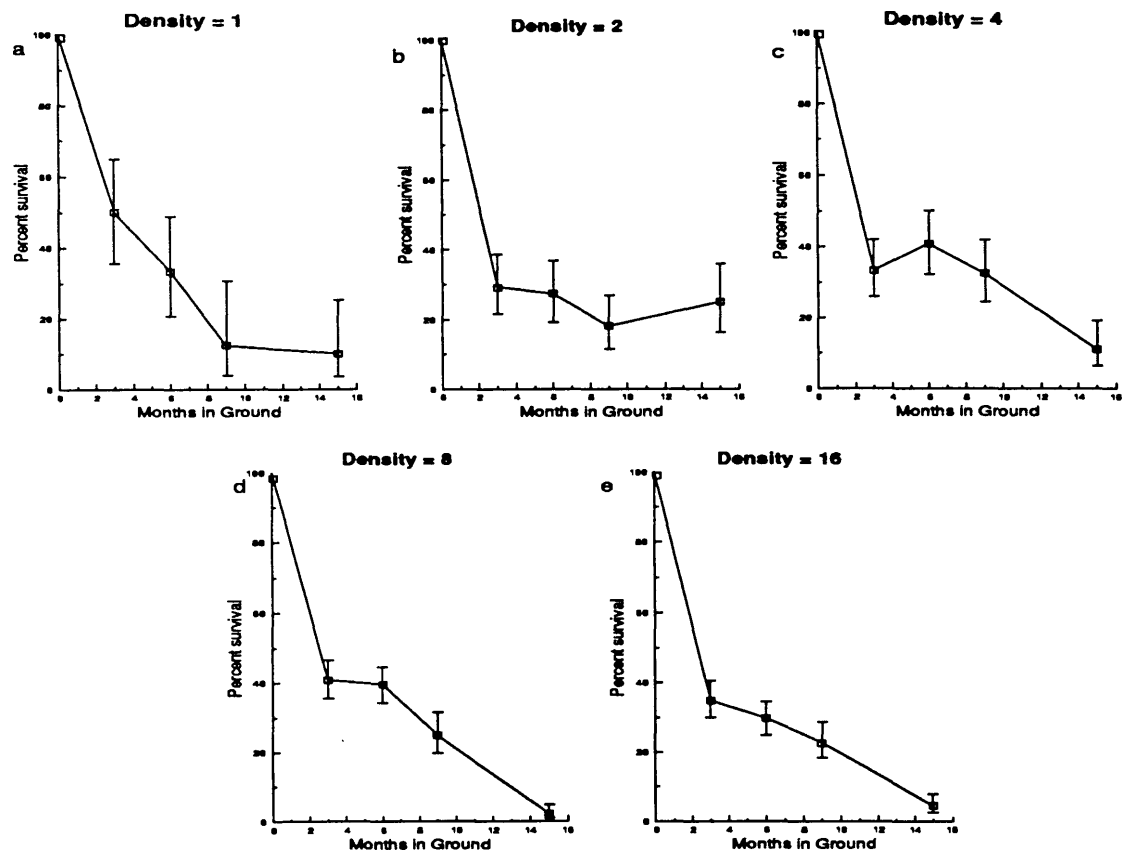


Fig 2.8 Survivorship (%) of weevil larvae at various densities, data were pooled over all 4 blocks.

2.4 Acorn trap experiments

The questions addressed in this series of observations concern the weevil-infested acorns that fall from the trees to the litter layer under the canopy. 1) Is the proportion of weevil infested acorns remaining on the ground, different from the proportion falling from the tree? 2) Are the proportions of weevil infested acorns higher in low fruiting years than in high fruiting years? 3) were the larval densities used in the burial experiment (above) realistic?

2.4.1 Methods

The acorn traps were large plastic dustbins (diameter 50 cm) weighted down with bricks. The lid of the dustbin was punctured to allow rain to drain through and positioned in the dustbin in an inverted position. A two-inch chicken-wire guard was placed over the traps to prevent squirrels from entering (Fig. 2.9).

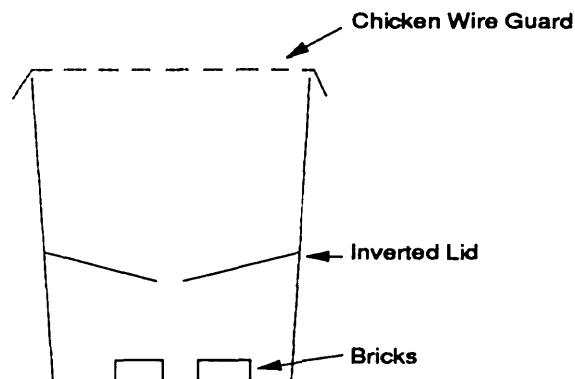


Fig. 2.9 Schematic diagram of the acorn traps, modified from a plastic dustbin with a 50 cm diameter

In 1987 8 trees were chosen for observation. Underneath each of these trees 6 traps were placed as illustrated in Fig. 2.10, along the North-South axis of the tree canopy. One metre from the traps six quadrats of 0.5 x 0.5m were marked out. During the low acorn year of 1988 the number of trees studied was reduced because some of the trees used in the previous years had either no acorns or the few acorns they had were galled by *Andricus quercuscalicis*. Because the acorn crop was so low it was decided to increase the number of traps beneath the five remaining trees.

Each day during seed fall (late August through early October) the number of acorns falling into the traps and quadrats were counted and removed. From the data information was obtained on the proportion of weevil-infested acorns on the ground and in the traps, and between year differences in proportion of weevil-infested acorns could be estimated.

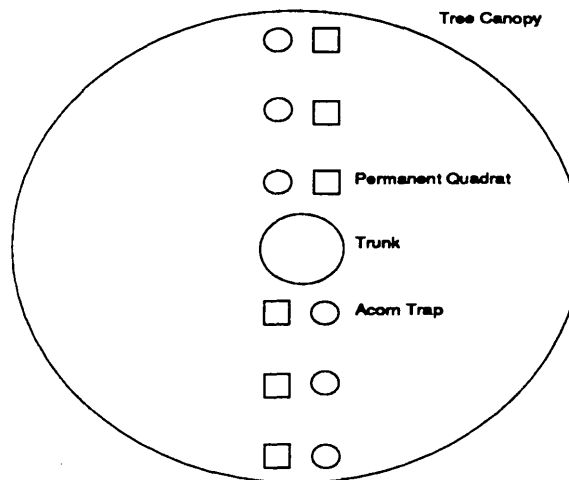


Fig 2.10 Lay out of the 6 acorn traps under the canopy of a tree during the 1987 study. During 1988 the 9 traps were arranged around the tree in 3 rows at 120 degrees to one another.

2.4.2 Results

The results of the acorn trap study were analysed in two separate ways. First, the proportions of weevil-infested acorns in the traps and on the ground were compared. Second, an estimate of the density of weevil larvae on the ground was made for each of the trees in both of the years.

1) Proportion of infested acorns in the traps and on the ground.

During 1987 the proportion of weevil infested acorns in the open quadrats on the ground was either significantly greater than in the acorn traps or not significantly different (Table 2.8). This lends some support to the observation made by Crawley (personal communication) that small mammals can detect and preferentially reject weevil-infested acorns.

Differences in the proportions between trap and quadrat samples were assessed using GLIM with binomial errors. The value of t was obtained by dividing the differences of the estimates of the trap and quadrat logits by the standard error of the difference between the two logits. 1988 was a very poor acorn year and there were no significant differences in the proportion of weevil infested acorns in the traps and quadrats.

Tree	Trap	Quadrat	t	p
806	5/9 (0.55)	3/10 (0.30)	1.11	N.S.
814	12/115 (0.10)	23/181 (0.13)	2.25	0.012
1009	9/27 (0.24)	33/61 (0.54)	1.77	0.038
1020	35/205 (0.17)	66/449 (0.15)	0.78	N.S.
1024	12/188 (0.06)	54/162 (0.33)	5.74	<0.0001
1025	10/57 (0.17)	26/79 (0.33)	1.98	0.024

Table 2.8 The number of infested acorns (first number) out of the total number of acorns (second number) and the proportion of infested acorns recovered from quadrats compared to those from acorn traps in 1987. Probabilities are approximate (see McCullagh and Nelder 1983).

Tree	Trap	Quadrat	t	p
809	0/7	0/2	-	-
814	0/0	0/2	-	-
1020	7/8 (0.87)	3/6 (0.50)	1.45	N.S.
1022	22/35 (0.63)	36/51 (0.71)	0.75	N.S.
1024	5/7 (0.71)	2/3 (0.66)	0.15	N.S.

Table 2.9 As table 2.7 for acorns recovered in 1988. No significant differences are seen between the proportion of infested weevils in the quadrats and the traps.

2). *Density of weevil larvae under trees.*

The density of larvae under different trees varied significantly between trees, largely because different trees bear significantly different acorn crops (see section 3.2). The number of larvae per square metre is shown in Fig 2.11, as analysed in GLIM with Poisson errors.

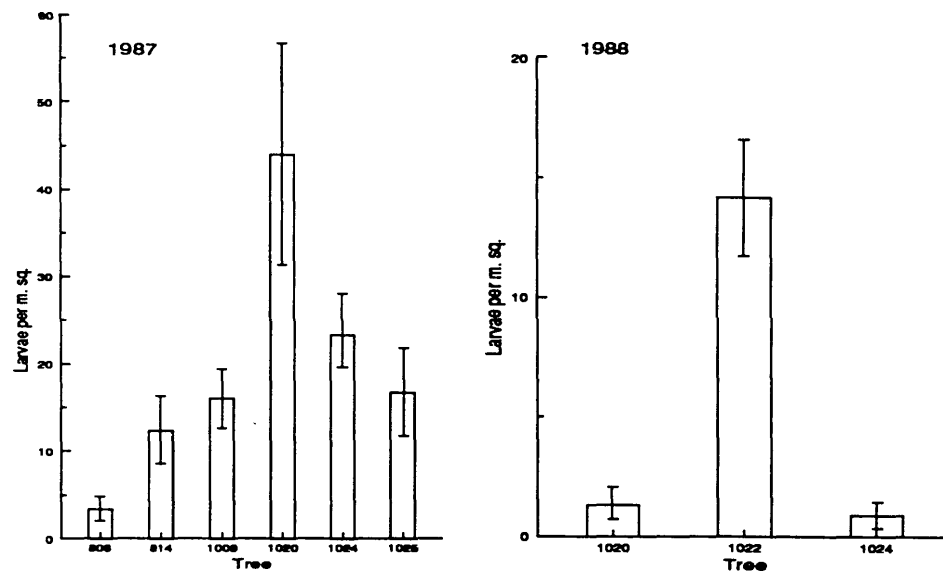


Fig 2.11 Larval densities per square metre of ground beneath trees bearing acorns in 1987 and 1988. In 1987 the quadrats below trees 811 and 809 yielded no acorns. In 1988 the quadrats below trees 814 and 809 yielded no acorns, and trees 806, 811, 1009, and 1025 were omitted from the study because they had so few acorns. Means are presented $\pm$ standard error.

2.5 Discussion

The life cycles of some of the members of the genus *Curculio* are hard to understand in terms of classical life history theory (Stearns 1976, Fisher 1930). They appear to miss the opportunity for early reproduction by remaining dormant in the ground for an extra year or more. It is known that some members of this genus are capable of completing their life cycle in 1 year (e.g. Kumpe and Isely 1936, Fang 1981), so the genus *Curculio* as a whole does not appear to be constrained to a supra-annual life history strategy. There is variation in life cycle duration within the genus.

In the remaining Chapters of this thesis I shall attempt to quantify the factors that influence the evolution of the extended life cycle, and to identify the practical benefits that extended dormancy confers on *C. glandium* feeding on the acorns of *Q. robur* at Silwood Park.

The life cycle of *C. glandium* is very similar to those of other *Curculio* species inhabiting seeds (Martin 1949; Bovey, Linder & Muller 1975). The complement of eggs appears to be similar to estimates from other species (Popova 1962; Alkan 1960). Superoviposition has been observed in *Curculio* species (Alkan 1960, personal observation) but there is no mention of larval survival being affected by competition within the seed. Individuals emerging from acorns containing more than one larva weighed significantly less than individuals that had sole occupancy of an acorn and these smaller individuals had a lower survival, at least in the insectary. That *C. glandium* larval survival is positively related to acorn size is not surprising, but the fact the number of larvae surviving within an acorn is not reduced at higher densities is somewhat surprising.

One might suppose that females should lay their eggs in larger acorns, but this was not observed to occur. Eggs were consistently laid in *smaller* acorns, and the variance in size of infested acorns was significantly lower than the variance in size of uninfested acorns. This same pattern was observed in two successive years. The female weevils appear to be extremely discriminating about where they lay their eggs.

Observations by Fabre (1927) suggested that with the largest acorns female beetles were unable to gain sufficient leverage on their rostra to enable them to pierce the skin of the acorn. He even reported that some females were trapped by their rostra, after having lost their grip on the acorn with their feet. Such females invariably died.

It appears that not all acorns on any given tree fulfil the oviposition requirements of female weevils. Individual oak trees have characteristically different shapes and sizes of acorns and these acorn attributes are consistent between years. It would be valuable to test whether the variance in attack rate was lower for large-acorn bearing trees, but the data are not available from the present study.

The major problem that must be faced by a weevil larva before emerging as an adult 18 months later is to survive in the ground within its earthen cell, relying on its fat reserves. The robustness of the cell is the larva's protection against desiccation and predators. Larval survival in the ground over the 15 months of the burial experiment was approximately 10% and there was only a very slight effect of enhanced density on the proportion of larvae dying. These experimentally elevated densities were much higher than at any natural densities found during the two years the acorn trap observations were carried out (up to 1414 m⁻² in the 16 larvae treatment) and are probably biologically unrealistic. However, the results do show that spatial density dependent mortality in the ground is not likely to be an important factor in the population regulation of *Curculio*. It was not possible to carry out this study in the low acorn years of 1986 or 1988 because of the scarcity of weevil larvae, and by the next good acorn year (1989) the study had finished (see section 3.2). Even if the study had been carried out using natural densities of larvae, a three year study of these natural densities may not have been sufficient to detect temporal density dependence (Hassell, Latto, and May 1989).

3 Fruiting and Acorn Abortion in *Quercus robur*

The purpose of the series of experiments and observations described in this chapter was to determine the factors affecting the pattern of seed production in *Q. robur*. Data were available from ten years of a long term study and in detail for the three years of the present study.

3.1 Pollination Biology

A hand pollination experiment was carried out in 1987 to test the hypothesis that fruit production in *Q. robur* is pollen limited. This was seen as a potentially important mechanism of crop size limitation which should be assessed before any further studies on seed abortion were initiated.

3.1.1 Introduction

Previous work on the abscision of fruit on *Q. alba* in Wisconsin (Williamson 1966) reported that between 16 and 57% of the aborted flowers had received pollen. Other work on *Catalpa* species (Bignoniaceae) showed that artificial pollination did not increase fruit set when compared ^{with} naturally pollinated control inflorescences (Stephenson 1979). Other *Mangifera* and *Cassia* species in which artificial pollination experiments have been carried out have increased the number of flowers that set fruit but not the number of seeds that matured (Lee 1980, Singh 1960). One reason why the abortion rates in artificially pollinated flowers was so high may be that they have received pollen that is incompatible with the recipient stigma or the timing of stigma receptivity was incorrect (Stephenson 1981, and Willson & Burley 1983).

3.1.2 Methods

Three trees were selected for the experiment. Each was known to have borne fruit in previous years, and each had low branches for easy access. Within each tree 60 shoots bearing peduncles were marked in each of the northern and southern aspects of the tree. At random 30 of these shoots were allocated to treatment or control groups. Pollen from five other trees was gathered, mixed together in a petri dish and applied to the stigmas of the treatment group using an artist's paint brush. The pollen from five different trees was used in an attempt to decrease the likelihood that the pollen was incompatible with the particular stigma on the experimental shoots (Stephenson 1981, and Willson & Burley 1983). Another experiment was carried out using pollen exclusion bags. Here the treatments were: no pollen; own pollen; pollen from different trees; and unbagged controls. Unfortunately, acorns were initiated in the bags with the 'no pollen' treatment and so this part of the experiment had to be abandoned.

The number of aborted peduncles, recognisable by the characteristic scar they leave, and the number of acorn-bearing peduncles were counted at the end of the summer, just before acorn fall.

3.1.3 Results

The response variable in the GLIM analysis was the proportion of peduncles surviving the season to bear acorns. The binomial denominator was the number of peduncles on the shoot at the start of the experiment in spring. The fitted model was a nested design, with the effect of pollination nested within aspect Nested within trees. This model explained a mere 3% of the total deviance in abortion rate. The differences between trees and aspects within trees are discussed in greater detail in the following section.

The result is presented graphically in Fig. 3.1, where it is clear that there are only small differences between the pollination treatments, and none of these is significant.

Source	Change in Deviance (χ^2)	d.f.	p
Pollination	17.07	11	>0.05

TABLE 3.1 Results of the pollination experiment. The pollination effect is the full nested model of pollination within aspects within trees. None of the effects are significant. Error deviance 498.9 with 342 d.f., total deviance 516.1 with 353 d.f.

Log-odds proportion peduncles surviving	S.E.	Tree	Aspect	Pollination
-0.8754	0.3755	1	N	Y
-0.6466	0.3715	1	N	N
0.1112	0.3337	1	S	Y
-0.1001	0.3166	1	S	N
-0.9614	0.3258	2	N	Y
-0.6650	0.2900	2	N	N
-0.9268	0.2710	2	S	Y
-0.4055	0.2357	2	S	N
-0.6931	0.3391	3	N	Y
-0.1542	0.3212	3	N	N
-0.7221	0.2956	3	S	Y
-1.196	0.3163	3	S	N

Table 3.2 Log-odds ratios of the proportion of peduncles surviving to produce acorns in the pollination experiment, classified by treatment. The standard errors vary with treatment because of unequal numbers of peduncles on the various shoots.

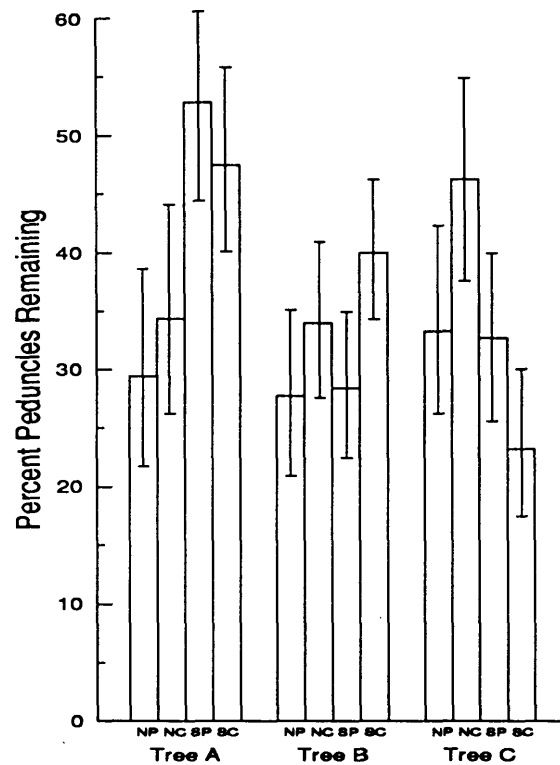


FIG 3.1 Percent peduncles (mean of thirty shoots) surviving on three trees, classified by north/south, and by hand pollination/control: NP= north hand pollinated, NC= north control, SP= south hand pollinated, SC= south control. Error bars are ± 1 standard error, back transformed from the logit scale.

3.2 Census of individual trees

This section addresses the following questions: 1) Are there any differences between the number of peduncles per shoot initiated by trees each spring, and are these differences consistent between years? 2) Are there differences between the rates at which trees and branches within trees abort peduncles throughout the year, and are such differences consistent over the three years of the study? 3) Does the long term pattern of acorn production relate to weather patterns, and can acorn production be enhanced by experimentally manipulating certain weather conditions (e.g. early summer rainfall) that were associated with years of high acorn production?

3.2.1 Nomenclature of modules of *Q. robur*

Observations in the following sections were made at several different spatial scales within each tree, each scale corresponding to a different module. The first level of strat-

ification was the branch, with branches defined on the criterion that they originated from the bole of the tree. The next level of stratification was the twig. A twig was taken as the previous year's growth and could bear between 1 and 20 or more buds. Buds bursting in the spring could produce either male catkins, leafy shoots bearing catkins, or leafy shoots bearing both male flowers and peduncles. Peduncles within these leafy shoots constitute the final level of sampling stratification.

3.2.2 Spring Peduncle Count

The peduncles on 4 trees (numbers 1004, 1008, 1022 and 1024;) were counted during the spring of 1987, two weeks after bud burst, when all peduncles were fully expanded. The sampling regime was stratified by aspect, branch within aspect, twig within branch and shoot within twig. Five twigs were sampled from each branch and each twig had up to 10 shoots. The number of peduncles per shoot was recorded and used as the response variable in a GLIM analysis with Poisson errors. Differences between the different levels of nesting were assessed, with particular emphasis on differences between trees. Ideally a larger sample of trees would have been preferable, to allow a comprehensive assessment of the total population variability in peduncle dynamics, but the sampling regime was particularly time consuming.

This process was repeated during the spring of 1988 using two of the original trees (numbers 1022 and 1004). Tree 1008 was blown over during the great storm of October 16-17, 1987 and tree 1024 was defoliated by a late spring frost. Although only two trees could be compared between two years this did allow a tentative test of the hypothesis that there are consistent year to year differences in the number of peduncles initiated per shoot. The series of observations was finally abandoned in the spring of 1989 when tree 1007 was discovered to have been struck by lightning, with its branches dying and in a generally poor state of health.

3.2.3 Selection of trees for continuous census

1). The 1987 season.

Eight trees (five smaller and three larger) were chosen to investigate the abortion rates of acorns and peduncles. Trees were stratified into quadrants corresponding to north-east, north-west, south-east and south-west aspects. Two major branches were chosen within these four canopy sectors. This procedure was followed in an attempt to detect whether there were any within-tree differences between branches in the rates of acorn abortion, as a test of Gill's (1986) genetic mosaicism hypothesis. Finally, two twigs were selected on each branch. Each twig had at least two shoots with developing peduncles present. This selection procedure was carried out in the early spring, prior to anthesis, and hence before pollination. The shoots were marked, and the number of flowers on each peduncle and the position of the peduncle on the shoot were recorded. The position of the peduncle was recorded as the number of the axil in which it originated, counting from the shoot apex (i.e. if there were 15 leaves on a shoot and the peduncle was in the 4th axil from the apex of the shoot then the position was recorded as 4/15).

The numbers of surviving flowers were counted weekly from 12 May 1987 to the 12 October 1987. After this date the great storm dislodged many of the acorns from the experimental trees. Tree 801 was badly damaged in the storm losing two of its major branches, and tree 1008 was blown over and killed.

2). The 1988 season.

Where possible the same trees as 1987 were used but three of the trees were unusable. Two were lost in the storm, and trees 1001 and 1024 suffered frost damage in the early spring, before the initial selection of shoots (i.e. it was impossible to know how many peduncles and flowers there had been at the start of the season). The effect of late spring frosts is discussed in Section 3.5

Preliminary analysis showed that there were few differences in abortion rates within trees during the 1987 and so a slightly modified sampling regime was employed in 1988. First, only two aspect categories were used (on the north and south sides of the tree). Second, although two branches were again chosen in each aspect of the tree, ten twigs were chosen from each branch, and the shoots on each twig were assigned to one of five experimental treatments at random:

i) *Control*, all leaves present.

ii) *Axil leaf absent*, the leaf subtending the peduncle was removed.

iii) *Axil leaf present*, all leaves removed except the leaf subtending the peduncle.

iv) *All*, all leaves removed.

v) *Insecticide*, application of insecticide to the entire shoot was applied weekly using a fine artist's paint brush. The insecticide used was a domestic, garden variety with the active ingredient, primicarb-methyl, this was applied at the recommended rate.

3). The 1989 season

The sampling regime in 1989 was different again, and involved a scaled down version of the census of the previous two years. This was because an additional set of observations were being carried out on one of the blocks of trees in the watering experiment, described in Section 3.4. Four of the original eight trees were used (see Table 3.2). Again, 1988 results showed that aspect within tree and branches within aspect showed only slight differences in the abortion rate of the flowers, so these levels of stratification were abandoned in 1989. At least thirty shoots bearing peduncles were chosen for the census, making sure that at least ten twigs were included in the count.

Tree	1987	1988	1989
1001	*	F	F
Southwood	*	*	*
1024	*	F	*
801	*	dead	
1004	*	*	*
1008	*	dead	
1007	*	L	L
1025a	-	*	
Elm Row	-	*	**
End Elm	-	*	E
1022	-	*	*
Recog	-	-	**

TABLE 3.3 The demise of trees used during the 3 year study of acorn abortion rates: *, tree used during particular year; F frost damage; L, lightning strike; Dead, lost during the great storm of October 1987; E, used as one of the control trees in the watering experiment.

3.2.4 Results

3.2.4.1 Results of the spring peduncle counts

The following two sections describe the analysis of the average number of peduncles per shoot at the beginning of the season which was carried out using GLIM with Poisson

errors (Aitkin *et al.* 1989).

1). The 1987 season

The differences in the average numbers of peduncles per shoot on each tree were highly significant (Table 3.4). The inclusion of between-tree differences in the model accounted for 12% of the total deviance in peduncle densities. The change deviance, expressed as χ^2_3 , accounted for by trees was 96.5, and the error deviance was 818.5 with 624 d.f. (marginally, but not significantly over-dispersed).

The largest difference in the average number of peduncles per shoot was between tree 1022 with 1.16 peduncles per shoot, and tree 1008 with only 0.58 peduncles per shoot. The only comparison that was not significant was between the mean peduncle densities on trees 1007 and 1008.

Tree	Log _e Number of Peduncles	Standard Error
1022	0.4762	0.0664
1008	-0.5458	0.1169
1007	-0.4353	0.0869
1024	-0.1317	0.0860

TABLE 3.4 Mean log_e number of peduncles per shoot in 1987 with their standard errors back-transformed from logits.

2). The 1988 Season

The same type of analysis was carried out on the data gathered in 1988. As before the tree differences were highly significant (the change in deviance, expressed as χ^2_1 , accounted for by trees was 41.1, the error deviance was 679.8 with 473 d.f.). The mean numbers of acorns per shoot are given below in Table 3.5.

Tree	Log _e Number of Peduncles	Standard Error
Tree 1022	-0.1127	0.0641
Tree 1007	-0.9531	0.1246

TABLE 3.5 Mean log_e number of peduncles per shoot in 1988 with their standard errors back-transformed from logits.

3.2.4.2 Results of the Continuous Census

The following three sections deal with the analysis of the average time to death of the flowers on each tree. The analysis was performed using GLIM using methods for analysing survival times (Aitkin *et. al.* 1989) with exponential errors. The proportion of flowers that survived to bear fruit was analysed using GLIM with binomial errors.

1).The 1987 season

The tree-to-tree differences in the average survival times of flowers were highly significant even though the inclusion of trees only accounted for about 6% of the total deviance. (Table 3.7). The deviance accounted for by differences between trees, expressed as a change in χ^2 , was 199.4, with a total deviance of 3324.1 on 2661 d.f., ($p < 0.0001$).

Tree	Log _e Time to Death (Weeks)	Standard Error
Tree 1001	1.783	0.05096
Southwood	1.279	0.05064
Tree 1024	1.964	0.05164
Tree 801	1.44	0.05025
Tree 1004	1.35	0.05634
Tree 1008	1.078	0.06580
Tree 1022	1.367	0.05625
Tree 1007	1.698	0.06275

TABLE 3.6 Mean log survival time of flowers on each tree in the 1987 census with their standard errors back-transformed from logits.

Log_e time-to-death are given in Table 3.6 along with their standard errors. A major difference is seen between trees 1024 and 1008 (a significant difference of 4.2 weeks in their mean survival times). It was observed in the field that tree 1008 aborted many of its flowers very early in the season, and this is borne out by the analysis. Unfortunately it was impossible to follow through the difference between these two extreme trees because tree 1008 was lost in the storm of October 1987. The survival curves for the flowers on the 8 trees studied in 1987 are given in Fig. 3.2.

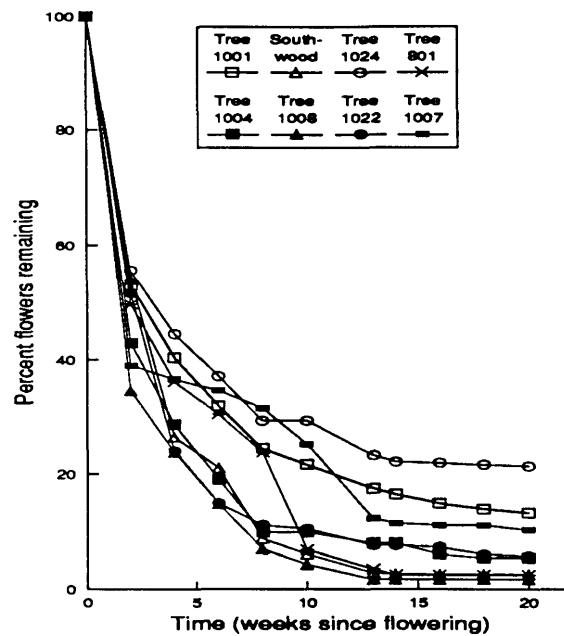


FIG 3.2 Survivorship curves for trees in the 1987 census. Proportions of the flowers remaining on each tree are plotted against the sampling date.

The proportion of flowers surviving on branches within aspects within trees was analysed using binomial errors. The response variable was taken as the number of acorns produced on each peduncle and the binomial denominator was the total number of flowers present on the peduncle at the beginning of spring.

Source	Change in Deviance (χ^2)	d.f.	p
Tree	146.5	7	<0.00001
Aspect in Tree	38.35	24	0.032
Branch in Aspect in Tree	46.96	32	0.043

TABLE 3.7 Analysis of deviance table of the proportion flowers surviving through the summer to produce acorns, fitted in a nested model, with trees, aspects in trees, and branches in aspects in trees fitted sequentially. Error deviance = 591 with 855 d.f., total deviance = 822 with 918 d.f.

The major significant difference is between trees (Fig. 3.3) and there were slight but significant differences between the abortion rates of flowers between aspects within trees. There was also a very small but significant effect of branches within aspects within trees (Fig. 3.4), arising from the difference between the two branches on the south side of tree

1024.

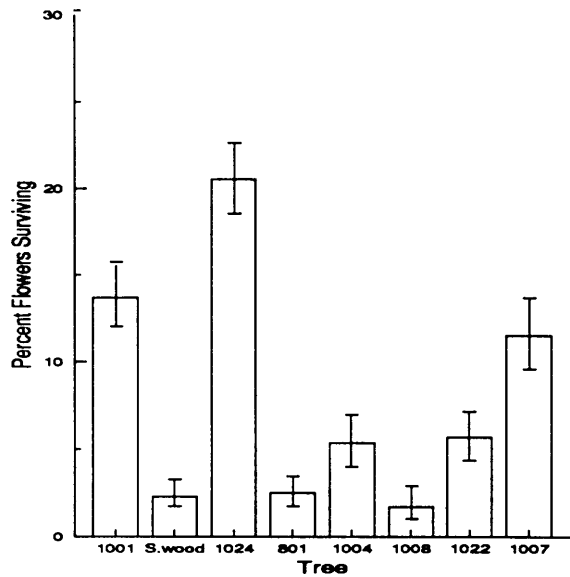


FIG 3.3 Proportion of flowers surviving to become acorns on the 8 trees of the 1987 census. Bars are ± 1 standard error, back transformed from logits.

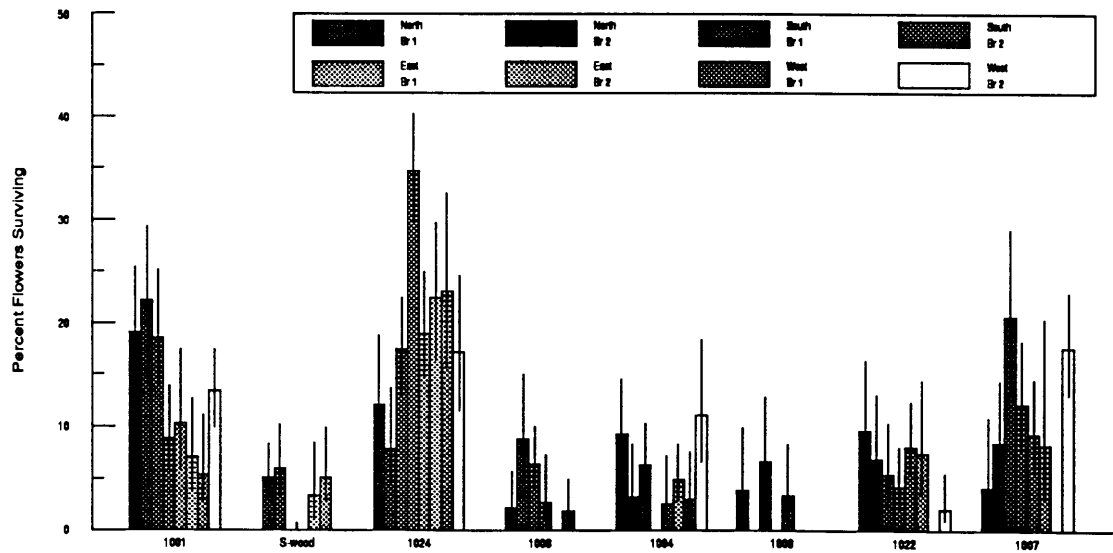


FIG 3.4 Percentage of flowers surviving to become acorns on the 8 trees of the 1987 census presented as the means of the individual branches. Standard error bars refer to pair-wise comparisons between branches, within aspects, within trees, back transformed from logits.

2). The 1988 Season

A similar analysis was carried out on the 1988 continuous census data, except that aspect and between branches within aspect were not considered (see above). The analysis concentrated on the differences between the experimental treatments. Contrary to earlier results from Silwood Park (Crawley 1985), the simulated herbivory and insecticide treatments did not have a significant effect on the rate of acorn abortion (Table 3.7 and Fig. 3.5), or on the proportion of flowers producing acorns (Table Appendix 3.1. And Fig. 3.5.). Even though the effect of treatment within trees was significant, the differences were not associated with any systematic patterns in the survival of acorns. As in 1987, there were significant differences between the proportions of flowers surviving on different trees (change in deviance $\chi^2 = 51.9$ with 5 d.f., total deviance = 830.1 on 1834 d.f., $p < 0.0001$).

Source	Change in Deviance (χ^2)	d.f.	p
Tree	112.4	5	<0.0001
Treatment in Trees	58.3	24	<0.001

TABLE 3.8 Analysis of deviance of the survival times of the female flowers in the 1988 census. Note that although the treatment effects are highly significant, very few acorns were produced in this year over the experiment as a whole. Error deviance = 2300.2 with 4017 d.f., total deviance = 2470.9 with 4046 d.f.

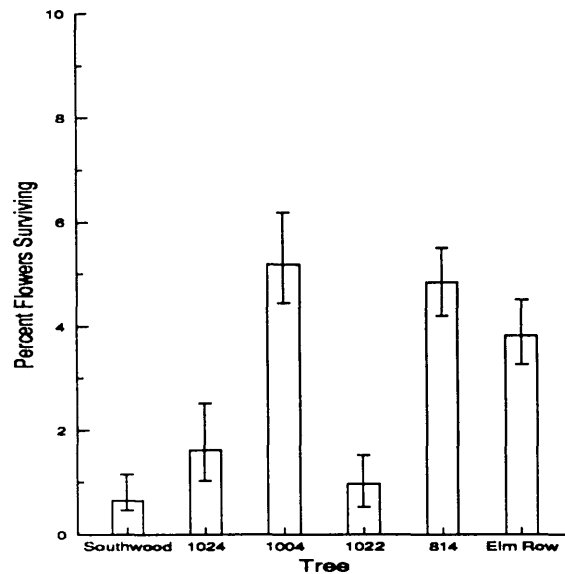


Fig. 3.5 Percentage of flowers surviving on individual trees in the 1988 census, means presented ± 1 S.E.

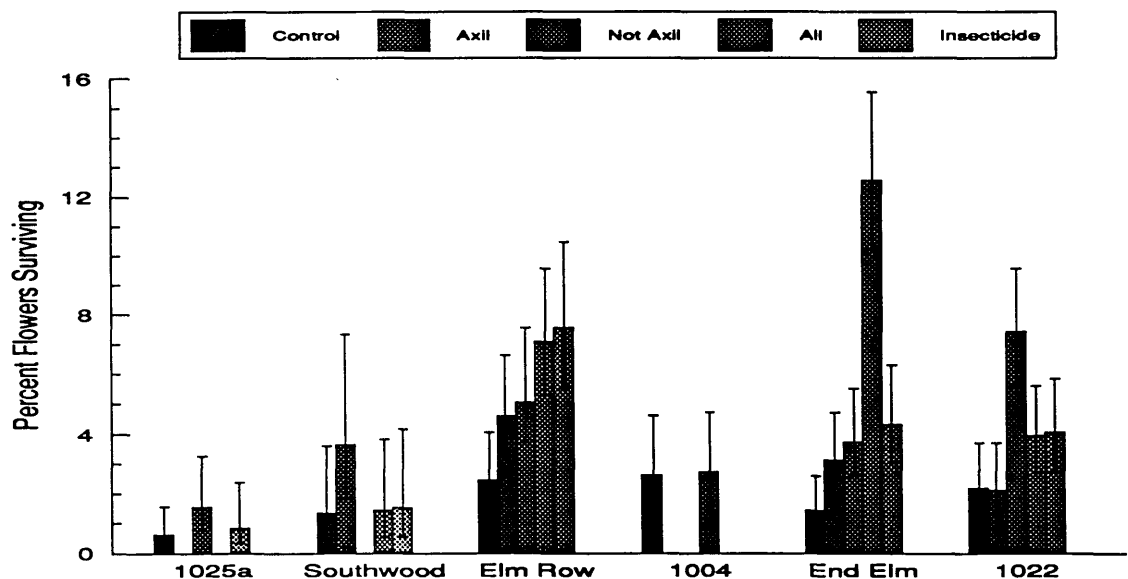


Fig 3.6 Percentage of flowers surviving on trees in the 1988 census, classified by leaf treatments. Note that in most trees only about 5% of flowers survive to produce acorns. Only one treatment on the Elm Row tree had a substantially higher flower survival. Standard errors back-transformed from logits. For explanation of treatments see text.

3). The 1989 Season

The analysis carried out on the 1989 data was essentially the same as the previous two years, except that trees were the only level of stratification. The previous year's work

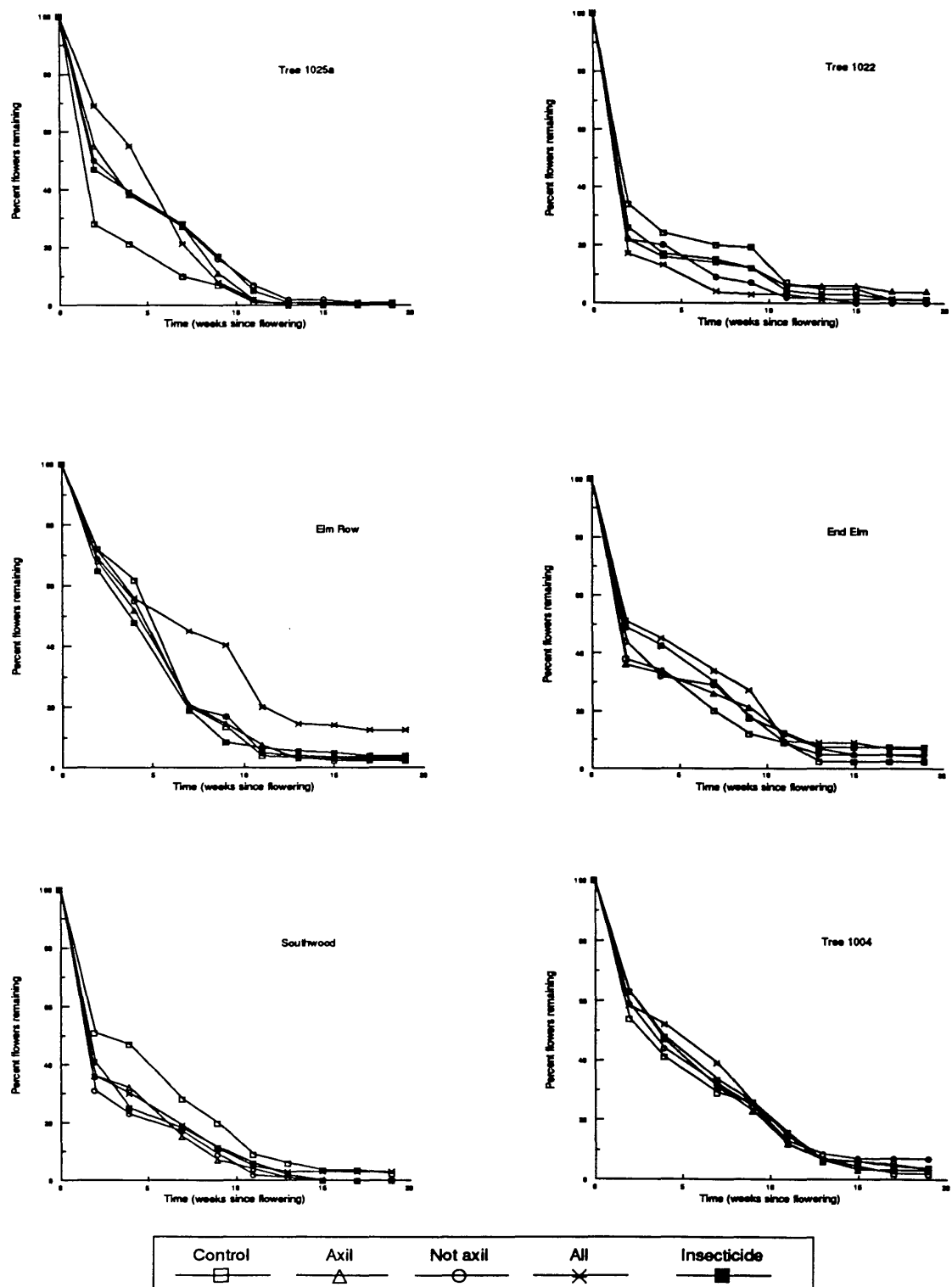


FIG 3.7 Survivorship curves for the flowers on the 6 trees in the 1988 census, classified by leaf treatments (for explanation of treatments see text).

showed that other treatments, accounted for a small proportion of the total deviance. The average time to death and the percent of acorns produced from the total number of flowers originally present were analysed.

As before, there were significant differences between trees in the average survival time of the flowers. Although the percentage of the deviance explained was small, (11%, see Table 3.8) the differences were highly significant, mainly as a result of the poor survival on the Southwood tree.

Tree	Log _e Time to Death (Weeks)	Standard Error
Southwood	1.728	.07738
Tree 1024	2.591	.07217
Tree 1004	2.357	.07692
Tree 1022	2.130	.07019
Tree 814	2.176	.07433
Elm Row	2.301	.08874

TABLE 3.9 Log_e survival times of flowers on trees in the 1989 census, with their standard errors back-transformed from logits. Note that tree 814 and the Elm Row tree were used as control trees in the watering experiment. The deviance accounted for by tree differences expressed as a change in χ^2 , was 69.8, with a total deviance of 616.7 on 1038 d.f., $p < 0.00001$.

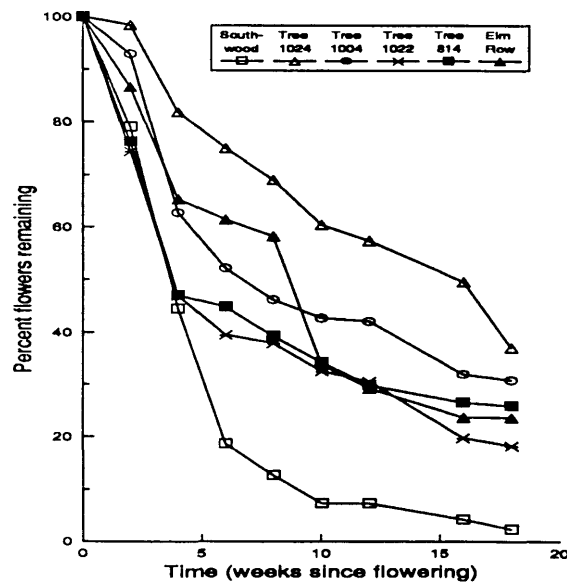


FIG 3.8 Survivorship curves of individual flowers for the 6 trees in 1989. Note that for the 3rd successive year the Southwood tree lost almost all of its flowers.

Note that for the 3rd successive

A similar pattern was observed in comparing the percentage of flowers surviving to produce acorns, across trees (table 3.10).

Tree	Log-odds proportion peduncles Surviving	Standard Error
Southwood	-3.706	0.4938
Tree 1024	-0.5331	0.1495
Tree 1004	-.8023	0.1668
Tree 1022	-1.468	0.1799
Tree 814	-1.048	0.1695
Elm Row	-1.174	0.2089

TABLE 3.10 Log-odds ratios of the proportion of flowers surviving to produce acorns in the 1989 census. The change in deviance explained, as χ^2_5 , was 86.8, with a total deviance of 724.4 on 447 d.f., $p < 0.00001$, by differences between trees.

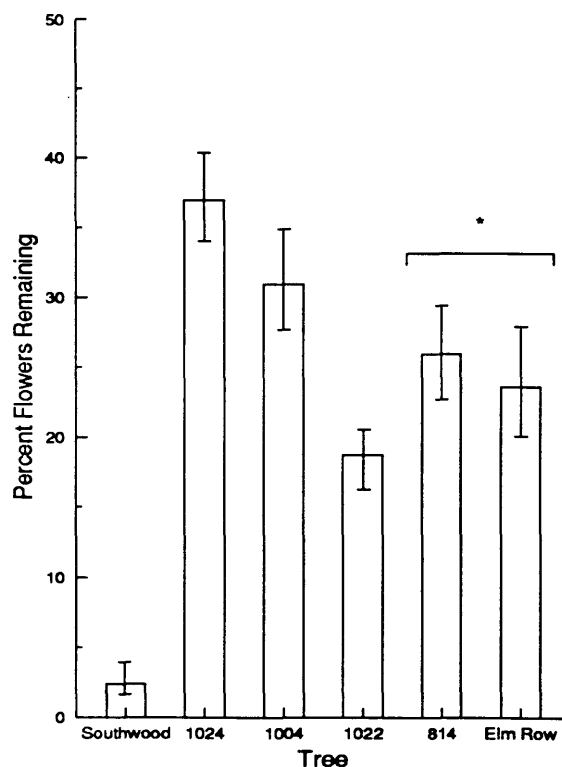


FIG. 3.9 Percent flowers remaining on the trees in the 1989 census $\pm$ standard errors, * trees also used as controls in the watering experiment (see section 3.4). Standard errors are back transformed from logits.

In each of the three years a count was made of the number of weevil infested acorns present; these results summed over all trees are presented in Fig 3.10. Also included in

the figure is the proportion of weevil infested acorns gathered from the ground beneath trees in Windsor Great Park during the very poor acorn year of 1986. Although the data from 1986 were not obtained by the same methods as the subsequent years, they imply that intraspecific competition may well be important in years of low acorn production.

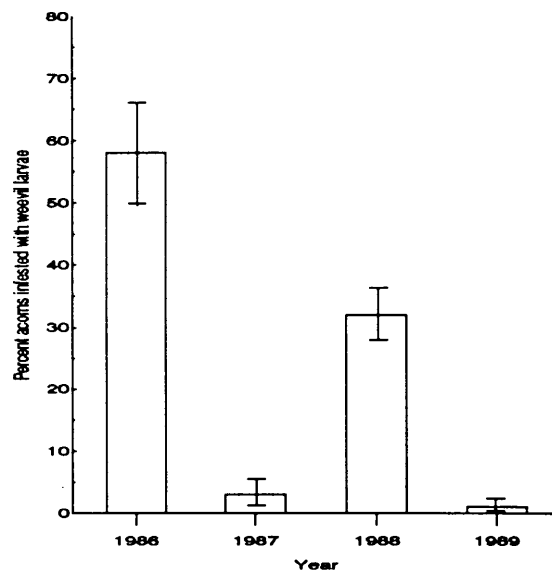


Fig 3.10 Proportions of acorns infested by weevils during the four years the continuous study. During good acorn years (1987 and 1989) the level of attack is very low, while in 1988, a very poor acorn year, the rate of attack by weevils is relatively high.

3.3 Long Term Tree Fecundity (10 year binocular count)

A long term study on the fecundity of *Q. robur* was initiated in the autumn of 1979 by M.J. Crawley, (Crawley 1983, 1985, 1987, 1991). Initially the study was carried out on 36 trees, but in 1987 six of them were felled as part of another experiment Crawley (1987) and one other (tree 1008) was blown over in the great storm of October 1987. Measurements continue on the remaining 29 trees, and a new set of 30 trees added in 1989.

3.3.1 Counting Methods

During the early years of the study, samples of 30 shoots were taken from each tree to obtain an estimate of the number of acorns per shoot. In most years, and for most trees, the majority of these shoots had no acorns. An additional count was made of 50 shoots in situ by searching different aspects of the canopy using binoculars. These two estimates were comparable (M. J. Crawley, unpublished results) but the binocular method of counting was chosen as all regions of the tree canopy were sampled, and the sample of shoots was larger (30 vs. 50) sampled. From 1986 onwards the size of the acorn survey was increased to 100 shoots per tree. The results of the survey from 1980 to 1988 are given in Table 3.11 and Fig 3.11.

Year	80	81	82	83	84	85	86	87	88
Acorns/Shoot	0.29	0.07	0.39	0.21	0.13	0.35	0.03	0.29	0.07

TABLE 3.11 Acorn production expressed as mean acorns per shoot of the 30 trees used in the long term observational study, up to 1988.

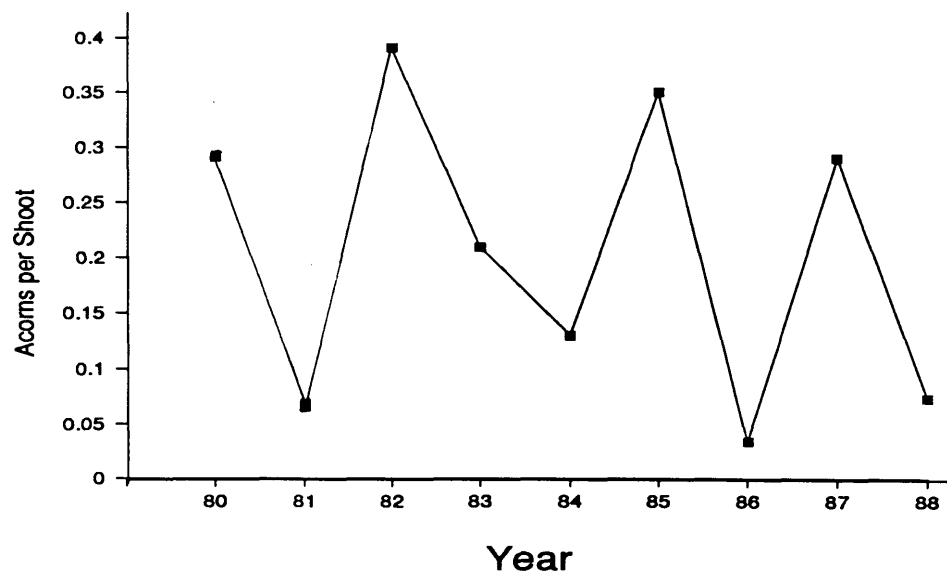


FIG 3.11 Acorn production over the 9 years up to 1988, note the two successive years of lower acorn production (1983-84).

3.3.2 Correlation with Meteorological Data

Previous studies (e.g. Mathews 1963; Puritch & Vyse 1972; Nielsen 1977) have presented evidence suggesting that years of mast fruiting are closely correlated with climatic variables. The trees are thought to use rare environmental cues in order to achieve synchronous fruiting (see section 1.4.2). After the very poor acorn year of 1988 (Fig 3.7) the meteorological data from Silwood Park were correlated with the acorn production records gathered over the previous 9 years. The variables used in the analysis were as follows:-

Monthly maximum and minimum temperatures;

Lowest monthly temperature;

Number of days the air temperature went below zero;

The average ground temperature in each month.

Simple correlation coefficients were calculated between these variables and the number of acorns per shoot over the course of the 9 years (Table 3.12).

3.3.3 Results

Several of the meteorological factors were correlated with acorn production: In total 84 correlation coefficients were calculated, (table 3.12) of which we might expect about 4 or 5 to be spuriously significant by chance alone. The temperature data are discussed later, and, for the moment the emphasis will be placed on the very high positive correlation between acorn production and June rainfall, (Figs 3.2a & 3.2b)

Month	Max t	Min t	Mean t	Low t	DBZ	Rain	Gnd t
January	-.53	-.57	-.68*	-.70*	.79*	-.79*	-.13
February	-.51	.49	.60	.31	-.53	.35	-.64
March	.21	-.46	.27	-.30	.51	.07	-.23
April	.65	.61	.72*	.28	-.66	-.30	-.20
May	.31	-.63	-.005	-.21	.35	-.14	-.15
June	-.42	-.23	-.25	-.64	M	.97***	0.43
July	-.02	-.17	-.04	-.03	M	.02	.06
August	-.15	-.001	.06	-.16	M	-.06	.66
September	.82**	.532	.82**	.21	M	-.05	.58
October	.28	-.32	-.50	.15	-.04	.27	-.36
November	-.44	.05	-.22	-.27	.09	-.01	.02
December	-.12	.15	-.07	.34	-.07	.28	.11

TABLE 3.12 Correlation matrix of acorn production (acorns per shoot) against the Silwood Park meteorological data, up to and including 1988. Abbreviations are as follows: Max t, mean maximum monthly temperature; Min t, mean minimum monthly temperature; Mean t, mean monthly temperature; Low t, lowest monthly temperature; DBZ, number of days below zero °C; Rain, total monthly rainfall, mm; Gnd t, mean monthly ground temperature. M = missing value. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

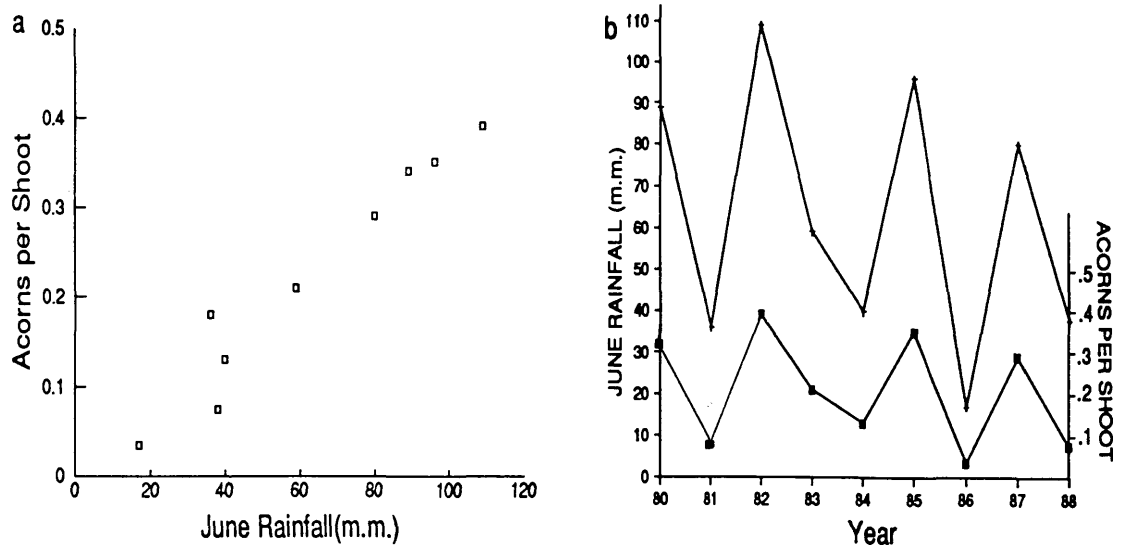


FIG. 3.12 a) The impressive correlation between June rainfall and acorns per shoot up until 1988: $r = 0.97$, $n = 9$, $p < 0.001$. b) The same data plotted as a time series, June rainfall (+) and acorns per shoot (•)

This result led to the design of an irrigation experiment to investigate the effect of experimentally enhanced June rainfall on the production of acorns. The summer of 1989 turned out to be an ideal time to test this hypothesis because it was the driest summer in the British Isles since the drought of 1976.

3.4 The Watering experiment

Thirty two trees in four blocks were chosen for the experiment. Two blocks containing mature trees (girth > 300 cm), and two blocks with trees approximately 35-40 years old (girth < 150 cm). Within each block one of four treatments was assigned at random to each tree, as follows:-

- i) Watering in May
- ii) Watering in June
- iii) Watering in July
- iv) Control, no water

3.4.1 Estimation of Volume of Water to be Applied

Weather records for Silwood park are available from 1952. It was decided to test the June rainfall hypothesis by simulating the maximum rainfall experienced in May, June or July during the last 37 years. These are:-

May 1984, 114mm

June 1971, 157mm

July 1956, 105mm

The amount of water to be applied was calculated by assuming that the area under the canopy of the tree was circular and that during the course of the month enough water had to be applied to fill the circle to the required depth (i.e. the to maximum recorded for that month in the last 37 years).

3.4.2 The Water Delivery System

Water was delivered to the tree by means of a 1.5 cm hose pipe fed from a standard garden tap. The greatest distance from tap to tree was approximately 150 meters. Below the canopy the water was introduced into a series of perforated lay-flat hoses, to ensure an even coverage of water below the entire canopy.

1) Delivery system for large trees.

The delivery system around large trees consisted of six radiating arms of lay-flat tubing with sealed ends, arranged to cover as large an area as evenly as possible under the canopy as in Fig. 3.13a.

2). Delivery system for small trees, 34-40 years old

The delivery system around the smaller trees consisted of two pipes of lay-flat tubing arranged with sealed ends to cover as much of the area under the canopy as possible (Fig. 3.13b).

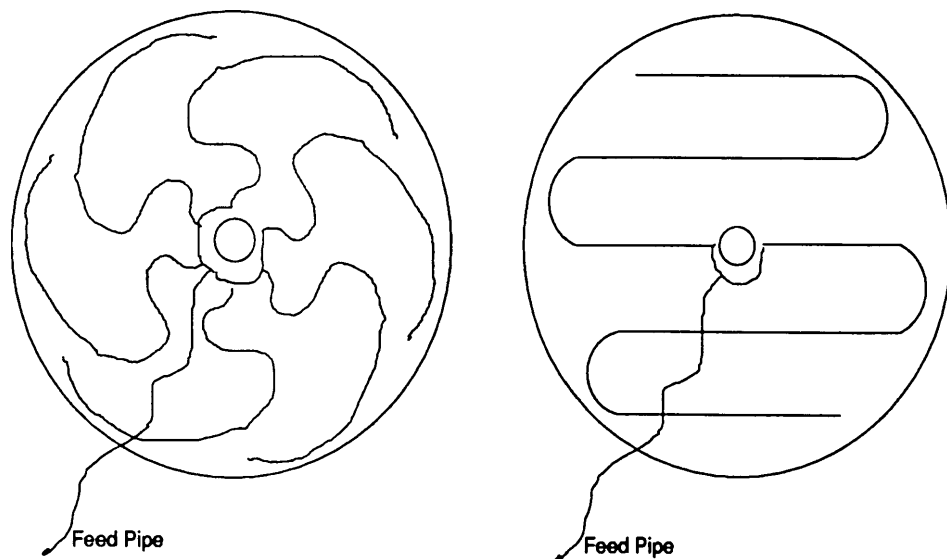


FIG 3.13 The arrangement of the lay-flat tubing around the bases of, left, mature trees and right, trees 35-40 years old. The feed pipe is connected to a tap by 1.5 cm hose no more than 100 metres away.

Water was applied each day to the 8 trees being watered in any month. The taps were left running long enough to deliver $\frac{1}{30}$ of the maximum rainfall for that month. Rainfall records were checked daily and if there had been any rain during the previous day, then the length of the delivery time was reduced accordingly.

Consider the Ashurst tree for example with a canopy diameter of 17 metres, giving an area of 227 m², so to simulate the rainfall of June 1971 this area had to receive a depth of 157 mm of water (approximately 5.2 mm per day). This works out at 35.6 m³ of water or 35600 litres over 30 days. Therefore 1187 litres of water had to be applied each day. The rate of water arriving at the base of the tree was measured at 12 litres per minute, so the tap was left running for approximately 1 hour 40 minutes, if there had been no rain the previous day. Meteorological records were checked daily and if there had been rain during the previous 24 hours the proportion of the maximum daily total of rain was calculated.

3.4.3 Recording of Acorn Production

1) Absolute count of acorns.

A binocular survey of the 32 trees was carried out (see Section 3.4). One hundred shoots were checked and the total number of acorns recorded. Any differences between blocks and treatments were assessed using GLIM with Poisson errors.

2). Relative loss of peduncles.

One hundred shoots were gathered from each of the 32 trees using an extendible pole-pruner. The number of surviving peduncles and the number of peduncle scars (scars left by a peduncle when it aborts) were counted. Differences in the proportion of peduncles surviving to produce acorns between blocks and treatments were analysed using GLIM with binomial errors.

3). Census of trees on Elm Row.

A detailed census of the death rate of flowers on the trees from the Elm Row Block

was carried out using the method already described for the census of peduncles on individual trees (Section 3.2). The method of analysis was also similar, calculating the average time to death of each flower, with surviving flowers censored at any sampling period (GLIM with gamma errors, a scale factor of 1 and a log link function, Aitkin *et al.* 1989).

3.4.4 What Happened in 1989

1989 turned out to be the hottest and driest summer since the drought year of 1976, and was ideal for testing the June rain fall hypothesis. In the late spring of 1989 it was recorded that about 70% of the flowers still remained on the trees, and in early summer there were still about 50% of flowers remaining. In previous years that had experienced low acorn crops (e.g. 1988) only about 30% of flowers remained 5 weeks after flowering. By the middle of June it was clear that the hypothesis was falsified, but the experiment was continued until the end of July and data were collected during the first week of September. The yearly acorn count on the 29 trees observed over the past ten years bore out the fact that far from being the lowest acorn crop on record this was in fact the heaviest acorn crop in the past 10 years!

Year	80	81	82	83	84	85	86	87	88	89
Acorns/Shoot	.29	0.07	0.39	0.21	0.13	0.35	0.03	0.29	0.07	0.43

Table 3.13 Acorn production expressed as mean number of acorns per shoot of the 29 trees used in the long term observational study, including the score for 1989.

Re computing the meteorological correlations gave the following Table 3.14, Fig 3.14.

Month	Max t	Min t	Mean t	Low t	DBZ	Rain	Gnd t
January	-.27	-.33	-.42	-.52	.58	-.81 *	-.07
February	.61	.56	.66 *	.37	-.60	.52	.67 *
March	.13	-.15	.11	-.34	-.20	.004	-.10
April	.32	.51	.46	.25	-.60	-.10	.15
May	.53	-.29	.36	-.08	.19	-.34	-.09
June	-.11	-.30	-.07	-.74 *	.48	.62	-.02
July	.20	.01	.25	.34	M	.06	.01
August	.04	.05	.08	.16	M	.02	.02
September	.85 **	.59	.86**	.28	M	-.22	.61
October	.03	.06	-.12	.38	.22	.20	.001
November	-.38	-.12	-.31	-.35	.16	-.22	-.11
December	.003	.10	.004	-.25	-.06	.50	.06

Table 3.14. Correlation matrix of acorn production (acorns per shoot) against the Silwood Park meteorological data, up to and including 1989. Abbreviations are as in Table 3.12.

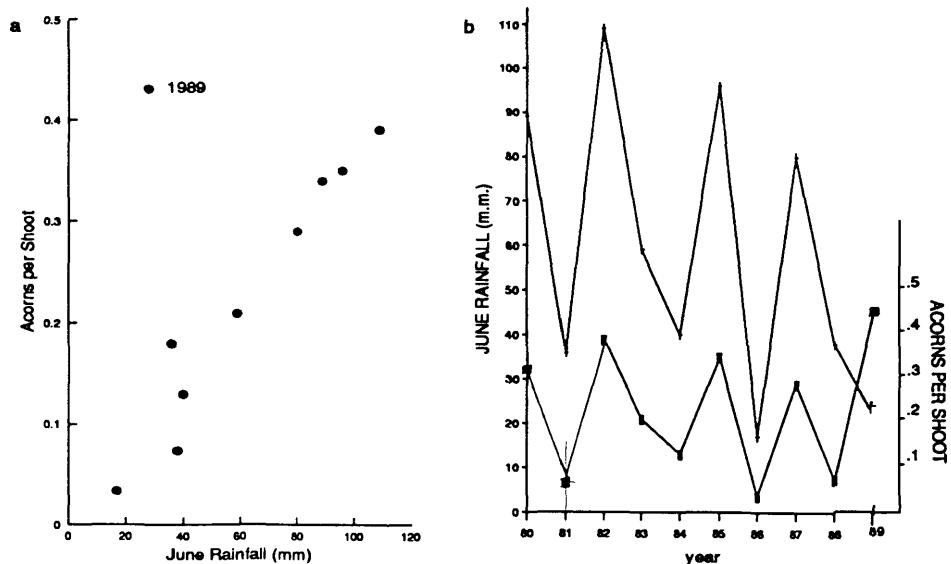


FIG 3.14 a). The disappearance of any correlation between June rain fall and acorns per shoot following the addition of the 1989 data: $r=0.62$, $n=10$, $p=0.056$. b). The same data plotted as a time series, June rainfall (+) and acorns per shoot (*), Showing the reversal of the rainfall and acorn trends, and highlighting the alternate-bearing pattern of fruiting in *Q. robur*. Note, also that the 1990 acorn crop was the lowest on record (not shown).

The very high correlation that existed up to 1988 ($r=0.97$, $n=9$, $p<0.001$) now disappears ($r=0.62$, $n=10$, $p=0.056$) Fig 3.14. The only correlations with acorn production that hold over the two years of the study are those with September temperature. These however may be spurious since by September all acorns are fully formed and nearly mature. It is possible, however, that September temperatures are associated with flower production in the following year (e.g. Ingle & Tamm 1988; P-G Tapper personal communication).

3.4.5 Results

1). Absolute count of acorns.

The differences between the number of acorns on the experimental trees showed neither a significant effect of blocks nor any significant effect of the watering treatments, and no pattern emerged when all treatments when pooled. Fig 3.15 shows the result graphically.

Source	d.f.	S.S.	M.S.	F	p
Block	3	1523	507.6	0.838	0.49
Water in Blocks	12	7269	605.8	0.709	0.72
Error	16	13671	854.4		
Total	3				

TABLE 3.15 Analysis of variance table of the absolute counts of acorns per 100 shoots. The experiment was analysed using a nested design, blocks and watering treatments within blocks. Analysis of variance was used as LSD bars could be calculated for graphical presentation. There are no qualitative differences in the model if Poisson errors are used.

The result shows that in all but one block, (block 1) the number of acorns in the June watering treatment was *less* than in the controls. Note, also that the error bars are large and any differences between acorn production between individual trees would need to be large in order to be significant.

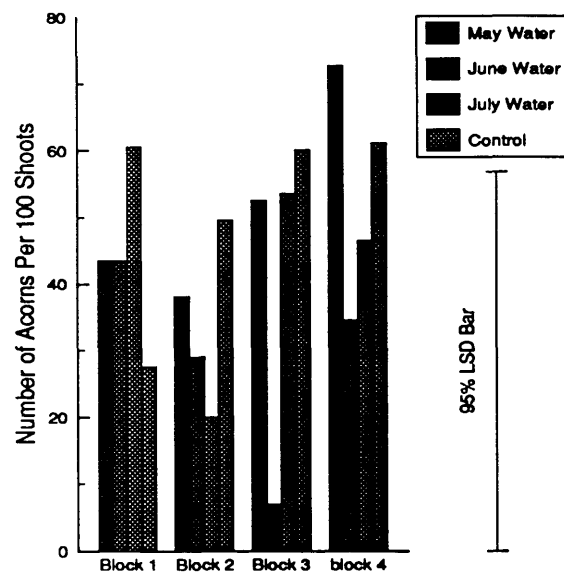


FIG 3.15 Means of acorn counts for the watering experiment, within each block the differences between each mean are smaller than the 95% least significant difference bar. M, May watering; Jn, June watering; Jl, July watering; and C, Control.

2). Percent of peduncles surviving.

Because the trees were likely to have had different levels of acorn production in previous years an analysis of the proportion of peduncles surviving to acorn production was undertaken. There was an effect of block on the proportion of peduncles surviving. There is also what appears to be a highly significant effect of the watering treatment, but differences between treatments are not in the direction predicted by the original hypothesis.

Source	Change in Deviance (χ^2)	d.f.	p
Block	42.12	3	<0.0001
Water in Blocks	231.3	12	<0.0001
Error	31.779	14	
Total	305.21	29	

TABLE 3.16 Analysis of deviance table of the proportion of peduncles remaining in the watering experiment. The model fitted is the same as in Table 3.15. Although there highly significant differences between blocks and treatments within blocks, these were not in the direction predicted by the original hypothesis (see Fig 3.16). Error deviance =31.8 with 14 d.f., Total deviance = 305.2 with 29 d.f.

The proportion of peduncles surviving in each of the experimental trees is shown in

Fig 3.16

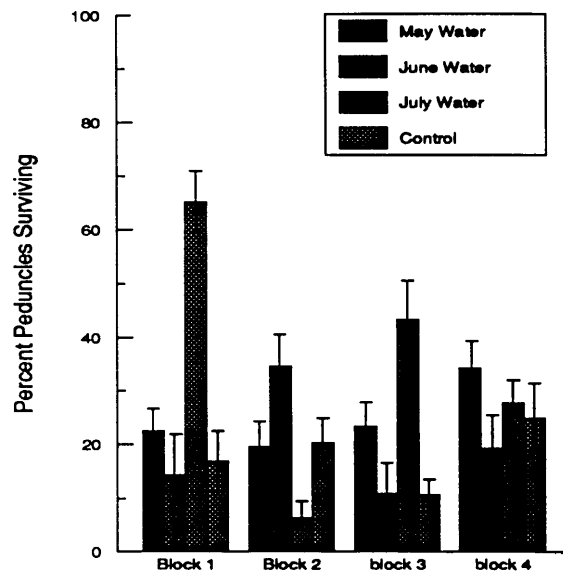


FIG 3.16 Proportion of peduncles surviving in the watering experiment $\pm$ their standard errors back-transformed from logits. M, May watering; Jn, June watering; JI, July watering; C, Control. There were two trees in each watering treatment in each Block. While July irrigation led to higher peduncle survival in Block 1 and 3 it led to a lower survival in Block 2.

The particularly high peduncle survival in Block 1 and 3 (Table 3.16, Fig. 3.16) is due to two particularly heavily fruiting tree that happened to be allocated to the July watering treatment.

3). *The census of individual experimental trees on Elm Row*

Fig 3.16 shows that the watering treatment had little systematic effect on the rate of flower abortion.

A GLIM analysis on the ^{time,} χ^2 in weeks, to death shows that although there were significant differences in peduncle survival, these did not vary systematically in the predicted direction. The deviance accounted for by trees, expressed as χ^2_7 , was 14.8, with a total deviance of 728.18 on 1131 d.f., $p=0.039$.

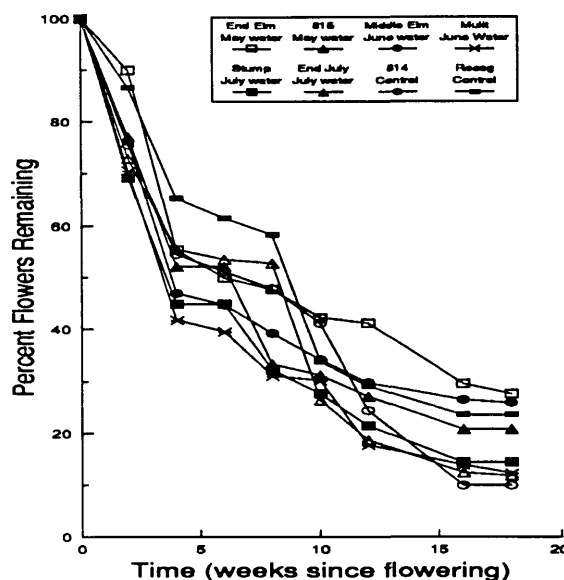


FIG. 3.13 Survivorship curves for flowers on the eight trees on Elm Row that were used in the watering experiment.

3.5 Discussion

The experiments described in this chapter have attempted to establish the factors controlling the fruiting behaviour of *Q. robur* at Silwood Park.

The first in the series of experiments demonstrated that acorn production in *Q. robur* was not limited by the availability of pollen, at least in 1987. Other workers (e.g. Singh 1960; Stephenson 1980) have carried out similar experiments on other tree species and report that although fruit set may be increased, there is rarely an increase in seed production. It is possible that pollen might be limiting during a year of heavy fruit set, but the census of individual flowers in a heavily fruiting year found only 20% of flowers produce acorns in 1987 and 40% in 1989. It has been reported (Williamson 1966) that in *Q. alba* 16-57% of aborted flowers had received pollen. Although figures on acorn production between years were not given, it appears that *Q. alba* produces a surplus of pollinated flowers, and that these may be aborted for a number of reasons (e.g. lack nitrogen or carbohydrate, pollen incompatibility, etc.; Levin 1986, Willson & Burley 1983). If *Q. robur* is behaving in the same way as *Q. alba* then pollination of flowers is not a limiting factor in acorn

production. Further discussion of acorn production therefore concentrates on meteorological patterns and I shall argue that there are innate (probably genetic) patterns of fruiting within the trees.

From the 1987 results the system is seen to be highly variable in that some trees abort most of their flowers while others retain their flowers and produce a very large acorn crop (Figs 3.2, 3.3 and 3.4). At the extremes tree 1024 had a 20% flower survival in 1987 while trees 1008 and the 'Southwood tree' had only, about 2.5% flower survival. Results from 1989 show a similar pattern.

Tree 1024 and the 'Southwood tree' had different acorn production, tree 1024 showing a 40% survival of flowers, and the 'Southwood tree' only 2%.

1987 saw a detailed analysis of flower abortion rates carried out between the branches of 8 experimental trees (Fig. 3.4). There was only 1 significant difference in the survival of flowers between branches (on tree 1024), and one pair wise comparison among 32, could be expected to appear to be significant on the basis of chance alone. Some authors (Withham & Slobodchikoff 1981; Gill 1986) have hypothesized that between-branch differences in fitness traits may arise in long lived modular organisms by the accumulation of somatic mutations. The phenomenon has been observed in tropical trees (Gill 1983) and in clonally reproducing quaking aspen trees, *Populus tremuloides* (Withham, Williams & Robinson 1984), but appears not to occur in acorn production in *Q. robur*.

The 1988 experiment using artificial defoliation and insecticide treatments gave contrary results to those obtained by Crawley (1985), and Torrent (1955). An explanation to this contradiction may lie in the fact that 1988 was such a low year for acorn production, and most of the flowers would have been aborted anyway. This explanation will become clearer in the light of the results of the long term observations. It is also possible that the defoliation was too small scale to have measurable impact on acorn production

The 1988 and 1989 observations ^{show} again that a consistent pattern in the ranking of the proportion of the flowers that survive to fruit, and the proportion of flowers surviving to acorns appears to be a characteristic of individual trees. Individual variation in phenology, particularly with late leaf flush, between oaks has been correlated with reduced fecundity (Crawley and Akhteruzzarman 1988), and local habitat differences may also exacerbate phenological differences.

Meteorological factors were thought to play an important role in controlling seed production in *Q. robur* in the early years of this study. That meteorological factors are associated with seed production in many tree species has been well documented (Maguire 1965; Pozzera 1959; Daubenmire 1960; Pawsey 1960; Matthews 1963; Lester 1967; Dewers & Moehring 1970; and Puritch & Vyse 1972; Nielsen 1977). The trees in these studies were all mast seeding species (Silvertown, 1980) and they appear to use rare environmental cues to achieve synchronous seed production over large geographic areas. In the Silwood Park meteorological data up to 1988, the best correlate of acorns per shoot was June rainfall in the same year. The proposed mechanism behind the rainfall hypothesis was that flower abortion occurred at a higher rate in dry weather. However, both manipulative experiment and direct observation during 1989 showed that there was, in fact, no causal relationship between fruit-set and June rainfall, and the original correlation was probably nothing more than an artifact of carrying out such a large number of correlations.

Trees 1001 and 1024 were susceptible to frosts in April and this had a pronounced effect on their acorn production because regrowth shoots do not produce acorns (M.J. Crawley, personal communication). Mean monthly temperature in April was significantly correlated with seed-set and the number of frosts (expressed as the number of days that

the minimum temperature reached 0 or below) had a marginal affect on seed production. As with June rainfall, however, the significance of the correlations was lost when the 1989 results were added to the data set.

The 10 year study of seed production in *Q. robur* allows us to obtain a reasonable picture of the seeding strategy of the tree and to consider the overall change in abundance of seeds in the environment in any particular year (up to a 14 fold change in abundance). The overall level of seeding in *Q. robur* appears to be synchronised over large areas. A study of red squirrels on the Isle of Wight over 5 years also detected the two low seeding years seen at Silwood Park during 1983 and 1984 (Kenwood and Holm 1989). Limited observations in continental Europe as far afield as central France and Yugoslavia (personal observation) suggest that synchronous seeding in *Q. robur* may be a widespread phenomenon.

The conclusion from this part of the study is that weather patterns do not appear to synchronize acorn production in *Q. robur*, although late frosts destroy the acorn crop of the earliest-flushing trees (e.g. tree 1001 in 1988 (personal observation) and tree 1004 in 1990, C. Long, personal communication, lost all its peduncles in a late spring frost). Perhaps the correct meteorological variable has not yet been discovered or perhaps this species has an internal clock. Biennial cycles of alternate-bearing have been noted in tropical trees (S. Hubbell, personal communication). The alternating seeding strategy and its possible evolutionary significance are discussed further in Chapter 5.

Appendix 3.1 log-odds ratios of proportions of peduncles surviving in the 1988 continuous census.

Log-odds percent peduncles surviving	Standard Error	Tree	Treatment
-5.100	1.003	1025a	Control
-11.01	13.68		Axil
-4.151	0.7127		Not Axil
-10.90	13.59		All
-4.787	1.004		Insecticide
-4.290	1.007	Southwood	Control
-3.277	0.7203		Axil
-11.00	22.07		Not Axil
-4.220	1.007		All
-4.174	1.008		Insecticide
-3.695	0.5062	Elm Row	Control
-3.031	0.3870		Axil
-2.936	0.4189		Not Axil
-2.573	0.3281		All
-2.503	0.3467		Insecticide
-3.620	0.5850	1004	Control
-10.97	12.73		Axil
-10.93	12.48		Not Axil
-3.584	0.5853		All
-10.96	12.78		Insecticide
-4.220	0.5861	End Elm	Control
-3.434	0.4544		Axil
-3.252	0.4161		Not Axil
-1.932	0.2393		All
-3.098	0.3861		Insecticide
-3.807	0.4522	1022	Control
-3.839	0.5053		Axil
-2.523	0.2684		Not Axil
-3.194	0.3607		All
-3.166	0.3859		Insecticide

TABLE A3.1 Log-odds mean ratios of the proportion of flowers surviving to produce acorns in the 1988 census, classified by treatment.

4 The Regeneration of *Quercus robur* under Field Conditions

The work described in this chapter sets out to test three hypotheses by direct experimentation: 1) Are weevil infested acorns capable of germination and if so, is there any selection pressure on acorn size to counter the effect of weevil infestation (e.g. do smaller acorns suffer disproportionately from weevil attack)? 2) Are acorns from different trees removed by vertebrate herbivores from artificial caches at differing rates, and does the presence of a weevil larvae have an effect on this removal rate? 3) Can weevil infested acorns establish as seedlings under field conditions and are such seedlings at a competitive disadvantage compared with seedlings established from healthy acorns.

4.1 Greenhouse Germination Experiment

This experiment was designed to compare the germination rates of weevil-infested and healthy acorns.

4.1.1 Selection of Trees and Acorns

During the autumn 1987 acorns were gathered from three heavily fruiting trees, two from Silwood Park and one from Ascot. The trees were chosen because they had different sized acorns (small 2.64g, medium 4.20g, and large 4.91g). Approximately one hundred healthy and one hundred weevil infested acorns were weighed from each tree. Within the healthy and weevil infested acorns from each tree, both relatively large and relatively small acorns were systematically chosen for use in the experiment. These correspond approximately to the upper and lower thirds of each group. The experiment consisted of three treatments:-

- a) Acorns from three trees differing in mean acorn weight.
- b) Relatively large and relatively small acorns selected from within these groups of acorns.
- c) Whether or not the acorn contains a weevil larva .

These treatments were planted in a 3 x 2 x 2 factorial combination.

4.1.2 Planting Methods

Acorns in each of the twelve treatment combinations were buried at a depth of 3-4 cm. in a 50:50 sand, peat mixture in seed trays. Six seed trays were planted in total, with the positions of the treatments independently randomised in each. The trays were placed in an unheated greenhouse for three months from November 1987 and allowed to germinate.

The experiment was repeated in the autumn of 1988 using three different trees, two from Silwood Park and one from Hartley Wintney in Hampshire (GR 14/767 572) because the trees used in 1987 did not have sufficient acorns. The tree with the heaviest acorns also had a very heavy weevil infestation rate, so only one of the six blocks could be planted with healthy acorns from this tree.

4.1.3 Data Collection and Analysis

After three months the acorns were recovered from the seed trays and the presence of a live radicle projecting beyond the seed coat was determined. An acorn was considered to have germinated if the radicle was visible beyond the seed coat. Acorns with the seed coat split but no radicle showing were not counted as having germinated. Acorns of *Q. robur* typically germinate within a few weeks of falling from the tree. The radicle is extended in autumn, so that by the time the first shoot appears in spring, the seedlings are very strongly anchored. It was previously believed that *Q. robur* acorns had no dormancy mechanism, but post-germination dormancy has been observed in the present study (see below).

During the 1987 experiment the sand-peat medium appeared to have been contaminated with a fungal pathogen and the emerging radicles became stunted and deformed. This did not appear to stop the radicles emerging and so the proportion of radicles emerging beyond the seed coat was used as a measure of germination success of the various classes of acorn.

During the 1988 experiment a serious problem was encountered which made interpretation of the experiment difficult. Many of the acorns were infected with the fungus *Sclerotium pseudotuberosum* (Morris and Perring 1974) and the smaller size classes of acorn were particularly infested, as were, the acorns from the tree from Hartley Wintney tree.

Analysis was carried out using GLIM with binomial errors (the number of acorns germinated was the response variable and the total number of acorns planted was the binomial denominator).

4.1.4 Results

1). The 1987 results

A full nested model was fitted to the data, with weevil infestation within acorn-sizes within trees. This model explained 71% of the total deviance in the system, and was used to predict the proportions of acorns germinating (see Figs 4.1a and b).

Source	Change in Deviance (χ^2)	d.f.	p
Weevil in Acorn Size in Tree	223.7	11	<0.00001

TABLE 4.1 Analysis of deviance for the full nested model, with weevil infestation nested in acorn size nested in tree, this model was chosen as it explains a highly significant proportion of the deviance. Error deviance = 91.0 with 60 d.f, total deviance = 314.8 with 71 d.f.

Healthy acorns had a higher germination rate than weevil infested acorns, regardless of the relative size of the acorn. Weevil infested acorns from trees bearing smaller acorns

had a significantly lower germination rate than the acorns from larger acorn bearing trees (Fig. 4.1a), and this difference was exaggerated in acorns that were relatively smaller (Fig. 4.1b).

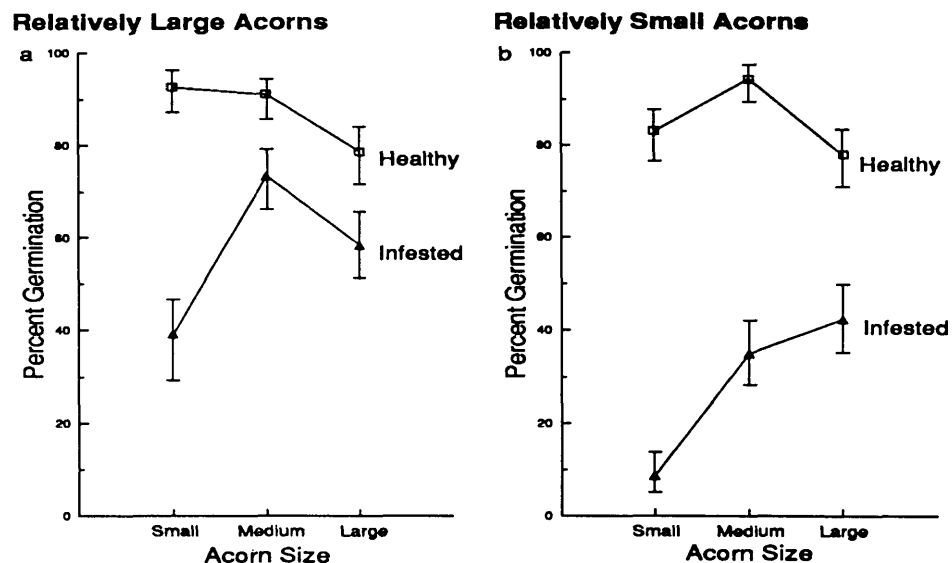


FIG 4.1 Results of the 1987 germination experiment, a) Relatively large acorns, classified by acorn size and by weevil infestation b) small acorns. All means are given $\pm$ their standard errors back-transformed from logits. Note that small acorns only show reduced germination when infested with weevil larvae.

The main effects and the lower order interactions were analysed separately. Fig 4.1a shows the main effect of weevil infestation, and as expected this has a highly significant negative effect on the probability of germination. Individual trees also show different germination rates (Fig 4.2b). This difference is probably caused by the disproportionately large effect of weevil infestation on the smaller acorns, an effect which is particularly striking in the tree-by-weevil interactions (Fig. 4.3a). Acorns from trees with smaller acorns suffered disproportionately heavily from weevil attack, and had a germination rate of only 23% compared with 54% and 50% for weevil infested acorns from trees with medium and large acorns. The effect of relative acorn size is also important (Fig. 4.3b); relatively smaller acorns suffer disproportionately when they are infested with a weevil larva.

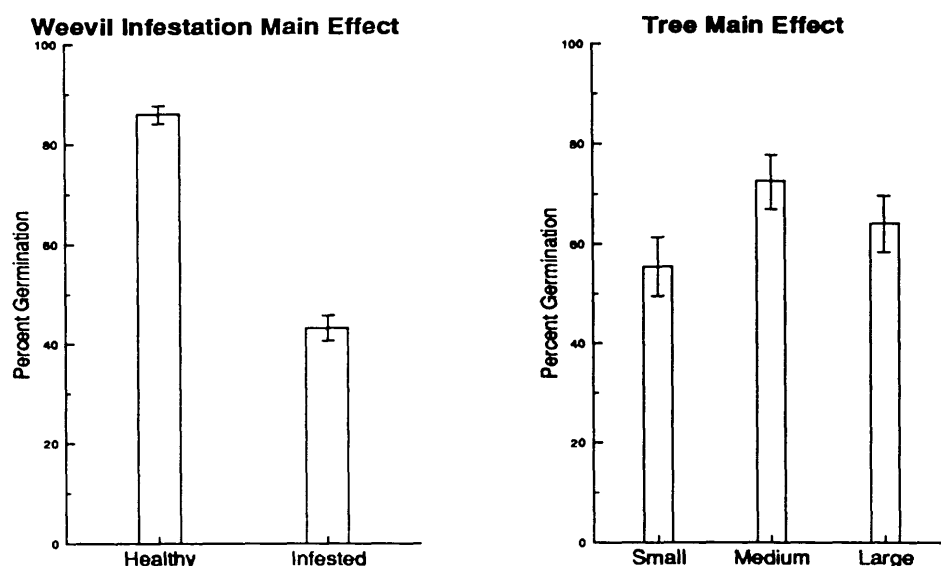


FIG 4.2 a) The main effect of weevil infestation in acorns on the percentage germination, across all classifications. b) The main effect of acorns from different trees on the rate of germination, acorns from the tree with the smallest acorns appear to have the lowest germination, but this is probably a statistical artifact of the increased risk of death from weevil-infestation suffered by smaller nuts. Means are presented $\pm$ standard errors back-transformed from logits.

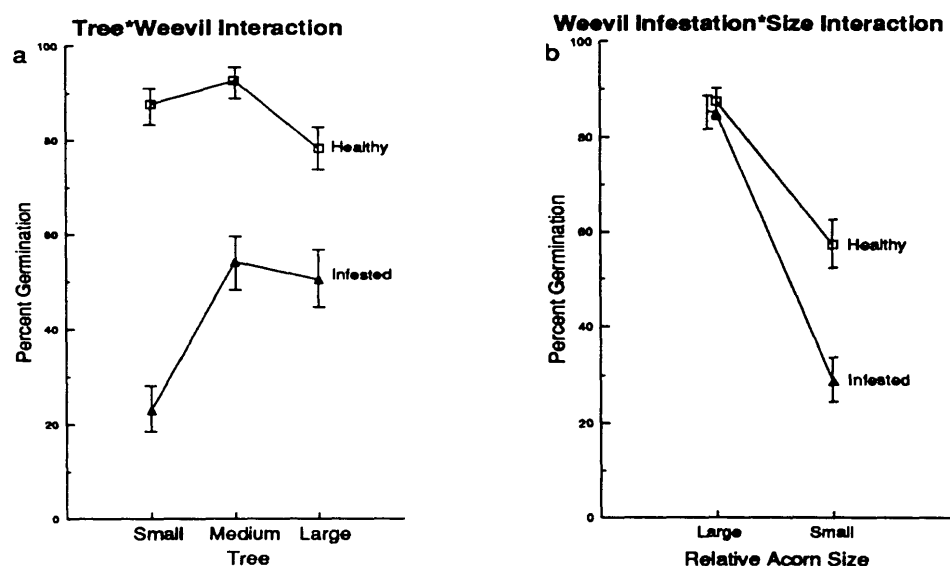


FIG 4.3 a). The interaction between weevil-infestation and acorns of different sizes from different trees. Trees bearing smaller acorns suffer disproportionately from weevil attack. b) The interaction between relative acorn size and weevil infestation. Proportionally more of the relatively small acorns fail to germinate in the presence of a weevil larva. Means are presented $\pm$ standard errors back-transformed from logits.

2). The 1988 results

The same statistical model was used as in 1987, but even though a significant amount of the deviance was explained (Table 4.2), the results were more difficult to interpret due to 1) the small sample size of the healthy acorns from Hartley Wintney; and 2) the high incidence of the fungus *Sclerotium pseudotuberosum* which causes blackening of the cotyledons. Only 35% of the acorns germinated in total, compared with 64% in 1987. The fungal infection of the cotyledons was so severe that the interactions with relative size and weevil infestation were lost, only the weevil main effect was significant (Fig. 4.5). As in 1987 the presence of a weevil larva significantly reduced the probability of germination.

Source	Change in Deviance (χ^2)	d.f.	p
Weevil in Acorn Size in Tree	113.8	11	<0.00001

TABLE 4.2 Analysis of deviance table for the full nested with model, weevil infestation within acorn size within tree. 59% of the total deviance is explained by this model in 1988, compared 71% in 1987. Error deviance = 80.0 with 50 d.f., Total deviance = 193.8 with 61 d.f. See text for explanation.

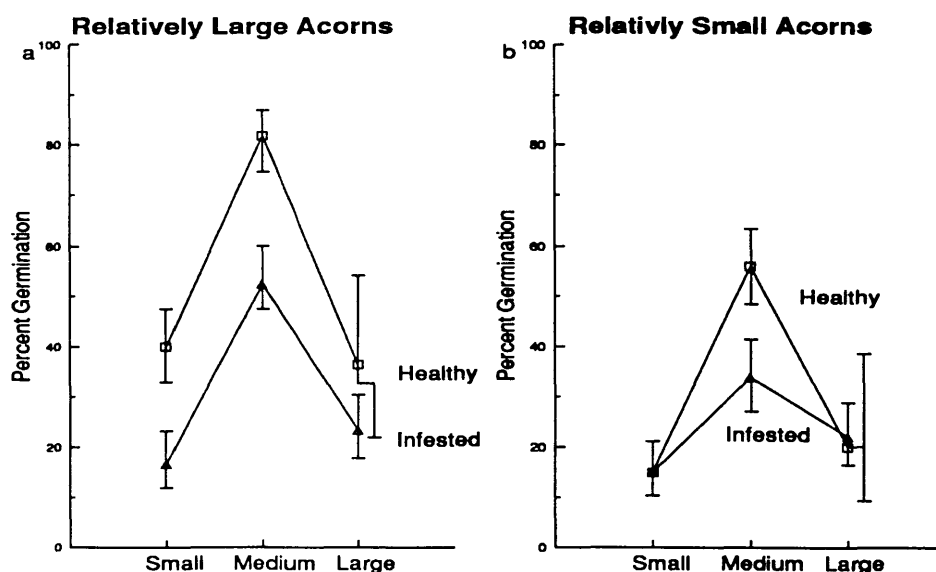


FIG 4.4 Results of the 1988 germination experiment, a) relatively large acorns, classified by acorn size and by weevil infestation b). Relatively small acorns. Note that the healthy acorns from the large and small acorn bearing trees have much reduced germination rates compared with 1987 as a result of infestation of the acorns by the fungus *Sclerotium pseudotuberosum*. Means are presented $\pm$ standard errors back-transformed from logits.

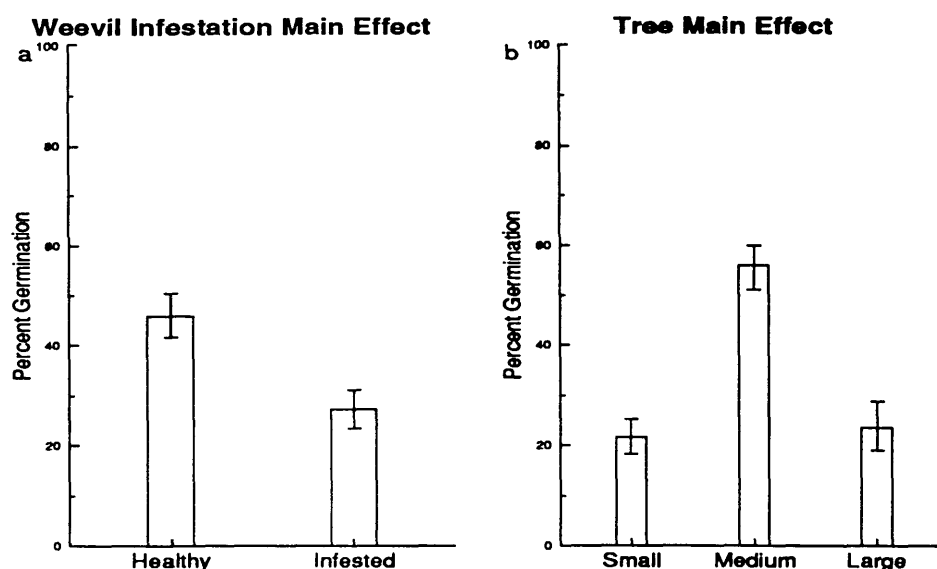


FIG 4.5 a) The main effect of weevil infestation on the percentage germination, across all classifications. b) The main effect of trees on the rate of germination. Note that the trees bearing the smallest and largest acorns have reduced germination rates, as a result of infestation by the fungus *Sclerotium pseudotuberosum*. Means are presented $\pm$ standard errors back-transformed from logits.

4.2 Removal Experiment

The idea that acorns require vertebrate herbivores as dispersal agents (e.g. jays Bossema 1979 and woodmice Jensen & Nielsen 1986) is well established. A factorial field experiment is described in this section which aimed to answer 3 questions: 1) Are acorns from different trees removed from artificial caches at different rates and are these rates affected by the presence of a weevil larva? 2) What is the effect of rabbit grazing on acorn-removal rates (by comparing areas that were fenced and unfenced)? and 3) What is the effect of ground cover on the removal rate (by comparing caches placed on open cultivated ground and on densely vegetated ground)?

4.2.1 Selection of Trees

During the autumn of 1987 acorns were gathered from three heavily fruiting trees (a different set from those described in section 4.1). No special attention was paid to the size of the acorns. Two trees were from Silwood Park and one from Ascot. The acorns were classified into six groups as follows:

- a) acorns from three different trees,
- b) whether or not the acorn contained a weevil larva.

4.2.2 Experimental and Censoring Methods

Plots of land in Nash's field, Silwood had been cultivated and fenced for the previous three years, as part of a study into the effects of rabbit grazing on plant recruitment (Crawley 1990). These exclosures provided an opportunity to carry out an experiment to examine the effects of rabbit grazing and ground cover on the survival of acorns. This enabled us to address the question as to whether acorns^{are} more or less likely to survive on early or later successional sites. The experiment contained five different factors:-

- a) Three blocks differing in distance from the edge of a woodland
- b) Acorns from three different trees
- c) Whether or not the acorn contained a weevil larva
- d) With and without rabbit proof fencing
- e) With and without ground cover (cultivated and uncultivated ground)

There were two replicates within each treatment combination. Acorns were placed in the plots in piles of ten on the surface of the ground. The position of each cache was randomized, and the number of acorns surviving was counted each day. All the acorns disappeared eventually from all the treatments, but at different rates. After about eighty days, no acorns remained in any of the treatments.

4.2.3 Results

All model terms were significant. The acorns in block C situated closer to the woodland edge than the other two blocks showed a slower loss rate (Fig. 4.6a).

An analysis of deviance on the survival times was carried out in GLIM assuming constant hazards and using gamma errors, a log link function and a scale factor of 1 (Aitkin *et al.* 1989). This model explained 64% of the deviance in removal times (see table 4.3).

Source	Change in Deviance (χ^2)	d.f.	p
Block	168.2	2	<0.00001
Ground Cover	123.8	1	<0.00001
Rabbit	394.1	1	<0.00001
Weevil infestation	346.0	1	<0.00001
Tree	44.1	2	<0.00001
Rabbit*Weevil	7.72	1	0.005

TABLE 4.3 Analysis of deviance of survival times of acorns from three different trees classified by block, presence or absence of ground cover, presence or absence of rabbits and weevil infestation. Error deviance = 598.64 with 1431 d.f., Total deviance = 1979.8 with 1439 d.f.

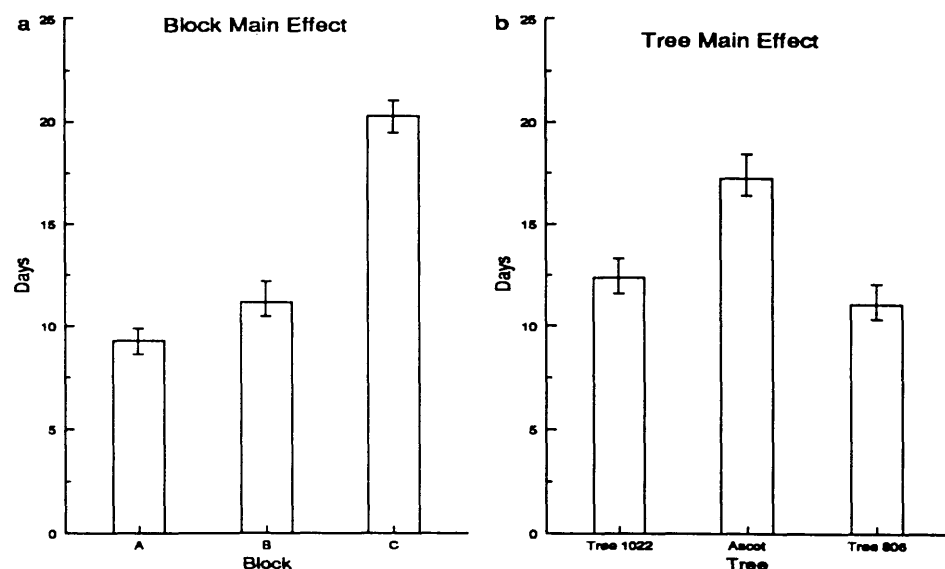


FIG 4.6 a) The effect of block on the time to removal of acorns from artificial caches. Note that block C has a significantly longer survival time. b). The main effect of acorns from different trees on removal rates.

Another interesting effect was that the acorns from the Ascot tree had consistently longer survival times in all treatments (Fig. 4.6b). The presence of ground cover had a significant effect on the survival of acorns, with acorns surviving about six days longer on the uncultivated ground where they were partially hidden by the grass (Fig. 4.7a). The

presence of a weevil larva had a substantial effect on removal rates (Fig. 4.7b), and weevil infested acorns remained on the ground for about ten days longer than healthy acorns. The factor accounting for the largest proportion of the total variance was fencing, with acorns surviving about twelve days longer on the side of the fence protected from rabbits (Fig. 4.7c).

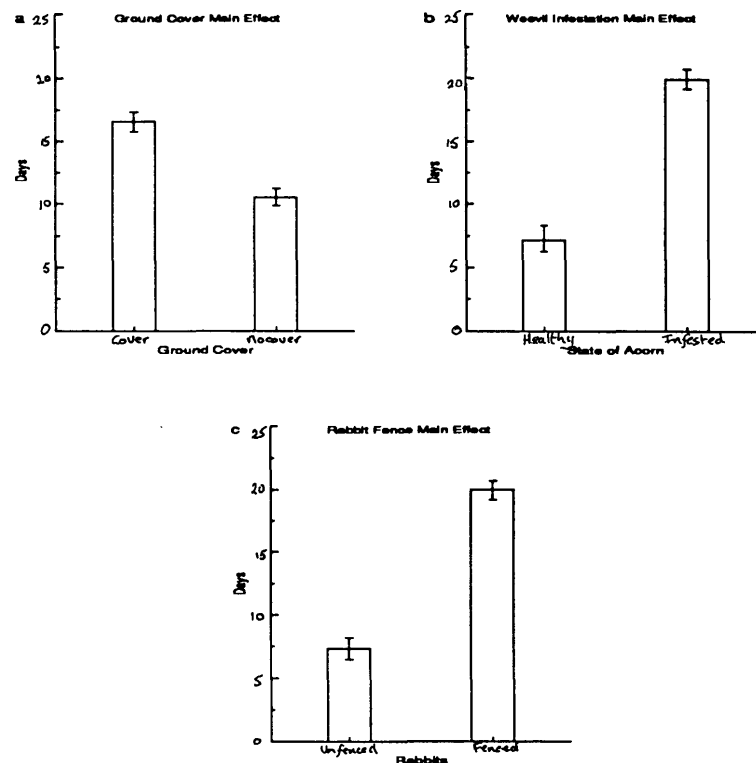


FIG 4.7 a) The effect of ground cover on the time to removal of acorns from artificial caches. b) The effect of weevil infestation on the time to removal from artificial acorn caches. c) The effect of the presence or absence of rabbits on the time to removal from acorn caches.

Three first order interactions were significant: 1) The fencing-by-weevil infestation interaction showed that weevil infested acorns have a proportionately longer time survival inside the rabbit fence, suggesting that rabbits were first to discover the fresh caches (compared with the birds and small mammals that were responsible for removing the acorns from within the fence Fig. 4.8a). 2) The weak ground cover-by-weevil infestation interaction (Fig. 4.8b) suggests that weevil-infested acorns placed on bare ground with no cover had a somewhat longer survival time. 3) The ground cover-by-fencing interaction showed

that acorns inside the rabbit fence with ground cover had a longer survival time presumably because the grass is proportionally taller inside the rabbit fence (Fig. 4.8c). Outside the fence there was very little difference between the mean time to removal with and without ground cover and the rabbits quickly found all the acorns.

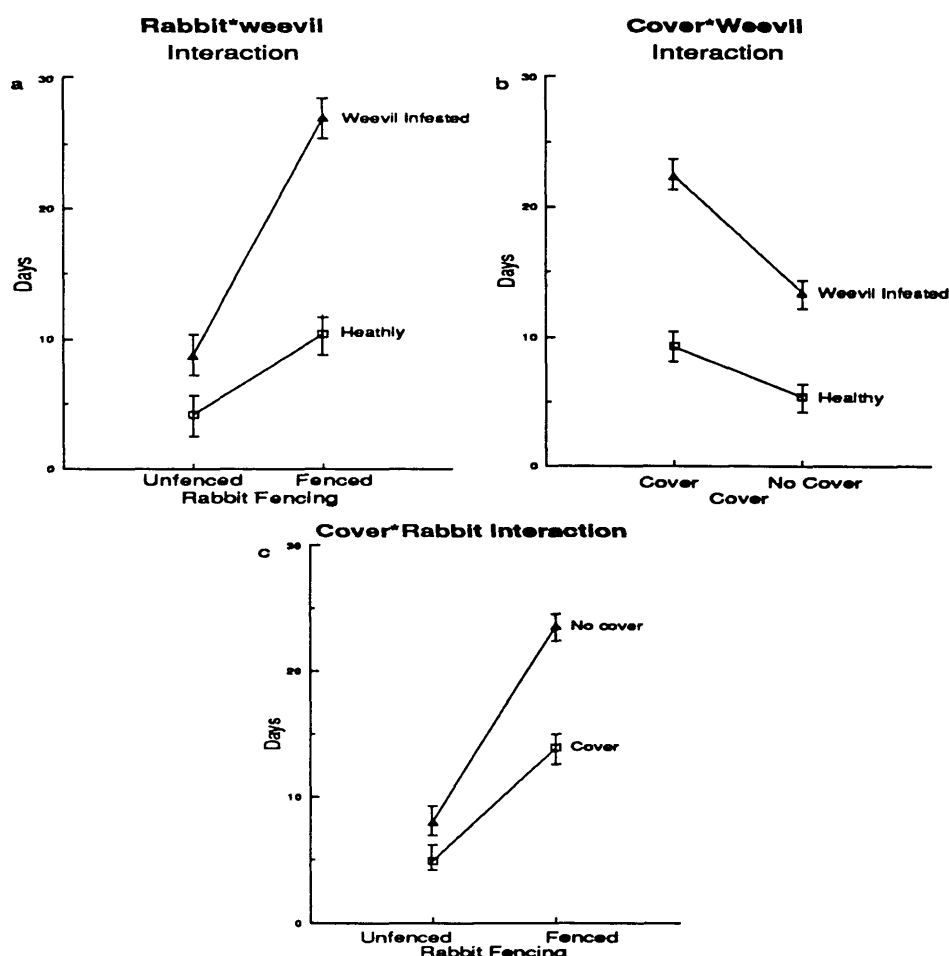


FIG 4.8 a). The interaction of rabbits and weevil-infestation on the average removal time. Note that inside the rabbit fence, small mammals found weevil infested acorns substantially more distasteful than did the rabbits. b). The ground cover-by-weevil infestation interaction on the average removal time, weevil infested acorns survived proportionately longer than healthy acorns when ground cover is absent. c). The ground cover-by-rabbit interaction on the survival time of acorns; acorns survived proportionately longer in the taller vegetation inside the rabbit fence.

4.3 Germination Experiments

Field experiments were designed to test the following hypotheses: 1) Weevil infested acorns are able to germinate and produce healthy seedlings under field conditions. 2)

Seedlings from weevil infested acorns are equally competitive with seedlings from healthy acorns. 3) The presence of rabbits affects the probability of survival of oak seedlings. 4) The burial of acorns affects the probability of seedling recruitment.

4.3.1 Methods in The three Years This experiment was Carried out

Experiments were carried out over three years in the fenced and cultivated plots in Nash's Field (see Section 4.2.2). In 1986 and 1988 I used three of the six blocks, and during the bumper acorn year of 1987, there were sufficient acorns to use all six of the experimental blocks. The experiments had slightly different designs in each of the three years.

a) The 1986 experiment.

During the autumn of 1986 the acorn crop at Silwood Park was particularly low, so the replication of this experiment was less than ideal. The experiment was designed to test the ability of healthy, weevil infested and experimentally mutilated acorns to germinate and to produce seedlings that emerged above ground. Acorns with 0, 30, 70, and 90% of their endosperm removed, leaving the embryo intact were used in the experiment along with weevil infested acorns and undamaged controls. The cotyledons of the acorns in the mutilated treatments were cut using a paper guillotine, and immediately taken to the field for planting so as to minimise the time that the damaged acorns were exposed to the air. The second aim of this experiment was to examine the competitive ability of the emerging seedlings. A series of healthy, weevil infested, and artificially mutilated acorns were planted out in factorial combinations in plots using the following treatment combinations:

- i) Rabbit grazing without cultivation
- ii) Rabbit grazing with cultivation
- iii) No rabbit grazing without cultivation
- iv) No rabbit grazing with cultivation

The level of interspecific plant competition was assumed to be greatest in the fenced uncultivated plots and least in the grazed cultivated plots. Levels of seedling predation by vertebrate herbivores were assumed to be highest in the unfenced cultivated plots and lowest in the fenced uncultivated plots. While the fences were rabbit proof, they allowed access to mice and voles (P. Hulme personal communication). The five acorn treatments were planted 5 cm below the soil surface in groups of five in each of the four grazing/cultivation treatment combinations. The experiment was replicated in blocks, A, C, and E. The positions of the various treatment combinations were randomized separately within each of the plots.

b) The 1987 experiment.

The experiment carried out in 1987 was larger because of the abundance of acorns. Mutilated acorns were not used, but otherwise the treatments were the same as in 1986. An additional treatment had unburied acorns on the surface in addition to fruits buried at 5 cm. This last treatment was intended to demonstrate the importance of burial by dispersal agents such as jays and small mammals for the regeneration of *Q. robur*.

Acorns were planted in groups of fourteen in each of four replicates at each treatment combination, in each of six blocks. A total 5376 acorns were planted out. As before, positions of the groups of acorns were independently randomized.

c) The 1988 experiment.

A slightly modified experiment was carried out in the autumn of 1988. In the previous years, all acorns left on the surface were removed by birds or small mammals, even inside the rabbit fence. A new treatment was added in 1988 to see if acorns placed on the surface but protected from seed predators with fine wire-mesh, roofed exclusion cages would produce seedlings. Because few acorns were available, only two replicates of each treatment were planted out in three blocks with ten acorns in each replicate.

4.3.2 Data Collection and Analysis

a) 1986 experiment

After one year's growth the number of seedlings in each of the treatment combinations was counted and the seedlings were dug up. A record was made of their height and the dry weight of the above ground portion of the seedling. The above ground portion of a seedling was taken as that tissue above the point of insertion of the old cotyledons on the stem. It proved very difficult to extract the deep tap roots of these plants, and an accurate record of the root weights was not obtained (but see below).

b). 1987 experiment

Again after a period of one year the number of seedlings in each of the treatment combinations was counted, but the seedlings were left to grow for a further year. During the autumn of 1989, the seedlings were counted again and dug up. This time, the tap roots were carefully excavated so that accurate root and shoot weights and root:shoot ratios could be calculated. Seedling height, root length, root diameter, number of shoots and the number of leaves were also recorded.

c) 1988 experiment

The summer of 1989 had the highest temperatures and lowest rainfall since 1976. As a result, very few seedlings emerged above the ground surface, and for those that did emerge, the shoots were so badly desiccated that all the seedlings appeared to be dead. On digging up the plots, however, it became clear that many of the seedlings had in fact, survived. Some had just a root protruding from the acorns and no shoot, while others had formed secondary shoots from the crown of the root following desiccation of the primary shoot.

In each year analysis was carried out on the proportions of acorns emerging above ground using GLIM with binomial errors. Results are tabulated as % of acorns that emerged above ground. The mortality of acorns that occurred between planting and the first census

includes two components: 1) the non-viability of acorns due to such factors as fungal infection from *S. pseudotuberosum*, malformation or damage to the radicle; and 2) seed predation, seedling predation, and plant competition (the experimental treatments). In 1987 an estimate of acorn inviability was obtained from the germination experiment (section 4.1).

4.3.3 Results

a). 1986 experiment

The mean proportion of seedlings emerging above the ground was analysed using GLIM with binomial errors, and the analysis of deviance is presented in Table 4.4.

Source	Change in Deviance (χ^2)	d.f.	p
Mutilation	41.54	4	>0.0001
Competition	2.74	1	N.S.
Rabbits	2.354	1	N.S.
Block	0.899	2	N.S.
Mut*Comp	4.52	4	N.S.
Mut*Rab	4.893	4	N.S.
Comp*Rab	5.583	1	0.019

TABLE 4.4 Analysis of deviance table for the number of seedlings emerging. Of the main effects, only mutilation had a significant effect on seedling emergence. The only significant interaction was the plant competition-by-rabbit effect, which occurs again in the experiment in the following year. Error deviance = 40.5 with 42 d.f.; Total deviance = 103.0 with 59 d.f.

As might be expected, mutilation had a highly significant negative effect on emergence (Fig. 4.10a). Weevil infested acorns had a probability of emergence similar to those with about 70% of the cotyledons removed. The fate of an acorn is highly dependent on whether or not the weevil larva eats the emerging embryo. Analysis of variance on the weights of the seedling shoots showed that there were no significant differences between any of the treatments except for the main effect of mutilation.

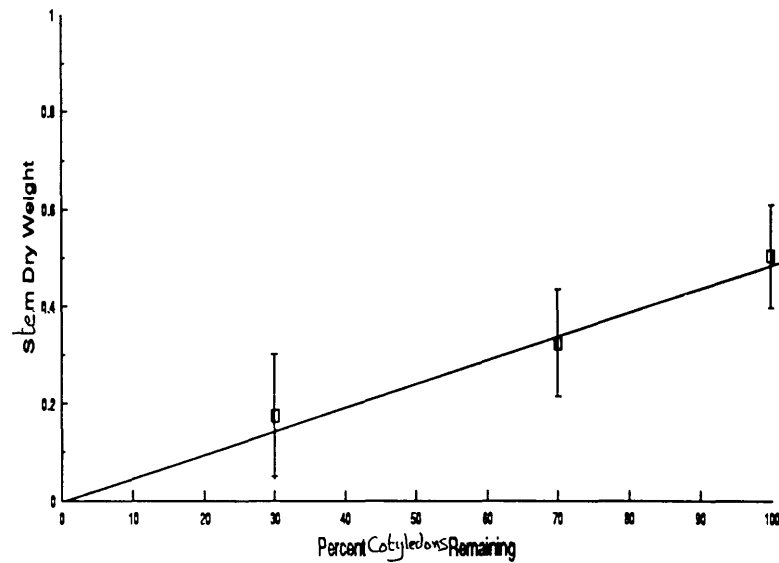


Fig 4.9 Regression of seedling dry weight on mutilation level. Intercept = -0.0036, $SE_a = 0.017$, $t = 0.21$, $p = 0.836$; slope = 0.00526, $SE_b = 0.0017$, $t = 3.05$, $p = 0.004$.

Contrary to expectation, neither plant competition nor the presence of a rabbit fence had any effect on the numbers of seedlings emerging. There was, however, a significant interaction between plant competition and the presence or absence of rabbits on the number of seedlings surviving after 1 year (Fig. 4.10_b).

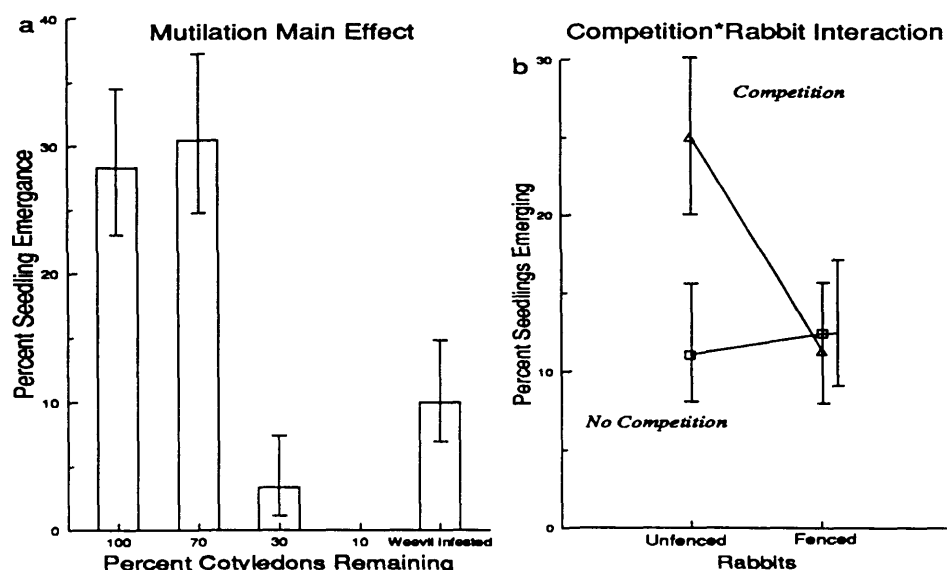


FIG 4.10 The effect of removing varying fractions of cotyledon mass on the probability of seedling emergence a) The mutilation main effect. b) The plant competition/rabbit-grazing interaction. In a low competition regime in the absence of rabbits there is a greater probability that a seedling will emerge. Means are presented $\pm$ standard errors back-transformed from logits.

As in the 1986 experiment, neither plant competition nor rabbit grazing had any effect on the probability of a seedling emerging (Fig. 4.11 a & b). A large proportion of the total deviance was accounted for by the burial treatment. Out of more than 2500 acorns placed on the surface, only one produced a surviving seedling (Fig. 4.11d). Weevil infestation had a major effect on the probability of emergence (Fig. 4.11c). There were two significant interactions. 1) The surface-by-weevil infestation interaction was just an artifact; almost all acorns above ground disappeared irrespective of infestation, whereas buried acorns had different survival rates depending on their infestation. 2) The rabbit grazing-by-competition interaction (Fig. 4.12a) is interesting because it gives the same counter-intuitive result as was obtained the 1986 experiment. Rabbit grazing and cultivation main effects were non-significant. Rabbit grazing had a *positive* effect on seedling emergence in grassland and a negative effect in cultivated land.

b). 1987 experiment

The mean proportion of seedlings emerging above ground after one year was analysed using GLIM with binomial errors, the analysis of deviance table is given below:

Source	Change in Deviance (χ^2)	d.f.	p
Block	25.75	5	>0.0001
Weevil Infestation (W)	230.06	1	>0.0001
Surface/Burial (S)	871.05	1	>0.0001
Rabbit Fence (R)	0.0004	1	N.S.
Plant Competition (C)	0.92	1	N.S.
C*R	16.56	1	>0.0001
C*W	0.29	1	N.S.
R*W	0.87	1	N.S.
C*S	0.82	1	N.S.
R*S	1.56	1	N.S.
W*S	19.23	1	>0.0001

TABLE 4.5 Analysis of deviance table for the proportion of acorns emerging as seedlings. Neither the presence of a rabbit fence nor the effect of plant competition was significant when considered alone. The presence or absence of a weevil account for a large proportion of the total deviance, as did the burial treatment. The interaction between plant competition and rabbit grazing was again highly significant. Error deviance 719.0 with 368 d.f., Total deviance 1886.0 with 383 d.f.

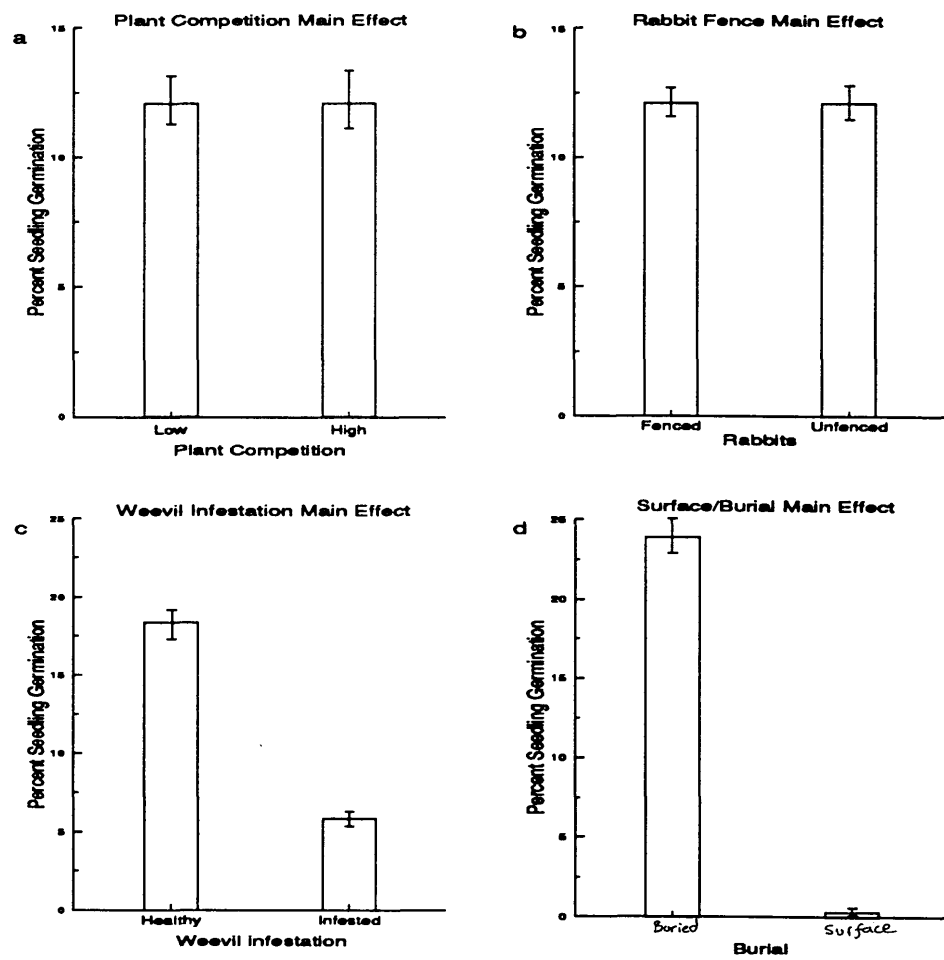


FIG 4.11 Main effects of the 1987 emergence experiment after one year in the field. a) Plant competition main effect; b) Rabbit grazing main effect; c) Weevil infestation main effect; d) Surface/burial main effect. Standard errors are back-transformed from logits.

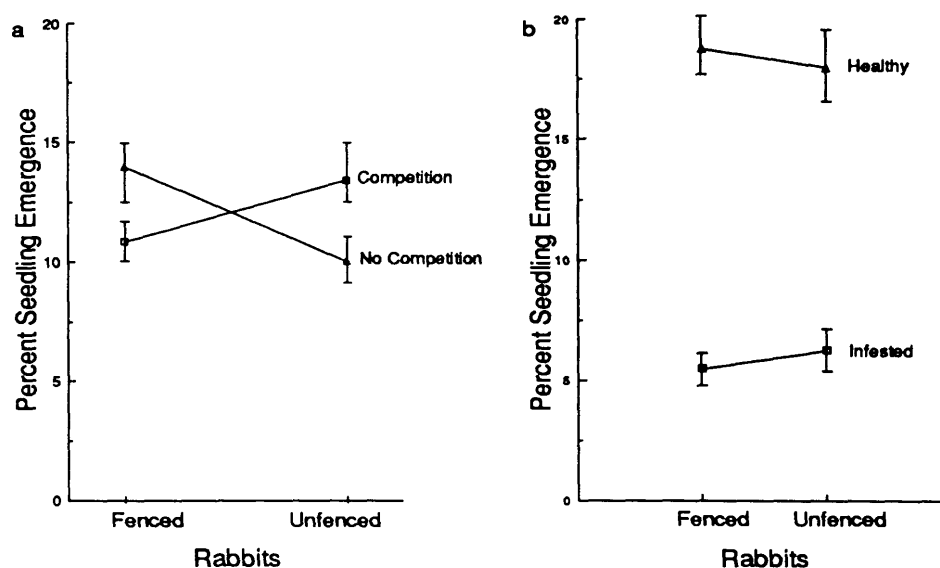


FIG. 4.12 The emergence experiment 1987. a) The rabbit/cultivation interaction, showing that the presence or absence of rabbits can influence the outcome of competition between oak seedlings and the surrounding vegetation (see text for further details). b) The interaction between rabbits and weevil-infestation although this was not significant in 1987, the interaction became highly significant in 1988, after a further year in the ground (FIG 4.14 b).

The same analysis was carried out on the proportion of seedlings present one year

later:

Source	Change in Deviance (χ^2)	d.f.	p
Block	35.18	5	>0.0001
Weevil Infestation (W)	197.16	1	>0.0001
Surface/Burial (S)	621.69	1	>0.0001
Rabbit Fence (R)	1.83	1	N.S
Plant Competition (C)	3.48	1	N.S
C*R	7.69	1	0.006
C*W	0.084	1	N.S.
R*W	12.89	1	>0.0001
C*S	1.65	1	N.S.
R*S	2.13	1	N.S.
W*S	3.09	1	N.S

TABLE 4.6 Analysis of deviance for the 1987 emergence experiment, after two years in the ground. The only different result is that the interaction between rabbits and weevil infestation has now become highly significant. Error deviance 581.8 with 368 d.f., Total deviance = 1468.6 with 383 d.f.

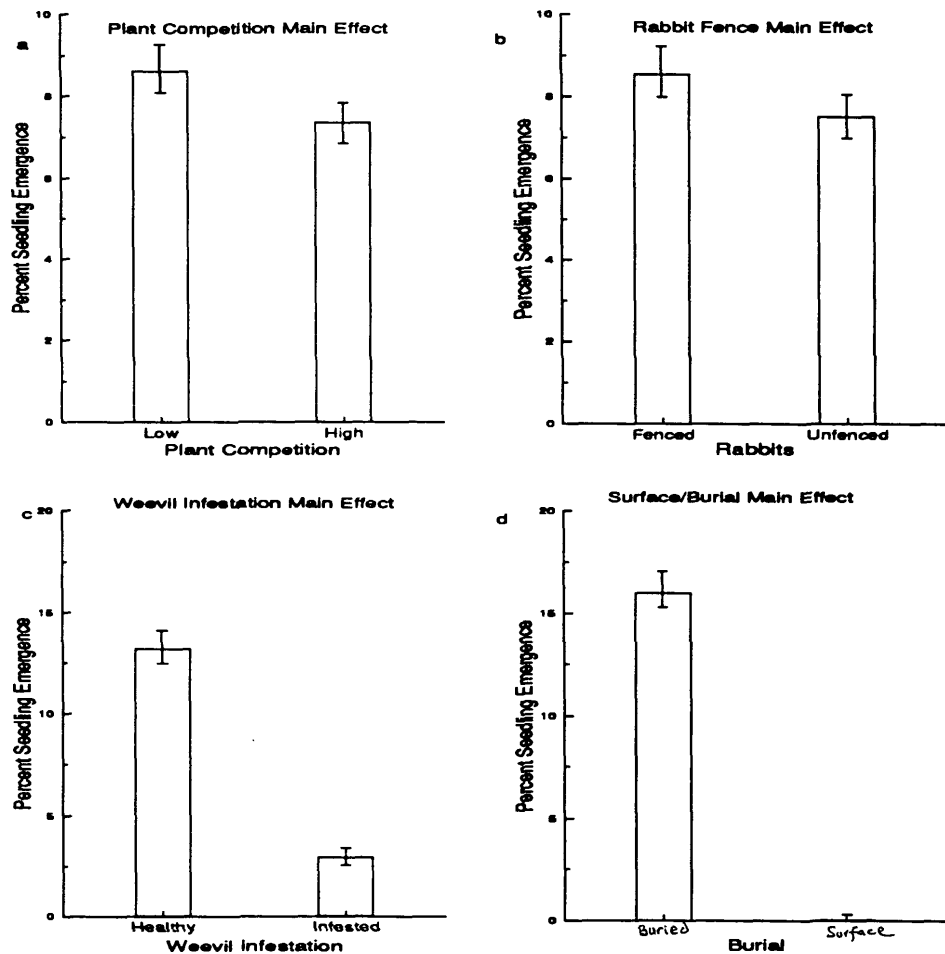


Fig 4.13 Main effects of the 1987 emergence experiment after two years in the ground. a) Plant competition main effect; b. Rabbit grazing main effect; c). Weevil infestation main effect; d) Surface/burial main effect. Standard errors are back transformed logits.

An exponential survival curve was fitted to the number of surviving seedlings over the (constant hazard) three years with and without rabbit grazing (Fig. 4.15b) and cultivation (Fig. 4.15c). The mean time to death (fitted using GLIM with gamma errors) is affected by neither treatment. However, there is a significant effect of the presence of a weevil larva on the subsequent survival of seedlings (Fig 4.15a).

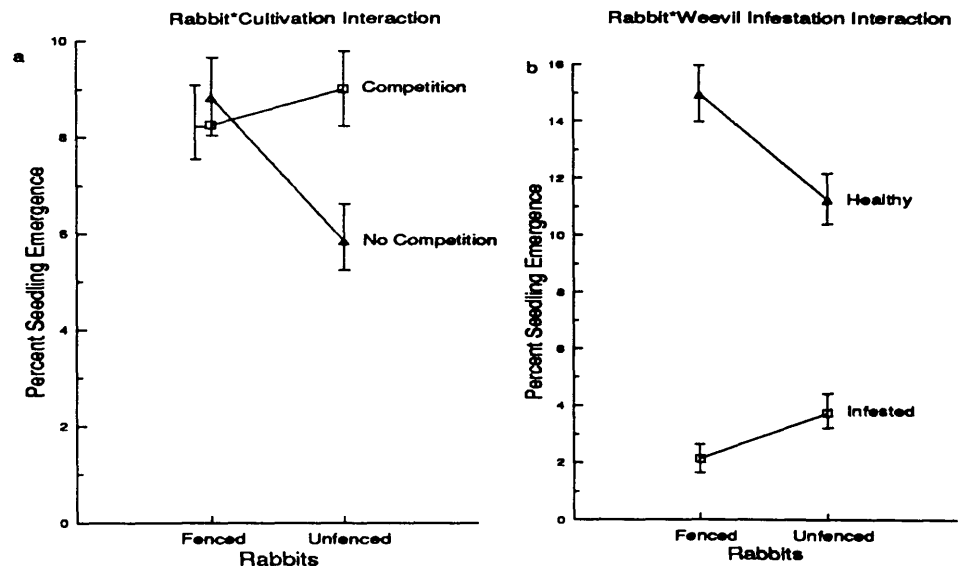


Fig 4.14 The significant interactions observed in the 1987 emergence experiment after two years in the ground. a) The rabbit-by-cultivation interaction is still significant, although there is now no difference between the competition treatments inside the rabbit fences. b) The interaction between rabbits and weevil-infestation. Standard errors are back transformed logits.

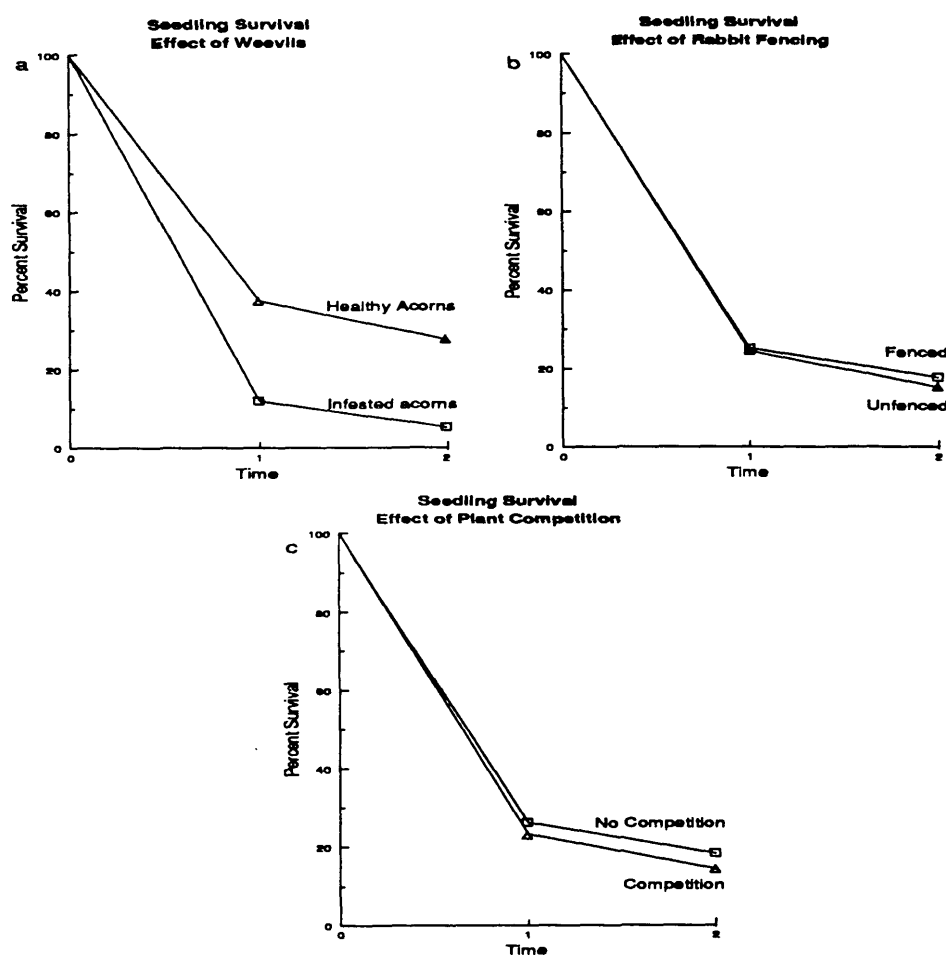


Fig. 4.15 Survivorship curves for the main effects of the 1987 emergence experiment. a) The effect of weevil infestation still has an effect on the survival of seedlings two years after planting, the proportion of seedlings surviving from healthy acorns is greater in both years of the experiment. b) The effect of rabbit fencing on seedling survival (N.S.). c) The effect of plant competition on seedling survival.

The proportion of dry weight allocated to shoots and roots was examined. Differences in root/shoot ratios between treatments should show up as an allometric relationship in a plot of log root weight against log shoot weight. Double regression (Morris 1959) showed that there was no significant allometric relationship with either grazing, cultivation or weevil infestation treatments.

The dry weights of the above ground parts of the oak seedlings were analysed by analysis of variance. The effect of blocks was significant, but the effect of surface burial was spurious because only one seedling recovered from the surface treatment plots. (Table 4.7).

c). 1988 experiment

The hot, and dry summer of 1989 appeared to kill many of the shoots of emerging seedlings, making interpretation difficult. As in the previous year's experiments, burial

Source	d.f.	S.S.	M.S.	F	p
Block	5	7.009	1.402	4.642	0.0014
Competition (C)	1	0.578	0.578	1.914	N.S.
Rabbits (R)	1	0.556	0.556	1.841	N.S.
Weevil Infestation (W)	1	0.113	0.113	0.440	N.S.
Surface/Burial (S)	1	6.710	6.710	22.218	>0.0001
C*R	1	0.256	0.256	0.848	N.S.
C*W	1	0.080	0.080	0.265	N.S.
R*W	1	0.280	0.280	0.297	N.S.
Error	90	27.154	0.302		
Total	103	42.735			

Table 4.7 Anova of log_e shoot dry weight after two years in the field. Note that the one significant result, surface/burial main effect, is probably, since it results from the comparison of a single seedling from the above ground treatment being compared with all the other seedlings.

had a highly significant effect on seedling emergence. Acorns placed on the surface but protected with a fine wire cage also showed no germination (all protected, surface-placed acorns were completely desiccated). The buried acorns emerged at an average rate of 5%. A further 19% remained below ground with only their roots developing. This result may explain why during the 1987 experiment more seedlings were found in some plots in 1989 than were counted in 1988.

4.4 Discussion

This series of experiments provides a convincing demonstration of the impact of weevil-infestation on seedling recruitment (Fig 4.1 and 4.2a). Subtle aspects of the process emerge when other factors such as acorn size and tree of origin are taken to account. The germination of acorns from different parent trees confirmed that nuts from small-acorn trees had a reduced probability of germination. Smaller acorns suffer disproportionately

higher mortality in the presence of a weevil larva (Fig 4.3a) But small healthy acorns are equally likely to produce a seedling. This suggests there is some disadvantage to a tree bearing small acorns that are attacked by these seed predators and selection might be expected to favour trees that had larger acorns. There are two main reasons for this: 1) a larger seed has a greater chance of surviving weevil infestation; and 2) female weevils exhibit a preference for ovipositing in smaller acorns. This begs the question as to why the weevils and the oak trees are not engaged in a Red Queen conflict (Van Valen, 1973) with the trees attempting to produce larger acorns to avoid oviposition by weevils, and the weevils adapting to oviposit in larger acorns. Bossema (1979) presents evidence that jays, the major dispersal agent of the acorns of *Q. robur*, prefer acorns in the size class of 28-29 mm a figure close to that obtained from acorns found growing naturally in Nash's Field, at least 100 meters from the nearest oak tree (M.J. Crawley, unpublished data). Jensen and Nielsen (1986) report that mice moved acorns into a Danish heath at about 35m per year, and although they did not give any indication that the mice exhibited size preferences, it is clear that the mice inflicted very heavy mortality on their caches.

The removal experiment demonstrated that even in a heavy fruiting year all seeds were removed from the surface of the ground, although at different rates according to the particular treatment. Although the majority acorns were eaten at the site of the cache, a considerable number disappeared, presumably to be eaten or cached elsewhere. Removal of an acorn from the artificial cache can not be equated with acorn death.

The germination experiments bear out the fact that acorns placed on the surface have a very low probability of surviving to produce a seedling. Out of 2500 acorns placed on the surface in the 1987 experiment only 1 produced a surviving seedling. The results from the germination experiments were also remarkably consistent. The 1986 experiment and the 2 years of the 1987 experiment showed that neither plant competition nor the effect of rabbit grazing had any appreciable effect on either the number of seedlings or the final dry

weights of the seedlings. The significant rabbit fencing-by-plant competition interaction is interesting in that it shows that rabbits can have a beneficial effect on the proportion of seedlings emerging, if interspecific plant competition is intense and the young seedlings are competing with a dense sward of vegetation (Fig. 4.14a). There is no effect of rabbit fencing on survival on the cultivated plots. *Q. robur* is clearly not a pioneering species, and requires the presence of vegetation to enable its conspicuous^{seeds} to escape from herbivores and to reduce the risk of desiccation. Oak seedlings are tolerant of competition with other plants during the first two years of life, as demonstrated by the fact that neither plant numbers nor the final plant dry weight were reduced by competition in a mature grassland sward. Fenner (1985 and 1987) presents evidence that large seed size such as exhibited by *Quercus* are adaptations to survive in a highly competitive environment (and see Grime and Jeffery, 1965).

The 1988 experiment appeared initially to have failed, because of the particularly dry summer of 1989. In fact, it produced some novel insights into the biology of *Q. robur*. Despite the fact that the growing shoots were completely desiccated, the below ground parts of the seedlings survived the drought and appeared to be in good health. This allows the possibility that a subterranean 'seedling bank' may buffer the population against complete recruitment failure in hot dry years, despite the absence of any seed dormancy.

5 Life History Strategies of *Curculio*

Taking the life cycle of *Curculio* as described in Chapter 2, and the pattern of acorn production as described in Chapter 3, I present a simple theoretical model of life history strategies, in an attempt to understand the reproductive biology of the weevil. A simulation model of weevil population dynamics was run on a computer to test the predictions of the analytical model, and the results are interpreted using bet-hedging theory.

5.1 Does the weevil live in a predictable or an unpredictable environment ?

Two contrasting hypotheses about the temporal pattern of acorn availability can be envisaged. They can be encapsulated in two questions: 1) does *Q. robur* behave as an alternate seed bearer; or 2) do meteorological factors drive the fluctuations in acorn production in *Q. robur*?

5.1.1 An unpredictable environment (acorn production controlled by the weather)

Up until the autumn of 1989 our working hypothesis was that acorn production was controlled by June rainfall (Section 3.5). The watering experiment and direct observation showed that this was not the case. Other observational data suggested that frosts in late April had some effect in reducing acorn production, especially in early flushing trees (regrowth shoots produced after loss of the primary shoots do not produce flowers; see Section 3.4). This correlation also disappeared with the inclusion of the 1989 meteorological data. Many other meteorological variables were tested against acorn production, but only September temperature showed any consistent significant correlation with the production of acorns. Since the acorn crop is determined well before September, the only biological meaning that this correlation could have is that, given the alternate bearing

pattern of *Q. robur*, high September temperatures are associated with *lower* acorn production in the following year. This seems unlikely, since high summer temperatures are typically associated with higher seed production in the following year (Harper 1977), but there are reports of reduced fruiting in herbaceous perennials following dry (and presumably hot) summers (Inghe & Tamm 1985, 1988).

5.1.2 A Predictable Environment (*Q. robur* as an alternate fruit bearer)

The pattern of acorn production over the ten years of the study appears to show alternate bearing, and only 1 year out of 10 (1983) was out of sequence. This hypothesis was tested by plotting $\log(N_t/N_{t+1})$ against $\log N_t$, where N is the number of acorns per shoot at time t .

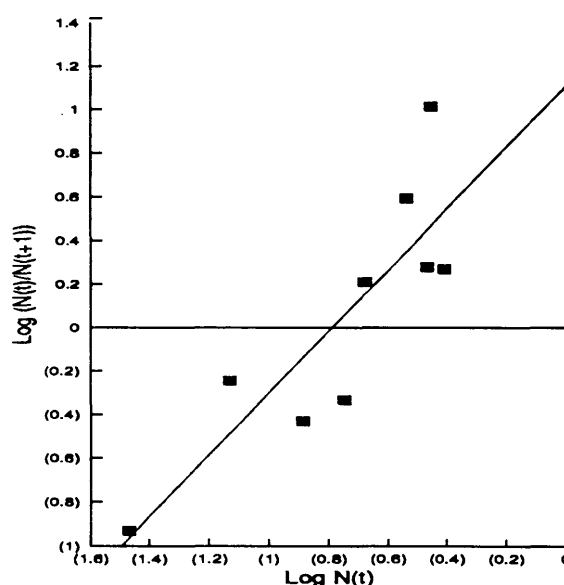


Fig 5.1 Plot of $\log(N_t/N_{t+1})$ against $\log N_t$, showing a significant linear trend, supporting the hypothesis that large seed crops in *Q. robur* follow small seed crops and vice versa. Slope = 1.411, S.E. = 0.327, $t = 4.31$, $p = 0.0035$.

Given the limited data available, the alternate bearing hypothesis seems the more plausible, subject to the caveat that successive low acorn years can occur with a low probability. Alternate bearing is the pattern of reproduction assumed in the following life history strategy model. The occurrence of two bad years in succession, will be referred to as a 'phase shift' in the resource, and is assumed to occur with a probability S .

5.2 The Analytical Model

Consider two populations, one growing exponentially and the other stable. The optimal fitness strategy in the exponentially growing population would be to breed without delay. Suppose we have an annual organism with a net multiplication rate of 10 at low densities. Each year each one of the offspring will produce 10 more. The genotype will increase exponentially, and to have an equivalent rate of increase a 2-year life cycle would need to have the square of the fecundity of the annual (Kelly 1985, Crawley 1986). In contrast, if the population is constant, then an individual only has to replace itself in order to maintain its representation in future generations. Under these conditions there is no necessary evolutionary penalty to delayed reproduction (Woolfenden & Fitzpatrick 1984).

An important assumption of the analytical model is that the weevil population is at equilibrium, and that birth and death rates are equal on average. The model investigates the fitness of an individual that puts a proportion p of its offspring into a two year life cycle and a proportion $(1-p)$ into a three year life cycle. The host plant is assumed to be alternate-bearing, but with a probability S that the resource level undergoes a phase shift in any given year (Section 5.3.1).

Now we compare the fitness of the p and $(1-p)$ strategy against a rare mutant that puts a proportion p' into a two year life cycle and $(1-p')$ into a three life cycle. Consider the relative success of this mutant against the wild type.

For a two year life cycle $\frac{p'}{p}$

For a three year life cycle $\frac{(1-p')}{(1-p)}$

These proportions give the fitness ratio of the two life history strategies. If $p > p'$, p will be the more successful life history strategy and when $p < p'$, p' will be favoured in the population. When $p = p'$ we have the ESS proportion, because p is uninvadable by any other strategy.

Now the probability that the resource will undergo a phase shift in any given year is S , so the average reproductive success, Q , is given by

$$Q = \frac{p'}{p} \cdot S + \frac{(1-p')}{(1-p)} \cdot (1-S)$$

To find the maximum fitness, we set $\frac{dQ}{dp'} = 0$ and find the value of p such that no value of p' can make Q any larger

$$\frac{dQ}{dp'} = \frac{S}{p} - \frac{(1-S)}{(1-p)} = 0$$

This can only occur when $p = S$, and so the weevils should put a fraction S of their eggs into a 3-year larval period, with a larger fraction when the probability of a phase shift is higher.

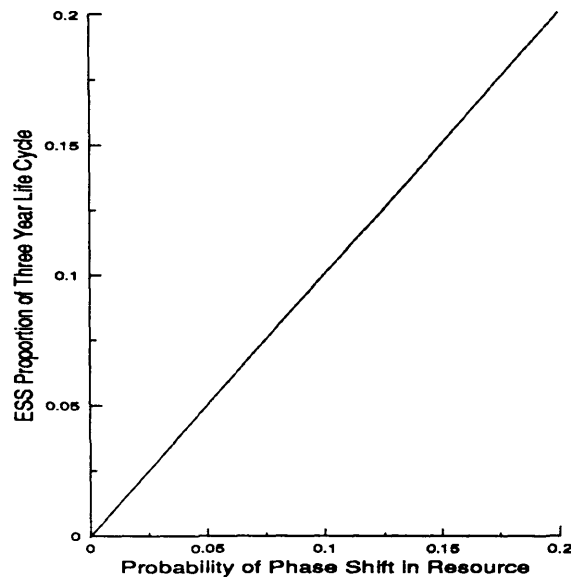


Fig 5.2 The results of the analytical model, extended over biologically realistic phase shifts in resource. Higher values in the probability of phase shift would result in the pattern of alternate bearing breaking down, and the environment becoming essentially random.

The ESS proportion of offspring allocated to a three year life cycle should be equal to the probability of a phase shift in the resource. This strategy would be uninvadable by any other, and is the evolutionarily stable strategy (Cohen 1966, Parker 1984, Ellner 1987).

5.3 The Simulation Model

A simulation model was constructed to investigate the behaviour of populations of weevils living in a fluctuating environment. The life history parameters used in the model were estimated from field observation and experiments.

5.3.1 The Model Environment

The model environment consists of a sequence of good and bad years. Fig. 3a illustrates a perfect alternating environment, where, if we assume that the population started in the correct phase, the best strategy for any weevil population would be to breed only during the years when the resource level was high (intraspecific competition notwithstanding). But there is a non-zero probability that the resource will undergo a phase shift

(Fig. 3b), so that any weevil breeding strictly in alternate in years would end up breeding only in the poor resource years, so that its reproductive rate would be much reduced, until the next phase shift occurred

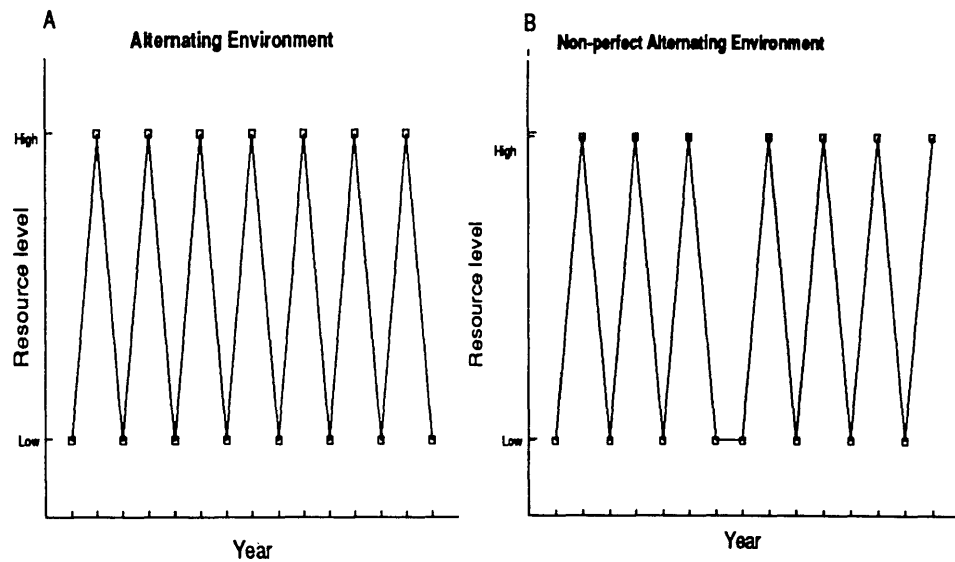


Fig 5.3 Schematic representation of a perfectly alternating environment used in the simulation model where the best strategy for an organism would be to emerge every other year, during years of high resource availability and an environment that under goes a one year phase shift in resource availability. The best options for an organism now is different.

Two strategies can be envisaged: 1) to predict, using environmental cues, when there is likely to be a resource phase shift and then to extend the period of time spent as a resting stage; 2) to allocate a fixed proportion of each clutch to a further year in the larval stage in all generations. Under female control this strategy would allow an individual to increase the likelihood that at least some of her offspring would emerge in a year of plentiful resources. The aim is to predict the optimal fraction of offspring that should spend a further year in the larval stage, as a function of S (the probability of a phase shift in resource availability).

5.3.2 The Model

The number of adults produced in any year is a function of the number of adults two and three years ago.

$$N_{t+3} = F(N_t) + F'(N_{t+1})$$

where F is the fecundity discounted for two years of larval mortality in the soil, and F' is the fecundity discounted for one year of larval mortality. The model assumes: 1) a constant annual mortality, estimated from the larval burial experiment; 2) a fixed proportion of the larvae from each cohort breed after two and three years; and 3) the fecundity of the weevils in any year is determined by the ratio of adult weevils to acorns in that year. The number of eggs in the fecundity equation was taken to be an hyperbolic function, declining with the decreasing ratio of weevils to acorns in that particular year (the linear regression from Section 2.2.2 was not used because it would predict negative fecundities at high densities of weevils per acorn).

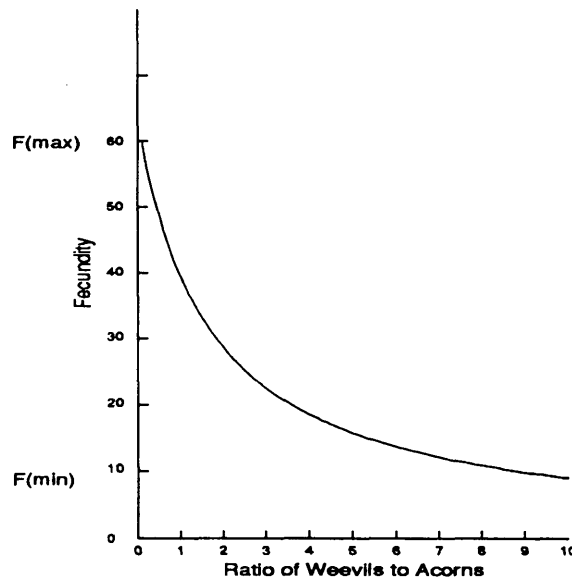


Fig 5.4 Hyperbolic regression of weevil fecundity against number of females per acorn. Parameter estimates by regression from Fig. 2.4.

The full model is then given by:

$$N_{(t+3)} = ((1-d)^3 \cdot (1-p) \cdot N_t \cdot f_3) + ((1-d)^2 \cdot p \cdot N_{(t+1)} \cdot f_2)$$

where, d is the death rate per year in the soil and p is the proportion of weevils in a two year life cycle. The two fecundity predictors are:

$$f_3 = \frac{m}{\left(1 + c * \left(\frac{N_t}{A_t}\right)\right)}$$

and

$$f_2 = \frac{m}{\left(1 + c * \left(\frac{N_{(t+1)}}{A_{(t+1)}}\right)\right)}$$

where m and c are the constants of the hyperbolic regression.

The overall probability of a resource phase shift can be calculated as follows. Consider the matrix;

		resource level @ t+1	
		high	low
resource level @ t	high	α	$(1 - \alpha)$
	low	$(1 - \beta)$	β

where α is the probability that two heavy acorn crops occur in consecutive years, and β is the probability that two poor acorn crops occur in consecutive years.

5.3.3 Results

The analytical and simulation models agree well for low (and apparently realistic) values of the probability of a phase shift in the pattern of acorn production. However, the simulation model departs from the analytical solution above a phase shift probability of about 0.25. The rate of increase of the proportion of weevils in the three year life cycle slows until the probability of a phase shift in resource is 0.3. After this point the simulation model tells us that a two year life cycle will be favoured, in direct contradiction to the analytical solution. For higher probabilities of a phase shift, the model environment becomes more and more unpredictable and the favoured life history strategy is the one that involves early reproduction (Stearns, 1976).

Given that we have only an 11 year run of data (the acorn crop was very low in 1990, as predicted; C. Long personal communication) and that there has been one observed phase shift in resource, it is far too early to obtain a reliable estimate of S from field data.

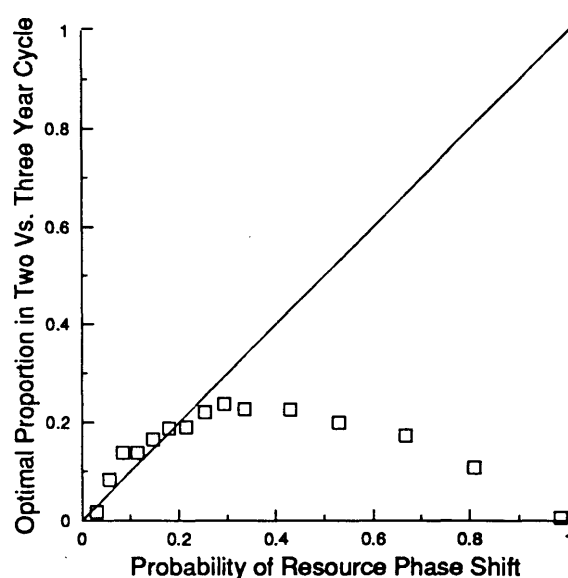


Fig 5.5 The results of the simulation model compared with the analytical solution over the full range of probabilities of phase shifts. Note that there is always some advantage to producing a few long-diapause larvae, except at $S=0$ (all proportions are > 0), but the magnitude of the advantage declines above $S=0.3$. For explanation see text.

5.4 Discussion

The results of the simulation model do not differ qualitatively from those of the analytical model for low values of S . If the probability of a phase shift is low then the ESS proportion in a three year life cycle is equal to the probability of a phase shift in resource. The results of the simulation model do differ from the analytical solution for $S > 0.3$. Over the lower portion of the graph (Fig 5.5) the simulation consistently gives an ESS proportion in a three year life cycle slightly higher than predicted by the analytical solution. This is most likely to be due to the additional parameters in the simulation model. First, there is the annual mortality rate in the soil and second, the fecundity of the weevils is variable in the simulation model, whereas it was assumed to be constant in the analytical model.

Given that the models are in close agreement for low (and apparently realistic) values of S we can now go on to address the question as to whether the models give us a clearer picture of the life history strategy of the weevil? If the assumption of an alternating environment is sound, as statistical analysis of acorn production in Silwood Park suggests, then the weevil could be seen to be hedging its reproductive bets in the sense of Seger and Brockman (1987) and Philippi and Seger (1989).

Bet hedging is seen as a trade off between the mean and variance of fitness. In the current example, consider a weevil breeding only in good years of acorn production. Its mean fitness will be at a maximum as long as the line continues to breed in years of high acorn production. But the weevil lives in a temporally varying environment, and so the offspring of one generation may find themselves emerging into a resource-poor environment, with the consequence that they suffer dramatically reduced fitness. As a result, the between-generation variance in fitness is greatly increased, and if the generation emerging in the bad year is unable to reproduce, that particular line of weevils will become extinct because the genotype has zero fitness. This is why the geometric mean fitness is the appropriate measure, rather than the arithmetic mean (Philippi and Seger 1989). The geometric mean is extremely sensitive to variance, and it equals zero if any one of the terms in the series is equal zero (See table 5.1). Now consider a weevil living in the same environment but putting proportion of its offspring into delayed emergence. The line will have a lower fitness than a line breeding only in the good years in the short run. But as soon as a phase shift in the resource occurs, the line with the mixed strategy will be buffered against large changes in its overall fitness. In particular, it is much less likely to suffer zero reproduction during any given run of years.

Table 5.1 Table adapted from Philippi and Seger (1989). Even though it has a lower arithmetic mean fitness, the mixed strategy has the higher geometric mean fitness. The mixed strategy would therefore be stable against the other two strategies. If the animal breeding in this system had an annual life cycle over the three years it would have a geometric mean fitness of 0.2154 or 0.4642 depending upon whether it bred in two bad or two good years. This figure is less than the geometric mean for the mixed strategy, and so the mixed strategy is still the ESS.

Breeding	Phenotype			
	All 2	Mixed	All 3	
In Sync	1.0	0.5	1.0	
Out of Sync	0.1	0.5	0.1	
Arithmetic mean	0.55	0.5	0.55	$\bar{Y} = \frac{\sum y_i}{n}$
Geometric mean	0.316	0.5	0.316	$\hat{Y} = \sqrt[n]{\prod y_i}$

This type of diverse life history strategy was first described by Cohen (1966) for desert annual plants in the simple case where there were two year types, good and bad. Here the fraction of seeds germinating is proportional to the frequency of good years for seed production. Diverse life history strategies have also been described in insects. At the onset of unfavourable conditions the insects arrest their development and enter a diapause. If the onset of unfavourable conditions is unpredictable, then a proportion of the population may enter diapause (Wipking and Neumann 1986). When the environment is unpredictable between years as in Cohen's (1966) example, the insects may enter an extra long diapause (Hanski 1988). An extreme example of a variable environment is the production of *Leccinum* fungi in Finnish Lapland where mushroom production can vary from 363 to 0.3 kg/ha between years (Ohenoja and Metsanheimo 1984). In southern Finland this large variation in mushroom production between years is not seen (Ohenoja and Koistinen 1982). They are food for seven anthomyid flies of the genus *Pegomya*. All seven of the fly species inhabiting these fungi display an extra long diapause in the northern parts of their ranges, where the 4 orders of magnitude difference in the level of resource between years is observed. In the south of the range, however, only one of the species

displays extra long diapause, and then only rarely (Hanski 1988 , 1989).

The control of the proportion of individuals entering an extra long diapause is a more difficult problem. Two mechanisms are possible: 1) the individual larva controls whether or not it enters into an extra long diapause; and 2) the control of the proportion entering extra long diapause is exerted by the mother. Westoby (1981) argues that in plants diverse germination behaviour is under selection pressure to give the mother control over the proportion of seeds germinating now or at a later date (see also Cohen 1966, 1967, 1968).

Given our present knowledge of the life cycle of *Curculio* and the fruiting pattern in *Q. robur* it is plausible to assume that any decision an individual weevil makes about breaking diapause is done without knowledge of the prevailing environmental conditions (e.g. the acorn density or the number of competing weevils). An individual female will be under selection to maximise the number of her grandchildren, and the best way to achieve this is to put a certain fixed proportion into an extra long diapause. There is no active female choice involved, because the proportion entering long diapause will have been under natural selection, and is likely to be close to the ESS proportion as defined in the models above. We do not know the mechanism whereby diapause duration is determined, but it is likely to involve the endocrine system (J. Hardie, personal communication).

6 General Discussion and Conclusions

The aim of this study was to understand how the interaction between *Quercus robur* and *Curculio glandium* has shaped the evolution of the life history of the insect and the reproductive biology of the tree. Models were produced in an attempt to explain the apparently paradoxical life history strategy of *Curculio* in which an extra year of larval development appeared to be 'wasted' underground. A solution was found by reference to the alternate-bearing pattern of acorn production by *Q. robur* and the bet-hedging strategy of the weevil.

I shall begin by discussing acorn dispersal before turning to a consideration of the evolution of mast-fruitle and alternate bearing in trees. I conclude the discussion with an assessment of the role of invertebrate seed predators in oak population dynamics and in shaping the evolution of the reproductive biology of oak.

Oak seedlings appear to originate from jay rather than small mammal caches. Also, the diameter of the acorns attached to naturally recruiting oak seedlings fell into the range of sizes that jays have been described as preferring (Bossema 1979). Bossema also reported that acorns with holes (i.e. those that are weevil infested) are avoided by jays. Mice also reject weevil-infested acorns (M.J. Crawley, personal communication), leaving them where they find them, under the parent tree.

Acorns left on the surface are destined to die. Observation and experiment showed that removal rates of acorns from parent trees were different, and healthy acorns disappeared faster those that were weevil infested. Of course, removal of an acorn from an experimental cache does not necessarily mean that the seed is killed, because jays and

mice may take the nuts to a cache of their own. Acorns that are removed preferentially from certain trees may be at an advantage during a heavy seeding year, because they are dispersed and cached first, before the seed predators are satiated. This hypothesis requires further work.

Acorn predators can have a pronounced effect on the number of seedlings produced (Shaw 1968b, and this study), but acorns remaining on the surface only rarely produce surviving seedlings. Shaw (1968b) reported a 70-80 fold increase in numbers of seedlings emerging from acorns covered in leaf litter and protected from seed predators compared with unprotected surface-planted acorns. In this study I found no difference between the emergence rates of buried acorns between control plots and plots protected from seed predators, but only 1 seedling was produced from 2500 acorns placed on the surface of the experimental plots. Jarvis (1964) explained this lack of viability in acorns as resulting from desiccation of unprotected seeds. Death resulting from desiccation was noted in acorns placed on the surface of the ground, but was not a major source of mortality compared with predation.

Given that an acorn needs to be buried before it has a reasonably high chance of producing a seedling, we need to know how burial influences the other factors associated with seedling survival. Surprisingly, neither plant competition nor protection from rabbit grazing had any effect on the proportion of seedlings surviving or on their shoot dry weights. In both years, there was a significant rabbit fence-by- competition interaction, resulting from the fact in dense grassland, rabbit grazing *improved* seedling performance presumably as a result of competitor release outweighing the direct costs of partial defoliation. Over the long term, however, rabbits appear to have a major effect on the dynamics of oak recruitment at Silwood Park. Many of the smallest oak saplings have been repeatedly nibbled back by rabbits over many years, and their root stocks are gnarled by the constant production of regrowth shoots. Their survival may not be affected, but their growth is

stunted by repeated rabbit browsing. The myxomatosis outbreak of the mid 1950's reduced the population of rabbits to less than 1% of its former abundance and, as a result, many suppressed saplings were able to grow. A large cohort of oak trees in this age class now covers sizable areas of Silwood Park in what used to be experimental grasslands (N. Waloff, personal communication).

It is clear that there will inevitably be serious shortcomings to any three year study of the consequences of seed production, herbivory and competition on the performance of a long lived species like *Q. robur* (trees normally live between 250 and 450 years, Jones 1959; Molisch 1938 (in Harper and White 1974)). The conditions which prevail at the time of a short-term study will probably never reflect the geometric mean conditions under which the species responds over evolutionary time.

The information gathered in this study indicates that the key to understanding the *Curculio-Quercus* system lies in the fruiting behaviour of *Q. robur*. Independent data from southern England (Kenwood & Holm 1989) and personal observation in central and south-eastern Europe suggests that the synchronous alternate bearing of *Q. robur* may occur over large geographic areas. Whether climatic cues are important for maintaining the synchrony, given the inevitability of locally poor conditions leading to occasional successive low seed crops, is unclear and requires further study. Naturally, the strength of any inferences arising from such a short time series is limited, but the data so far are persuasive. After the heavy fruiting of 1989 we predicted that the crop would be low in 1990. Gratifyingly, the count turned out to be the lowest on record (see Fig. 6.1).

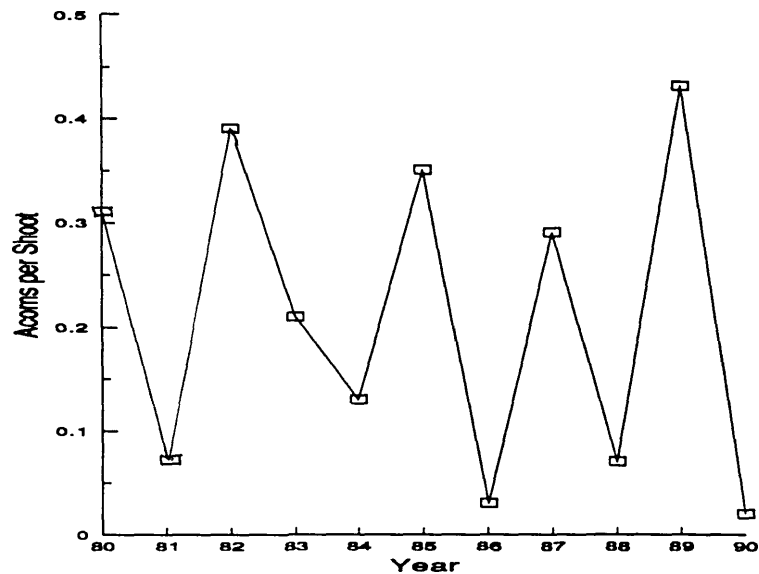


Fig 6.1 Acorn production over the 11 years of the study. 1990 was the first year when a successful prediction of the acorn crop was made. (1990 data courtesy of C. Long & M.J. Crawley, unpublished results).

Silvertown (1980) defined mast seeding as an inter-seeding period of >1.5 years. It is clear from the entomological literature that specialist seed-feeding insects have evolved mechanisms to survive protracted periods of unfavourable resource availability (Hanski, 1988). The fact that many specialist insects are capable of surviving for periods of >1.5 years, means that the threshold for the definition of mast seeding should be higher. Possibly a more realistic definition of mast seeding would include the inter-fruiting period of the tree as a random variable, where the inter fruiting period is long enough to ensure that specialist predators are sufficiently rare so as to be unable to mount a numerical response in the mast year. Also the amount of seed produced has to be enough to satiate any generalist predators in the area. Smith, Hamrick & Kramer (1990) list other potential advantages that accrue to mast-fruiting trees: 1) populations of specialist seed-predators are reduced during the inter-mast period; 2) dispersal by scatter-hoarding animals may lead to increased dispersal distances in mast years; 3) the weather cues used as a trigger for flowering might provide

optimum conditions for germination and subsequent seedling growth; and 4) concentration of pollen in mast years may lead to improved rates of pollination for wind-pollinated species.

It is worth considering alternate-bearing as distinct from mast fruiting because of: 1) the regularity of fruit production; and 2) the relative unimportance of meteorological cues in alternate bearing species. Both masting and alternate bearing appear to be effective defence strategies for the tree, because both give rise to predator satiation and hence to inverse density dependence in seed death rates.

The phase shift of seed production may be an adaptive response by the tree for predator avoidance. Seed predators in synchrony with the two year cycle of seed production would be vulnerable to this sort of tactical evolution by their host plant. Selection on the tree population to maintain synchrony between individuals is likely to be strong (as with true masting species) because an individual tree that fruits out of phase with the others would suffer disproportionately high seed mortality.

The life history of *C. glandium* appears to be well adapted to the fruiting strategy of *Q. robur*. The normal life cycle of the insect takes two years, but about 10% of the larvae remain in the soil for a further year. No larvae were found entering a fourth year, but this may be an artifact of the small sample sizes involved. There is no reason to suppose that *C. glandium* is incapable of passing a third year as a larva, because other *Curculio* species can live up to five years in the larval stage (Gibson 1969, 1977). The sacrifice of current reproduction can be seen as a trade off between the mean and the variance of reproductive success in a temporally variable environment, because the geometric mean fitness of a phenotype is increased by reducing the variance in fitness over generations (Philippi and Seger, 1989). Many members of the genus *Curculio* appear to be doing just that, by ensuring that a proportion of their larvae remain in protracted dormancy as an insurance against seed crop failure that would lead to zero reproduction.

The question of oak regeneration in Britain has a long and controversial history (Watt 1919, Shaw 1968b, Piggot 1983). It is clear from my studies that, in Silwood Park at least, there is no problem of oak regeneration. On the contrary, major exercises in oak clearance need to be carried out every 10 years or so to prevent the grasslands from turning into woodlands, despite heavy grazing pressure from rabbits (M.J. Crawley, personal communication). It is likely that in areas where oak is failing to regenerate, the cause is over-grazing by domestic livestock (especially sheep). While I have documented a substantial impact of *Curculio glandium* predation on acorn survival, and this must be added to an even larger impact due to the knopper gall wasp *Andricus quercuscalicis* which kills 30 to 90% of the acorns in Silwood Park each year (Hails & Crawley 1991), it is difficult to argue that invertebrate seed predators have an important role in oak population dynamics. The pattern of alternate bearing ensures that predator satiation occurs every other year, and in these bumper acorn years oak recruitment is certainly not seed limited.

The fact that invertebrate herbivores do not have a pronounced effect on tree population dynamics does not mean that they are irrelevant in terms of plant evolution. This study has documented pronounced differences between individual trees in their rates of acorn production and in the susceptibility of their acorns to attack by seed predators. If, as seems likely, these differences prove to have a genetic basis, then differential seed mortality inflicted by insect seed predators could prove to be a vitally important agency of natural selection, influential in determining seed size, seed chemistry and the pattern of seed production.

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