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ASPECTS OF THE DISTRIBUTION  
AND ECOLOGY OF GALL WASPS  
(HYMENOPTERA: CYNIPIDAE)  
OCCURRING ON THE AERIAL PARTS  
OF THE BRITISH OAK SPECIES  
(QUERCUS ROBUR L., Q. PETRAEA  
(MATT.) LIEBL.) AND THEIR HYBRIDS  
(Q. x ROSACEA BECHST) WITH  
PARTICULAR REFERENCE TO  
NEUROTERUS SPP..

MARTIN, MICHAEL HENRY

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University of Plymouth

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ASPECTS OF THE DISTRIBUTION AND ECOLOGY OF GALL WASPS  
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(MATT.) LIEBL.) AND THEIR HYBRIDS (Q. x ROSACEA BECHST)  
WITH PARTICULAR REFERENCE TO NEUROTERUS SPP..

Thesis presented by

MICHAEL HENRY MARTIN

For the degree of Doctor of Philosophy  
of the Council for National Academic Awards.

School of Environmental Sciences  
Plymouth Polytechnic  
Plymouth  
Devon

February, 1980

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A B S T R A C T

Mature oaks covering the full range of the indigenous Quercus species, from the oak woods of Dartmoor and its periphery, were sampled each month during the growing season for the presence of cynipid oak galls. The distributions of galls within sites, within trees and within leaves were recorded, and an investigation into the factors which affect them was made.

The distributions of galls on oaks were found to be influenced by climatic and topographical factors as well as by the behaviour of the wasps and the taxonomic status of the host oak.

Oaks in exposed situations tended to host more species of gall causing wasps, in higher numbers than oaks in sheltered situations within the woodland canopies. In addition, Q.robur hosts harboured more gall species and larger numbers of an individual species than Q.petraea hosts. Oaks of introgressed hybrid status (Q.x rosacea) had gall populations ranging from levels less than were found for Q.petraea to levels higher than occurred on Q.robur.

Partitioning of gall species occurred both vertically and horizontally within the canopy, and within individual leaves.

Work on the ecologies of the gall causing wasps indicate that the adults may be able to distinguish between the indigenous oak taxa, when selecting suitable oviposition sites. Some gall species are solely restricted to Q.robur, a situation probably determined by some unidentified physiological property of Q.robur favourable to cynipid gall induction.

An investigation into the life cycle of Andricus quercuscalicis Burgsdorff, and its effects on the natural regeneration potential of oaks was also undertaken. Up to 100% of acorns on oaks infested by A.quercuscalicis may be galled, which has serious consequences on the subsequent germination potential of the acorns. Only one or two trees in a wood are infested by A.quercuscalicis in any year, and as long as this pattern exists it is not thought likely to pose a serious threat to the natural regeneration of oaks.

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CHAPTER 1.INTRODUCTION1:1 Nature of Galls

Plant galls are structures which result from the abnormal growth of the host plant tissue, in response to the release of chemical substances by the gall causing agent.

Galls may arise as a result of the release of chemicals from an attack on the host plant by a parasitic agent, which include Bacteria, Fungi , Nematodes, Acarines and Insects (Darlington, 1968: Swanton, 1912). The largest numbers of gall species are induced by insects; of these the Aphididae, Psyllidae, Cecidomyiidae and Cynipoidea are the most represented (Cook, 1904) although Lepidopteran and Coleopteran gall causers are also known (Darlington, 1968). Many authors (Cook, 1904; Swanton, 1912; Mani 1964, 1973; Darlington 1968) comprehensively list gall-causing organisms and where they occur.

The work presented in this thesis is restricted to the study of galls induced by cynipid gall wasps (Hymenoptera:Cynipidae) on the British indigenous oak species (Quercus robur L. and Q. petraea (Matt.) Liebl.) and their hybrids (Q.x rosacea Bechst.) Cook (1904) states that "the cynipidous galls are the most highly developed and show a greater number of morphological structures peculiar to themselves than any other group". Oaks host far more cynipid induced galls than any genus. Of all the known species of cynipid gall wasps, 86% cause galls on Quercus, whilst 7% are confined to hosts of the genus Rosa and 7% to hosts of 35 differing genera from monocotyledons to the highest composites (Kinsey, 1920).

## 1:2 Chemistry of gall induction.

The chemical substances released by the gall causer induce both hypertrophy (overgrowth) and hyperplasy (excessive cell division) in the host plant tissue (Mani, 1973; Darlington, 1968). The nature of the chemical substances which induce gall formation is not clear, and they probably vary from species to species. Several workers (Martin, 1938, 1942; Lewis and Walton, 1947; Leatherdale, 1955) have obtained abnormal growths in plant tissue by injecting chemical extracts from gall inducing insects. Martin (1938, 1942) induced galls in the stems of sugar canes by injecting whole insect extracts of adults of the green leafhopper (Draculacephala mollipes), the corn leafhopper (Perigrinus maidis) and the pink sugar cane mealybug (Trionymus sacchari). Attempts have been made to determine the chemical nature of the gall inducing secretions (McCalla et al, 1962; Pelet et al, 1960); McCalla et al (1962) conclude that different gall causing species utilise different substances to stimulate gall growth in plants, and further that it is an interaction of gall causer chemicals and host plant growth hormones that combine to bring about the formation of galls. The site of production of the gall causer chemicals in insects has not been located, although Beyerinck (1887) found that sawflies of the genus Pontania, inducing the formation of galls on willow (Salix spp.), initiate the stimulus for gall production by the release of a fluid, formed in an accessory gland, which is injected by the adult into the host tissue during oviposition. This mechanism is, however, exceptional, for with the majority of hymenopterous gall insects there is no proliferation of host plant tissue until after the emergence of the larva from the egg (Went, 1940). Rossig (1904) stated that he could trace the site of gall-causing substances to the malpighian tubules of the developing larvae,

though I have seen no other evidence in the literature to support this claim. It is clear from the literature cited that not much is known about the nature of gall inducing substances, and their site of origin. More recent work of Okabayashi et al. (1972) on the induction of callus tissue from gall tissue caused by gall wasps of Dryocosmus kuriphilis on chestnut trees (Fagales castanea = Castanea sativa Mill.?), has shown that kinetin and indole-3-acetic acid concentrations effect the growth of callus tissue induced from gall tissue, and suggest that gall material is largely brought about by the incomplete dedifferentiation of the host tissue. No attempt was made to isolate and identify the gall inducing chemicals which are released by the insect larvae.

### 1:3 Structure of Cynipid Oak Galls

Cynipid induced galls on oak exhibit a wide diversity of forms, each being specific to the species which induced it. Oak cynipid gall-causing species may, therefore, be readily identified from the gall structures which they induce. Cynipid galls which occur on the indigenous British oak species may be found in a number of different parts of the host tree; on the roots (eg. Biorhiza pallida Olivier, agamic generation\*, and Andricus rhizomae Htg., agamic generation), on the bark (eg. A. testaceipes Htg., agamic generation), on the catkins (eg. A. quercusramuli L., and Neuroterus quercusbaccarum L. sexual generations), in buds (eg A. kollari Htg. agamic generation, B. pallida sexual generation, and A. callidoma Htg., agamic generation), and on leaves (eg. N. quercusbaccarum, N. albipes Schenck, N. tricolor Htg., and N. numismalis Geof. in Fourc.). Full lists and descriptions of

\* The Cynipidae in common with some other members of the Hymenoptera exhibit an alternation of generations in their life cycles; this is discussed in more detail in section 5:1.



cynipid galls occurring on the indigenous British oak species are given in Connold (1908), Swanton (1912), Cameron (1893), Eady and Quinlan (1963) and Darlington (1968). Lists and descriptions of cynipid galls occurring on non-indigenous oak species are given in Mani (1964, 1973), Adler and Straton (1894), Brookfield (1972), and Rolfe (1881, 1883).

As Cameron (1889) states, the forms of galls are diverse and may be round, oval, spherical, lenticular, reniform or flat. There are also large variations in the texture of the galls, some being perfectly glabrous and soft whilst others are pilose. Attempts have been made to histologically classify the types of gall tissue (Adler and Straton, 1894; Cook 1902, 1904; Cosens, 1912), from studies of a wide range of plant genera. All show a similar differentiation of the plant tissue into three areas- (a) the epidermal, (b) the parenchymal, and (c) the nutritive regions. Often in addition a fourth area may be recognised - (d) the protective region. As Kinsey (1920) points out "although all cynipid galls are formed fundamentally on the same pattern, the developments of that pattern are surely much more complex in certain cases than in others". Although outside the principal object of my work, histological and genetic work on the structure of galls would go far in answering certain questions about the co-evolution of the oak-cynipid gall complex. For example by what mechanism does the host Q. robur produce galls induced by the sexual generation of N. tricolor, which are pilose, when the host tissue is perfectly glabrous? And does the morphological character of the galls depend on the insect inducing it, as Cook (1904) states, or on the host on which it is induced?

#### 1:4 Gall evolution and the alternation of generations

An outline of the phylogeny of the zooecidia is given in Wells (1921) which goes far in answering questions on the structure of galls. Mamaev (1975) has comprehensively covered the evolutionary paths of the gall-causing insects.

The early work of Bassett (1873), Riley (1873), Adler (1881) and Adler and Straton (1894) went far in elucidating the alternation of generations displayed by some members of the Cynipidae. The more recent work of Peacock and Gresson (1931), Doutt (1959, 1960), Maynard-Smith (1968) Rosenthal and Koehler (1971a) and Slobodchikoff and Daly (1971) has further clarified the understanding of the phenomenon of alternating generations, and its evolutionary implications. It has been shown (Doncaster, 1910, 1911, 1916) that individual agamic females of N. lenticularis Oliv. (= N. quercusbaccarum L.) produce eggs which give rise to males or females, but never both. In contrast to this some species of the genus Andricus produce eggs which give rise to both males and females, from an individual agamic female (Patterson, 1928). Further it appears that some cynipids have lost the sexual generation, or rely on it very rarely (Wilkes, 1964; Patterson, 1928).

Slobodchikoff and Daly (1971) point out that arrhenotoky and the haplo-diploid system confers a considerable advantage upon the Hymenoptera; the advantages of diploidy are that it offers protection against the affects of somatic mutations, and confers heterozygosity and recombination, if the average fitness of the diploid population is greater than that of the haploid. A disadvantage is of bearing a greater genetic load (i.e. it allows recessive lethal mutations to accumulate in the population). And since all hymenopteran

males are genetically haploid, recessive lethal mutations cannot accumulate in the population. The genetic load in the males is reduced to a very low level, so while the females possess the advantages of diploidy any disadvantages are obviated by the males.

#### 1:5 Man as an agent of gall dispersal

Man by making use of certain insect induced plant galls has inevitably acted as an agent in their dispersal. Fagan (1918), in her review on the uses of insect galls from historical to more recent times, mentions that in the time of ancient Greece galls were used as a fuel which burnt without oil in lamps, as various medicinal cures and for making prophesies of the future. During the 18th and 19th centuries galls were of great importance in the manufacture of drugs, and up until the early 20th. century in the tanning and dyeing industries and in manufacture of inks.

D'Urban (1862, 1863) lists the English galls used in the manufacture of inks. The uses of galls by man would have inevitably resulted in their spread from one area to another. It is of interest to note that it is the gall containing the developing larva or pupa that is dispersed by man and not the adult insect, which is the natural agent of dispersal. The Devonshire or Marble gall A. kollari, is just such a case. Marble galls were introduced into Britain in the early 19th century for probable use in the cloth dyeing industry associated with Exeter and its environs. Marsden-Jones (1953), mentions that the Aleppo gall (Cynips tinctoria Mayr.) was imported for use in the dyeing industry in the early 19th century and that it seems likely that Marble galls were imported either accidentally or for experimental purposes at the same time. It seems unlikely that

galls of A. kollari had much commercial value as they contain only about 17% tannic acid compared to over 50% for C. tinctoria.

Today cynipid oak galls have no economic value in the manufacturing industries. A. quercuscalicis Burgsdorff, may have some effect on the regeneration potential of infested oaks, and bud galls like A. kollari may induce stunted oaks due to the galling of terminal buds. The effects and importance of A. quercuscalicis are discussed in section 4:4.

#### 1:6 The distribution of cynipid oak galls.

Much work has been carried out on the life-histories and the descriptions of cynipid gall-causing wasps (Cameron, 1893; Adler and Straton, 1894; Swanton, 1912; Bassett, 1873; Ashmead, 1903). However, relatively little work has been carried out on the geographical and ecological distributions of galls and the causes of such distributions that occur. The work presented in this thesis seeks to quantify gall distributions between sites, within sites and within trees, and in relation to the taxonomic status of the host oak.

##### 1:6:1 Within-tree distributions

Hough (1953, A.B.C.) looked at the within-leaf distributions of the agamic generation galls of N. quercusbaccarum. Askew (1962) extended this work (although at the time was not aware of Hough's publications) by investigating within-leaf and within-tree distributions, of the four species of Neuroterus which occur in Britain. The sample trees used in his work were young oaks (mainly Q. robur with some Q. petraea) with an average height of about 10 feet (3 metres). No work had been undertaken on the gall distributions on mature oaks and the way that they vary from site to site and between hosts of differing taxonomic status. Further, although several species of galls' life histories and economies had been investigated in detail (Blair, 1945;

Marsden-Jones, 1953; Askew, 1961; Duffet, 1969; Brookfield, 1972), apart from Hough (1953,A,B,C.) and Askew (1962) in Britain, and Rosenthal and Koehler (1971B) working on the inter-tree distributions of galls on Q. lobata in the U.S.A., no work had been done on the within and between-tree distributions of oak gall causing cynipids.

It has been stated (Connold, 1908; Swanton, 1912; Adler and Straton, 1894; Eady and Quinlan, 1963) that a number of species of cynipid oak galls occur on both the indigenous species of British oak (Q. robur and Q. petraea). Rolfe (1883, 1881) names a wide range of oak taxa which were infested by cynipid galls at Kew.

In order to discover if the distributions of cynipid oak galls in Britain may be related to the available host taxa, or if any preferential galling of one host occurs, it was decided to attempt to quantify differences in the degree of infestation, and the distributions, between the two indigenous British oak species.

#### 1:7 Taxonomy of the British oaks, Q.robur and Q.petraea.

In the British oak species there is a high degree of taxonomic character overlap, and as Carlisle and Brown (1965) point out this has in the past led to confusion in the identification of these species. The work of Jones (1959) and Cousens (1962) clarified the morphological differences between the two species, and the quantitative assessment of their taxonomic characters was extended by Carlisle and Brown (1965). In the South West of England the status of the oakwoods was further clarified by Wigston (1974, 1975) and his technique of analysis to determine the taxonomic status of the host has been used in this work (See section 2:1).

#### 1:8 Galling on exposed oaks

In addition to possible preferential galling of different oak taxa

by cynipid gall wasps, it had been noticed (Askew, 1961; Frankie personal communication) that isolated oaks in exposed places often tended to be more heavily infested with galls than similar, but less exposed oaks. In order to quantify any differences in the degree of infestation between oaks in varying site conditions, in this investigation sample oaks were chosen which were deemed representative of different site conditions and growth forms. These trees were then regularly sampled during 1976 and 1977.

#### 1:9 Andricus quercuscalicis Burgsdorff

An additional aspect of the work herein presented is the study of the distribution and ecology of the acorn knopper gall A. quercuscalicis. The first confirmed reporting of the presence of this gall in Britain was made by Claridge (1962), who found specimens of knopper galls on Q. robur at Salcey forest, Northamptonshire, in 1961. Connold (1908) stated that A. quercuscalicis was present in Jersey in some abundance at that time, but that it had not been found to occur in mainland Britain. However, there is evidence (Cobb, 1972) that A. quercuscalicis was present at Cromer, Norfolk, in the 1920's and at Charmouth, Dorset, in 1935. In view of the rapid spread and the large numbers in which it occurs in widely distributed sites, it may be possible that its presence in mainland Britain has been somewhat longer than is suggested by Claridge (1962). No parasites have been named as emerging from galls of A. quercuscalicis in mainland Britain, although Cobb (1971) mentions that he found a gall specimen from Wooton Woods, near Kings Lynn, with the remains of a hymenopterous parasite in it. The galls of A. quercuscalicis are stated as occurring on the cupules of acorns (Claridge, 1962) though in this work they have also been found on the acorns themselves.

In view of this it was decided to investigate whether the galling of acorns interferes with acorn germination, which may, therefore, affect the regeneration potential of oaks in woodlands. Watt (1919) and Shaw (1968) discuss the factors affecting natural regeneration of oak in British woodland, which are largely to do with pressures of grazing on seedlings and the consumption of acorns by birds and small mammals.

## CHAPTER 2

### MATERIALS AND METHODS

#### 2:1 Identification of Oaks by the analysis of Leaf Morphometrics

The two Oak species indigenous to the British Isles, Quercus robur L. and Q. petraea (Matt.) Liebl., can be separated and possible intermediate status recognised on the basis of leaf character (Wigston 1975). The technique requires the measurement of 2 leaf characters, petiole percentage and the leaf shape index, and the observation of 5 qualitative characters.

##### 2:1:1 Quantitative Characters.

(a) Petiole Percentage is the expression of the length of the petiole as a percentage of the total length of the leaf (lamina + petiole).

(b) Leaf shape index is an expression of the relative Ovateness to Obovateness of the leaf, and is calculated from the formula

$$\frac{W3 - W1}{W2}$$

Where W1, W2 and W3 are the widths of the lamina at points along its length of a quarter, half and threequarters respectively.

The values gained for petiole percentage and leaf shape index for individual leaves can be plotted as a point on a graph, with the values being the co-ordinates of the point. The distribution of a number of such points from a population gives a scatter diagram (Fig. 1).

##### 2:1:2 Qualitative Characters

The qualitative characters used in the analysis are scored as being either a Q. robur character or a Q. petraea character, or as is the case with three of the characters they may be scored as being of intermediate



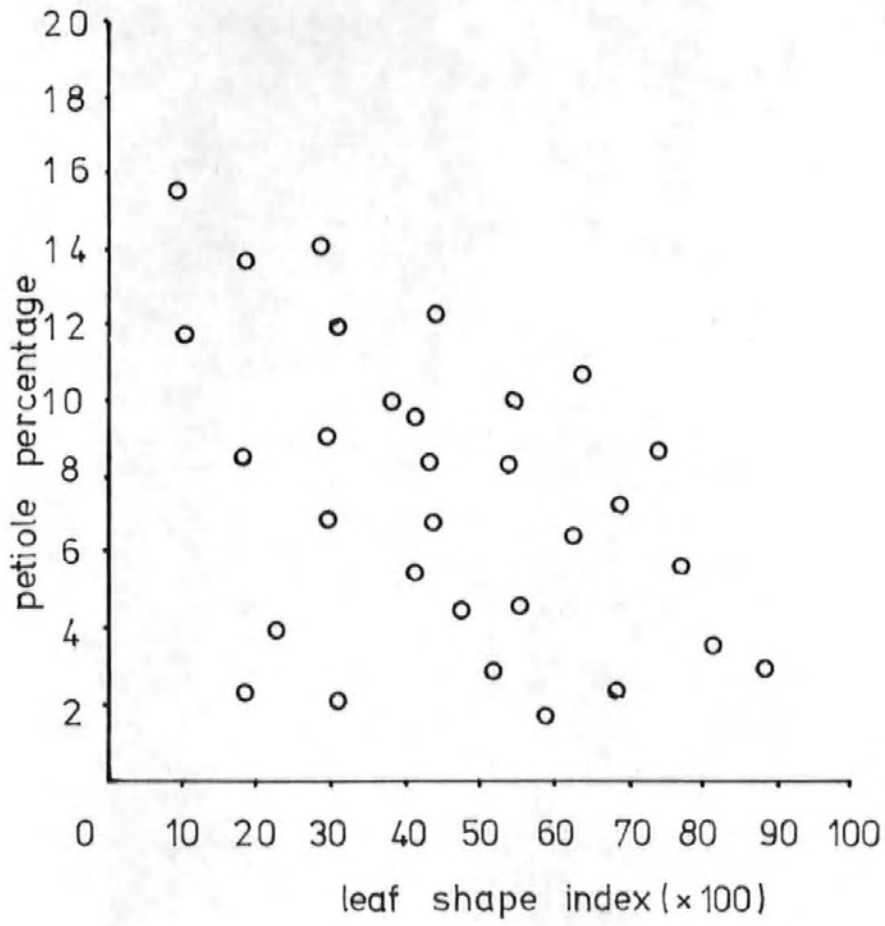


Figure 1. Scatter diagram for leaf morphometric analysis. (Data hypothetical).

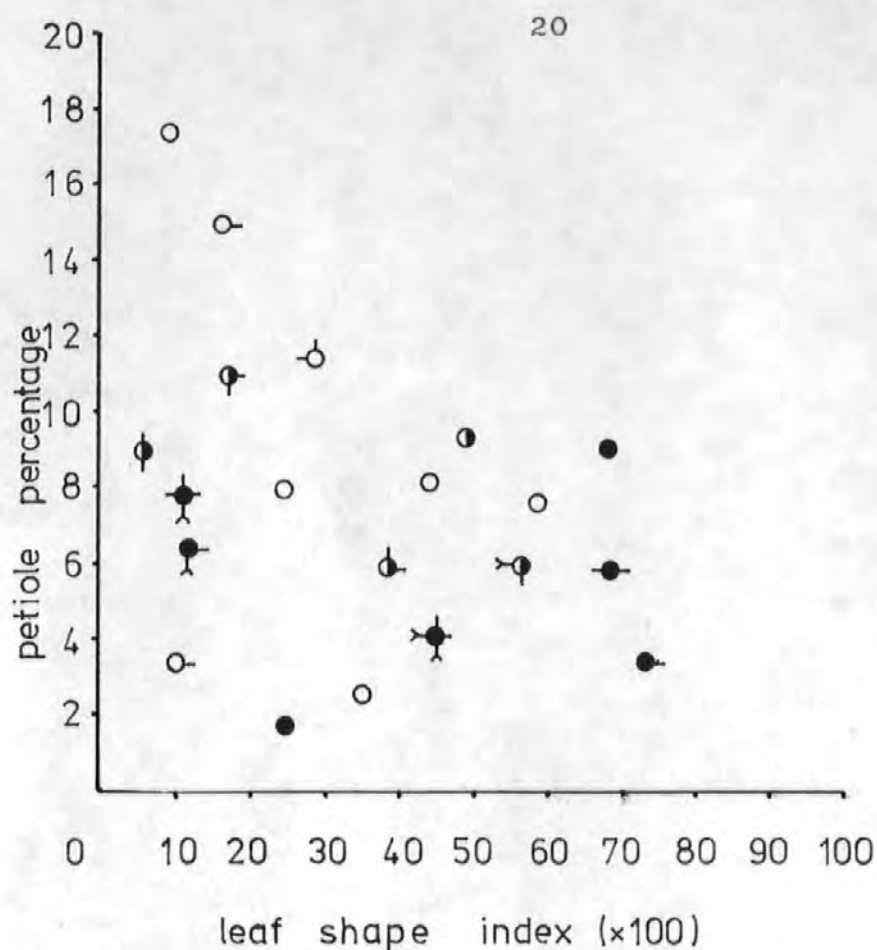


Figure 2. Pictorialised scatter diagram (PSD) of leaf morphometrics. (Data hypothetical to show all characters).

status. The scoring of these characters is summarised in Fig. 2 , from which it can be seen that each character is assigned a symbol, which when added to a point on the scatter diagram pictorialises it so forming a pictorialised scatter diagram (PSD). Pure Q. petraea is represented as an open circle, whilst Q. robur is represented as a filled circle adorned with symbols. This gives a clear visual separation of the species when the points are plotted as a PSD (Fig. 2). Leaves which have a high petiole percentage and a low value for leaf shape index are indicative of Q. petraea, whilst those with a low petiole percentage and high leaf shape index are indicative of Q. robur.

In order to determine the taxonomic status of the sample trees, 25 leaves from each of the sample trees were collected and analysed in this way. PSD's for each of the leaf samples were plotted which gave a quick visual assessment of the taxonomic status of the host tree. Combination class analysis of the secondary (qualitative) characters was used to determine whether any variability that occurred from the 'theoretical species type' (TST) was due <sup>to</sup> intraspecific variability or to hybridisation (Cousens, 1963, 1965; Wigston, 1974). From the use of these techniques an accurate assessment of the taxonomic status of each of the sample trees was made.

## 2:2 Sampling for the occurrence of gall species

Sampling for the occurrence of gall species on the full range of hosts of the British Oak taxa, was carried out along three transects. Two of the transects were through Yarner Wood National Nature Reserve in the Bovey valley (section 3:2:2). Transects were sampled from East to West and North to South across the reserve, using as guides the transect posts which are permanently positioned in the reserve at 50 metre

intervals. The tree nearest to each post along the two chosen transects were qualitatively sampled for the presence of cynipid oak galls each month. An estimate of the number of galls present, and the percentage of leaves galled, was gained from a random collection of a sample of 200 leaves from the lower 4 metres of each of the sample trees. Although both these transects through Yarner Wood were 'within site' they covered the full range of the host taxa from Q. robur through hybrids to Q. petraea, enabling gall occurrence patterns to be readily assessed between the different oak hosts without being biased by any substantial differences in the environmental conditions.

The third transect sampled covered a range of altitudes following a Q.robur - hybrid - Q. petraea pattern, as in Yarner Wood. Site 1 was taken as Wistmans Wood (section 3:3:1:1) which was also a quantitative sampling site. The other 10 sites along the transect all occurred along the valley systems of the River Walkham and the R. Tavy, from Heckwood to the estuary of the R. Tamar (see section 3:2:1). The transect was sampled monthly for the occurrence of gall species. An estimate of the percentage number of leaves galled and the numbers of galls occurring was obtained by taking a sample of approximately 200 leaves from the entire canopy of the sample trees. The presence of gall species other than those that occur on leaves were also noted. All the trees were either sampled manually from the ground or with the use of 3 metre pole pruners and by climbing, in order to secure a varied leaf sample from within the entire canopy.

In addition to the transect sampling for the occurrence of gall species, the presence of galls on any other oaks in South West Devon and East Cornwall were recorded in order to:-

(a) allow the spread of the Knopper gall Andricus quercuscalicis Burgsdorff , to be monitored.

(b) use the data collected to compile distribution maps of cynipid oak galls.

#### 2:3:0 Sampling for the spatial distributions of galls.

At four of the six quantitative sample sites two trees were chosen as being physiognomically typical of the site (see section 3:3:0).

One tree was within the canopy of the wood and the other was in a more exposed<sup>situation</sup> at the edge of the wood (see sections 3:3. 1:1, 3:3: 1:2, 3:3:1:3, 3:3:3:0). At the other two quantitative sites the oaks were widely spaced in an open situation and only one tree was sampled at each site (sections 3:3:2:1, 3:3:2:2).

The sampling routine followed allowed:- (a) a statistical analysis of gall numbers to be made, and their within leaf and within tree distributions to be readily recorded: and (b) galls whose growth rates were being monitored to be readily relocated within the canopy. Initially the random sampling of leaf bearing twigs was undertaken, but due to the inevitable variation in the size of the sample, an attempt was made to standardise the sampling. This was done by taking the measurements of a large number of twigs which would yield approximately 10 leaves/twig, in either a whorled or alternate arrangement. The lengths determined from these measurements were a twig length of 10 cm for twigs with an alternate leaf arrangement, and a twig length of 5.2cm for twigs with a whorled leaf arrangement. It was felt that by doing this field sampling would be facilitated, and that it would ensure that approximately equal numbers of leaves would be sampled from tree to tree. With the use of a rule twigs of these lengths were collected

and their positions recorded by three spatial parameters (Fig. 3):-

- (a) Aspect. This was measured in degrees with the use of a sighting compass.
- (b) The distance that the twig occurred away from the bole, measured in metres.
- (c) The height above the ground (taken from the base of the bole) also measured in metres.

The twigs collected were then assigned a sample number and taken to the Laboratory to record which gall species occurred, their numbers and their positions on the lamina. This was readily done for sample twigs having 10 or fewer leaves, but in the case of twigs with more than 10 leaves, only the galls on the apical 10 leaves were recorded. Each leaf was assigned a number from 1 (basal leaf of sample) to 10 (apical leaf) (Fig. 4). Information relating to species, numbers and the positions of the galls was recorded on prepared forms designed to facilitate subsequent data handling. Bud, bark and catkin galls were also recorded when encountered near the sample points in the canopy.

Each tree was sampled monthly during 1976 but in 1977 due to the extreme rarity of galls, sampling was only undertaken four times during the season from leaf burst to leaf fall. Because of the conspicuous nature of galls this sampling regime allowed changes in gall numbers, growth and predation rates, and species composition to be readily monitored. Any gall material which was brought to the Laboratory, in order to rear out occupants, was prepared as described in section 2:5.

In the seasons 1976 and 1977 systematic sampling of twigs within the canopies of the oaks was adopted in place of the previous random approach. Systematic recording involved the collection of a sample every metre along the branches. The heights and the aspect were recorded

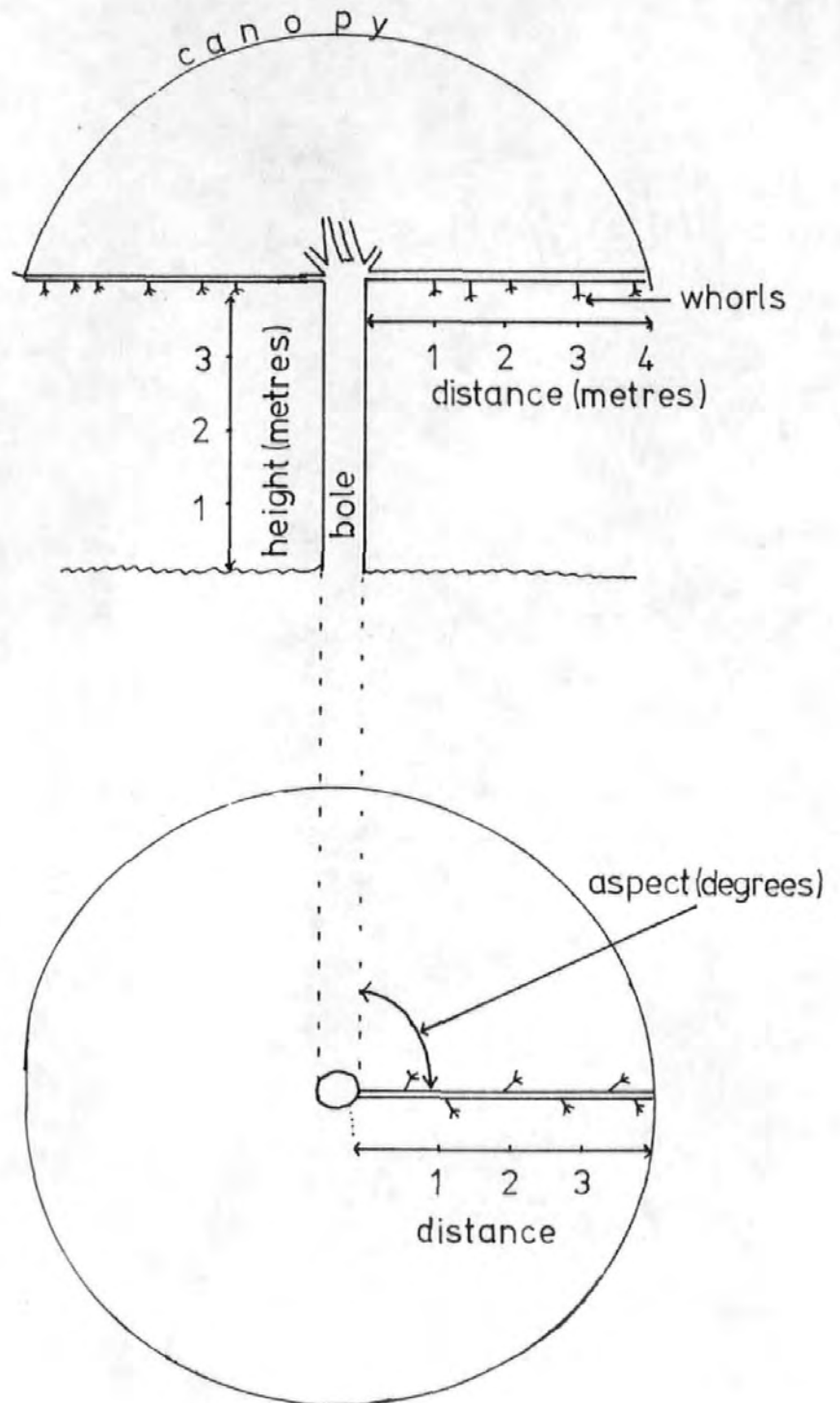


Figure 3. Diagram to show the measurements recorded during the within-tree sampling. (Aspect, height and distance).

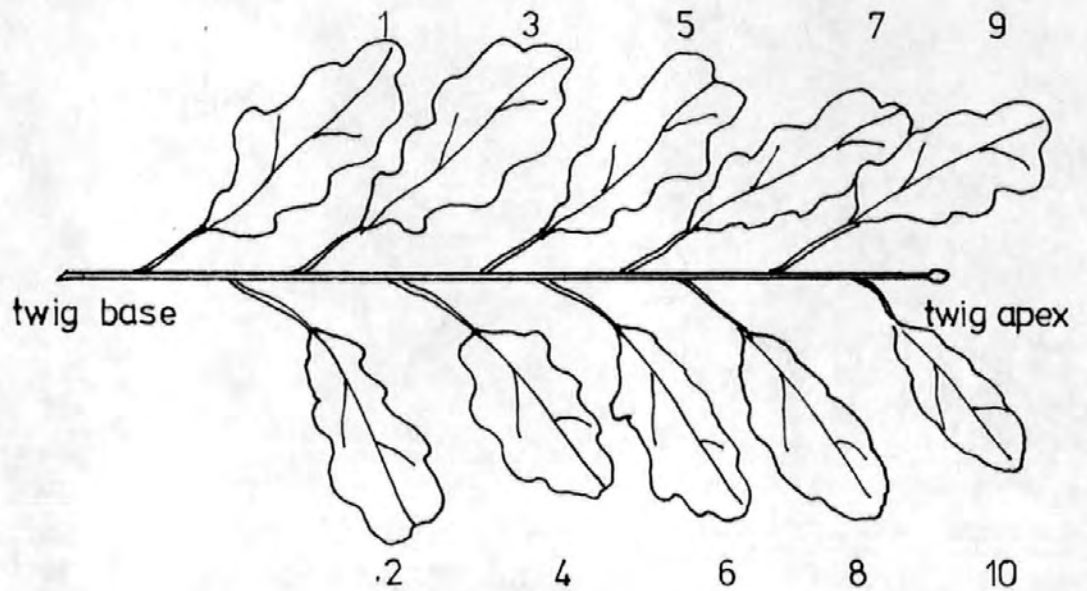


Figure 4. Diagram of a sample unit of 10 leaves.

(Leaf No.1 basal leaf - leaf No.10 apical leaf).



as described earlier in this section. Because of the variability of the arrangement of twigs along branches, twigs which occurred nearest to the metre mark were used, and their distance from the bole recorded. Once this recording method was adopted, all the recording was undertaken in the field, eliminating the need to transport large amounts of foliage and gall material to the Laboratory, which would have been prejudicial to the recording of changes in gall composition.

#### 2:4:0 Procedures for handling data on Spatial Distributions

All the raw field data for the within tree distributions of each gall species was subjected to an initial analysis in order to obtain seven sets of results:-

- (1) Number of leaves present in each of the groups 1 - 10.  
(basal to apical leaves).
- (2) Mean number of galls/leaf for each of the groups 1 - 10.
- (3) The variances for (2).
- (4) The total number of galls/sample routine, for each tree each month.
- (5) The mean number of galls/total leaf sample, and its variance for each tree/month.
- (6) The percentage of leaves galled.
- (7) The frequency distribution of numbers of galls/leaf.

This analysis was carried out on the data for Neuroterus quercusbaccarum L., which was the most abundant species of gall found, using a computer programme written in Algol (Appendix A), which was run using the ICL 1905 computer at Plymouth Polytechnic. All the field data for the within tree distributions of both generations of N. quercusbaccarum were punched onto computer data cards using the format given in Appendix A. Each sub-sample of 10 leaves was given a unique sample number facilitating information retrieval.

The data for all the other species which had been recorded during the spatial distribution sampling routine were analysed in a similar way. However it was not necessary to use the computer for these data, since in comparison with N. quercusbaccarum, low numbers were recorded and the time that would have been required to punch the cards was excessive in relation to the task at hand.

The second stage of the analysis was to calculate the variance/mean ratios giving an estimate of the degree of aggregation of each gall species (Southwood, 1966). The numbers of leaves with two or more species of galls and their relative positions on the leaves were then tabulated from the information stored on the field data sheets. Each leaf was divided into three sections along the length of the lamina, and the positions of the galls noted. Although each third of the lamina are not equal in area, an estimate of the relative distributions of the galls which occur is obtained (Refer to Askew, 1962; Hough 1953C).

From the information on the distributions and the occurrence of the differing gall species, it was then possible to calculate the degree of association between species using Jaccard's coefficient (Sokal & Sneath, 1963; Southwood, 1966).

Dendrograms of association were produced by single link cluster analysis (Everitt 1974; Cody, 1974). This is an agglomerative, hierarchical technique which proceeds by a series of successive fusions of the entities (gall species) into groups, from an association coefficient matrix. The clustering of sites was also undertaken to determine if any positive associations existed between them.

## 2:5 Methods of rearing Gall wasps, Inquilines and Parasites

Many species of galls were collected from a range of sites in South Devon and East Cornwall, as well as from other parts of the British Isles. Examples of those species which have soft gall tissue were placed in

specimen bottles on dampened blotting paper, and the lids were replaced with pieces of fine nylon gauze held in place by elastic bands (Darlington, 1968). On emergence the insects were preserved in 70% alcohol, prior to subsequent identification. In some cases the developing larvae were dissected out of the galls, in order to identify which part of the gall they were occupying and to make a preliminary assessment of their likely roles. Galls having a hard woody tissue were reared in a similar manner except that they were not placed on damp blotting paper. By the use of these techniques it was possible to rear gall occupants successfully from the majority of cynipid oak galls encountered in this work. Problems with mould growth occurred however on the agamic spangle galls of Neuroterus spp., and the rearing of agamic female adults was unsuccessful. An emergence technique involving the dissecting out of the agamic female larvae from the spangle galls of Neuroterus spp. and placing them in gelatin capsules (Shorthouse 1972) was tried for a number of individuals, but all failed to develop into adults. The timing of gall collection and the storage prior to dissection is probably very critical, especially if dessication occurs. The failure in this case is possibly due to the larvae being dissected out at too early a stage in their development. The sexual generation adults of Neuroterus spp., were readily reared as were their inquelines and parasites, by placing the galls on dampened blotting paper in mesh covered vials. By maintaining the rearing vials at room temperature the emergence of the adult insects was accelerated. In order to achieve a rate of development compatible with that which occurs under natural conditions, some galls were kept in mesh covered cylinders made of 'Miracloth' (Calbiochem) which were placed on trays in the open air.

Miracloth was chosen as it allows a free flow of air and moisture to the gall whilst avoiding any waterlogging which would have occurred if glass chambers were used. Once the adults had emerged from the galls they could be readily seen through the mesh covers of the vials, facilitating their collection.

### CHAPTER 3

#### DESCRIPTIONS OF SAMPLE SITES

##### 3:1 Introduction

All the sites used for the regular sampling of Cynipid oak galls were chosen from the oakwoods of Dartmoor and its periphery. The quantitative and qualitative sites were chosen to ensure that the full range of host taxa were sampled.

##### 3:2 Qualitative sampling sites

All the qualitative sites sampled lay along one of three transects, two of which were in Yarner Wood National Nature Reserve (within wood transects) whilst the third was along the River Walkham, R. Tavy valley systems (between wood transect).

##### 3:2:1 The River Walkham and River Tavy valley systems

Ten sample sites were regularly visited along the Walkham-Tavy system, from Heckwood (SX 545737) on Dartmoor to the Warleigh Wood Nature Reserve (SX 447608) on the banks of the estuary of the River Tamar (Fig. 5). The sites cover the full range of the indigenous oak taxa (Wigston 1971, 1974) with Q. robur at Heckwood, hybrids at intervening stations and Q. petraea at Warleigh wood. Wistmans wood, a high altitude Q. robur site on Dartmoor (section 3:3:1:1), was effectively regarded as part of this transect as well as being a quantitative site.

##### 3:2:1:2 Heckwood GR, SX 545737 (Q. robur)

This is the second highest site after Wistmans wood, and is at an altitude of 225 metres. Periodic coppicing has taken place at Heckwood, but from its irregularity it appears to have been done in order to obtain firewood, rather than as a part of a formal management policy.



Figure 5 .Sketch map of the Walkham and Tavy valleys showing the transect sample sites. (Scale: approx.  $2\frac{1}{2}$  miles to the inch).

- Legend:
- |                    |                   |
|--------------------|-------------------|
| 1. Heckwood.       | 6. Double waters  |
| 2. Ward Bridge     | 7. Denham Bridge  |
| 3. Dittisham.      | 8. Lopwell Dam.   |
| 4. Bedford Bridge. | 9. Blaxton Wood.  |
| 5. Grenofen.       | 10. Warleigh Wood |

The trees occur on granite clitter, and their form is tending towards a clitter oakwood, not dissimilar from Wistmans wood (section 3:3:1:1), Piles copse (3:3:1:2) and Ausewell Rocks which is a Q. petraea site (3:3:3:1).

3:2:1:3 Ward Bridge GR.SX 542721 (Q. robur).

The sample tree was a mature isolated oak standing on the bank of the River Walkham. It has been pollarded at regular intervals in the past, probably to prevent its branches from overhanging the road. The immediate area surrounding the tree has been highly modified with the planting of Cherry Laurel Prunus laurocerasus L. and Rhododendron spp., probably as an amenity feature connected with Eggworthy House which stands nearby. Originally the area would have been clitter Oakwood, but local clearing has occurred with the subsequent planting of Beech Fagus sylvatica L., Larch Larix decidua Miller and Sitka spruce Picea sitchensis Bong.

3:2:1:4 Dittisham GR.SX 538708 (Q. robur).

This site lies on a substratum of metamorphic aureolic clitter, in contrast to the granite clitter of the Heckwood and Ward Bridge sites. The wood in which the sample tree stands consists of mature Oak standards with Hazel Corylus avellana L. coppice, into which have been introduced Sweet Chestnut Castanea sativa Miller and Beech F. sylvatica. The sample tree was a tall, low branching mature Q. robur.

3:2:1:5 Bedford Bridge GR.SX 504703 (hybrid).

The sample tree was a mature, low branching Oak, standing on the edge of an old water meadow of waterlogged peat. It was one of several isolated trees and was surrounded by Hawthorn Crataegus monogyna Jacq. and Gorse Ulex europeaus L. scrub. Before the sites' current use as a picnic area open grazing took place, the trees exhibiting the classical cut-off canopy shape due to undergrazing.

3:2:1:6 Grenofen Weir. GR.SX 489708 (hybrid).

The sample tree at this site was a mature Oak with a high crown and some low lateral branching. It stands on a flood plain of the R. Walkham. The surrounding wood consists of mature trees which show no evidence of recent coppicing. A few exotic species of tree have also been planted in the past. The understorey is generally poor which is probably due to disturbance as the site is a popular picnic area. A recently felled stump (1977) was estimated as being 84 years old and was typical of the standing trees.

3:2:1:7 Double Waters. GR.SX 473697 (hybrid).

The sample tree was coppiced and stands on a bank associated with tailings from an old mine. The wood consists of a mixture of tall standard Oaks, and clitter forms which occur on the mine tailings. The wood displays a varied age structure and different growth forms. The understorey of the sample tree was very poor and confined to some moss and lichen, this was probably due to the nature of the old mine tailings.

3:2:1:8 Denham Bridge. GR.SX 478678 (hybrid).

The sample tree occurs in an area of mixed oak coppice, in which the last coppicing occurred about 15 - 20 years ago. The tree chosen at this site is atypical in that it was a young maiden oak with low branching. The tree stands on the bank of the River Tavy and has a dense undergrowth of brambles Rubus fruticosus L.agg.

3:2:1:9 Lopwell Dam. GR.SX 473651 (Q.petraea).

The sample tree is a standard Oak growing on a bank associated with an old hedge; it displays no evidence of having been stored up and is



therefore not derived from coppice. Cherry laurel, P. laurocerasus, and other exotic species are also present and were probably planted as an amenity feature for nearby Maristow House. Beech, F. sylvatica, has also been planted amongst the Oak standards.

3:2:1:10 Blaxton Wood GR.SX 472637 (Q. petraea).

The sample tree is a standard Oak growing on the edge of the Tamar estuary; it shows no evidence of having been stored up and is not of coppice origin. The wood has a very varied age structure and all the characteristics of a natural Oakwood, with a species-rich understorey and ground flora. If the wood has ever been managed it has only been on a very small scale and must have taken place some considerable time ago.

3:2:1:11 Warleigh Wood Nature Reserve GR.SX 449608 (Q. petraea).

The sample tree is a standard along the edge of the main ride, adjacent to an area which is actively coppiced as part of a conservation-coppicing management plan. The soil of the reserve consists of acid Brown Earths over a mass of slate and shale. The sample trees at this site is a mature standard Q. petraea.

Pictorialised scatter diagrams plotted from the analysis of the leaf morphometrics of sample trees in the Walkham/Tavy transect are given in Appendix B.

3:2:2 Yarner Wood National Nature Reserve GR.SX 780780

(Within Wood transects)

Yarner Wood N.N.R. is an example of mixed Oak woodland, which has a long history of management. It is situated adjacent to the valley of the River Bovey, and lies on the eastern periphery of the Dartmoor National Park. The reserve is situated on rocks of carboniferous age called the Culm Measures, which consist mainly of slates, shales,

coarse grits and lignite. There is some granite clitter towards the west end of the reserve as well as some areas of metamorphic aureole.

Today the reserve is managed with the principal long term objective of developing and maintaining a diverse woodland of mainly indigenous species, which would be comparable to that which might have occupied the site in the absence of serious intervention by man (Archibald 1976).

Two transects were sampled regularly for the occurrence of Oak galls across Yarner Wood. One transect running South-North across the reserve, whilst the other ran from West-East following the path taken by a small stream, the Woodcock, lying to the North of the central ridge (Fig. 6).

Although the Oak population of Yarner Wood is predominately Quercus petraea, both transects included specimens of Q. robur as well as Oaks of hybrid status Q.x rosacea. This allowed a within site comparison of Oak gall distributions between the different indigenous Oak taxa to be made. Scatter diagrams from the leaf analysis of the sample trees for Yarner Wood are given in Appendix C.

### 3:3 Quantitative Sampling Sites

#### Introduction

Sites for the quantitative sampling of the within tree distributions of Cynipid Oak galls, were chosen to cover the full range of the indigenous Oak taxa. All the sites were chosen from the Oakwoods of Dartmoor and the surrounding area. Six sampling sites were chosen, consisting of three Q.robur sites, two sites of intermediate status, and one Q. petraea site. At each of these sites with the exception of the two sites of intermediate status, two trees, one exposed and one sheltered, were sampled quantitatively each month for the occurrence and distributions of gall species within the canopy. At the sites of intermediate status, Roborough Down and Meavy, only one tree was sampled as all the trees were considered to be

Figure 6. Map of Yarner Wood National  
Nature Reserve, showing the  
transects sampled.  
(TG transect South - North;  
TN-TB transect West-East).

-  Oak forest, with Bilberry, etc.
-  Oak coppice or scrub
-  Birch, with Bracken, etc.
-  Conifers, pre-N.N.R.
-  Hardwood plantations, since 1955
-  Carr woodland
-  Heathland
-  Valley Bog
-  Fire breaks

x: hybrid  
 ⊙: Q. petraea  
 Δ: Q. robur

YARNER WOOD N.N.R.  
 MANAGEMENT PLAN, 1974

# VEGETATION

0 Metres  
 0 Yards

quite exposed and none to be in sheltered positions. The reason why both sheltered and exposed trees were sampled was because it was noticed during the preliminary survey that exposed, solitary oaks tended to be more heavily infested with galls than those in more sheltered situations. It was therefore necessary that both exposed and sheltered trees were sampled in order to determine whether any differences in gall distributions and numbers, was due to the status of the host, or whether it was due to a purely physical factor such as being in direct exposure to the prevailing winds, which play a part in the transporting of the gall wasps. Other workers (Askew 1962, Hough 1953C) have also made mention that young scrub Oak bushes were usually more heavily galled than mature oaks. Frankie (personal communication) reported heavier infestations of galls on isolated oaks occurring in urban environments in Texas, than was found in woodland situations. In order to attempt to even out the effects of exposure and the age of host trees, and to discover the effects of gall distributions due to the taxonomic status of the hosts, young and mature oaks from exposed and sheltered situations were sampled both qualitatively and quantitatively.

### 3:3:1 Quantitative *Quercus robur* sites

The three *Q. robur* sites chosen were (a) Wistman's Wood.

(b) Piles copse.

(c) Harford.

#### 3:3:1:1 Wistman's Wood GR.SX 613771

Wistman's Wood is a high altitude (405m) *Q. robur* site which is situated on the west facing side of the West Dart valley (Plate 1). The wood is typical of the high altitude granite clitter woods of Dartmoor and its trees exhibit two forms; stunted forms in the exposed wood margins, and taller, straighter forms in the more sheltered positions (Tansley 1939).

Plate 1. General view of Wistmans Wood  
from the south.





Two sample trees were chosen at Wistman's Wood, one from within the wood canopy (Plate 2) of the South wood (sheltered position), and the other an isolated oak to the south of the south wood (exposed position). The form of the wood is similar to that of Piles Copse, but due to greater effects of exposure the growth forms at Wistman's Wood are generally more stunted and disturbed.

### 3:3:1:2 Piles Copse. GR.SX 645620

Piles Copse is a high altitude (300m) Q.robur wood growing on granite clitter. It is situated on the west facing side of the valley of the River Erme (Plate 3), in a position comparable to that of Wistman's Wood. In the more exposed parts of the wood and on the granite clitter the oaks in their form resemble those which occur at Wistman's Wood (section 3:3:1:1) and Ausewell Rocks (section 3:3:3 ), but in the areas bordering on the river the oaks are quite tall and straight in their growth with very little low lateral branching (Plate 4). At Piles Copse two trees were sampled quantitatively each month; in an exposed situation just to the south of the main wood, and the other from a sheltered situation within the canopy.

The understorey at Piles Copse is regularly grazed by sheep, ponies and cattle and has little diversity, consisting mainly of a grass sward with some bracken Pteridium aquilinum (L) Kuhn and Bilberry Vaccinium myrtillus L.

### 3:3:1:3 Harford GR.SX 627603

The site at Harford is situated at 195 metres. It is a Q.robur site containing mature oaks with low canopies some of which display evidence of having been wind cut (Plate 5). Historically the site was agricultural, used as rough grazing, and the trees form part of the



Plate 2. Within the canopy of Wistmans Wood.

(Note stunted growth forms of oaks,  
and the clutter boulders).



Plate 3. General view of higher Piles Copse  
from the south.



Plate 4. Within the canopy of higher Piles Copse.





Plate 5. General view of the Harford sample site.





old field boundaries, with the occasional 'Parkland' tree situated in the middle of the old fields. The site has now been fenced off and secondary succession is occurring as a result of the elimination of grazing pressure. Two trees were quantitatively sampled each month. Both the sample trees were in quite exposed situations, and were associated with an old bank separating two fields.

The understorey of the site consists mainly of bracken P. aquilinum gorse U. europeus and U. gallii Planch, bramble Rubus fruticosus agg. with Juncus effusus L. J. conglomeratus L. and Molinia caerulea (L.) Moench in the wetter parts.

In many aspects the form of the oaks at this site are comparable with those at Roborough Down (section 3:3:2:1) which are of intermediate status and occur at a slightly <sup>lower</sup> altitude (180m).

### 3:3:2:0 Sites of intermediate taxonomic status.

Two sampling sites containing oaks of hybrid status were quantitatively sampled each month.

#### 3:3:2:1 Roborough Down GR.SX 503653

This site is in an exposed position with oaks reinvading and regenerating on what was formerly open Ulex moorland. The trees are wind cut and in their situation resemble 'parkland' trees, as they are regularly undergrazed by cattle, sheep and ponies. The ground flora is predominantly of close cropped grass with bracken P. aquilinum and some bramble R. fruticosus agg. One tree was quantitatively sampled each month at this site which was in a relatively sheltered position. Adjacent trees were also sampled qualitatively.

#### 3:3:2:2 Meavy GR.SX 546667.

Meavy is an exposed site containing an Oak of intermediate status.

The oak is situated in a small disused quarry in an isolated position and is partially sheltered by the sides of the quarry. The ground flora is grazed by domestic animals and consists of a grass sward with some gorse, U. europeaus and bramble R. fruiticosus agg.

The tree has a low canopy with low lateral branching (Plate 6), with branches reaching close to the sides of the quarry.

### 3:3:3 Quantitative *Quercus petraea* site

#### 3:3:3:1 Ausewell Rocks GR.SX 734716

Ausewell Rocks is a Q. petraea clitter oakwood which occurs at an altitude of 200 metres, and is situated in the Dart Valley. In many respects the morphology of the oaks at this site closely resembles those of other high altitude clitter oakwoods such as the Q. robur woods of Piles Copse and Wistmans Wood (Wigston 1971). Two oaks were chosen as sample trees, one from within the canopy of the wood, and the other from a more exposed situation at the edge of the wood. As at the other sample sites the trees were sampled monthly. The ground flora at this site consisted of bracken P. aquilinum and bilberry Vaccinium myrtillus growing from between the clitter boulders, and the oaks themselves were rich in epiphytes. During the early spring of 1977 the 'within' canopy sample tree was felled, and subsequently no data on the distributions of galls was obtained from this tree for the 1977 season.

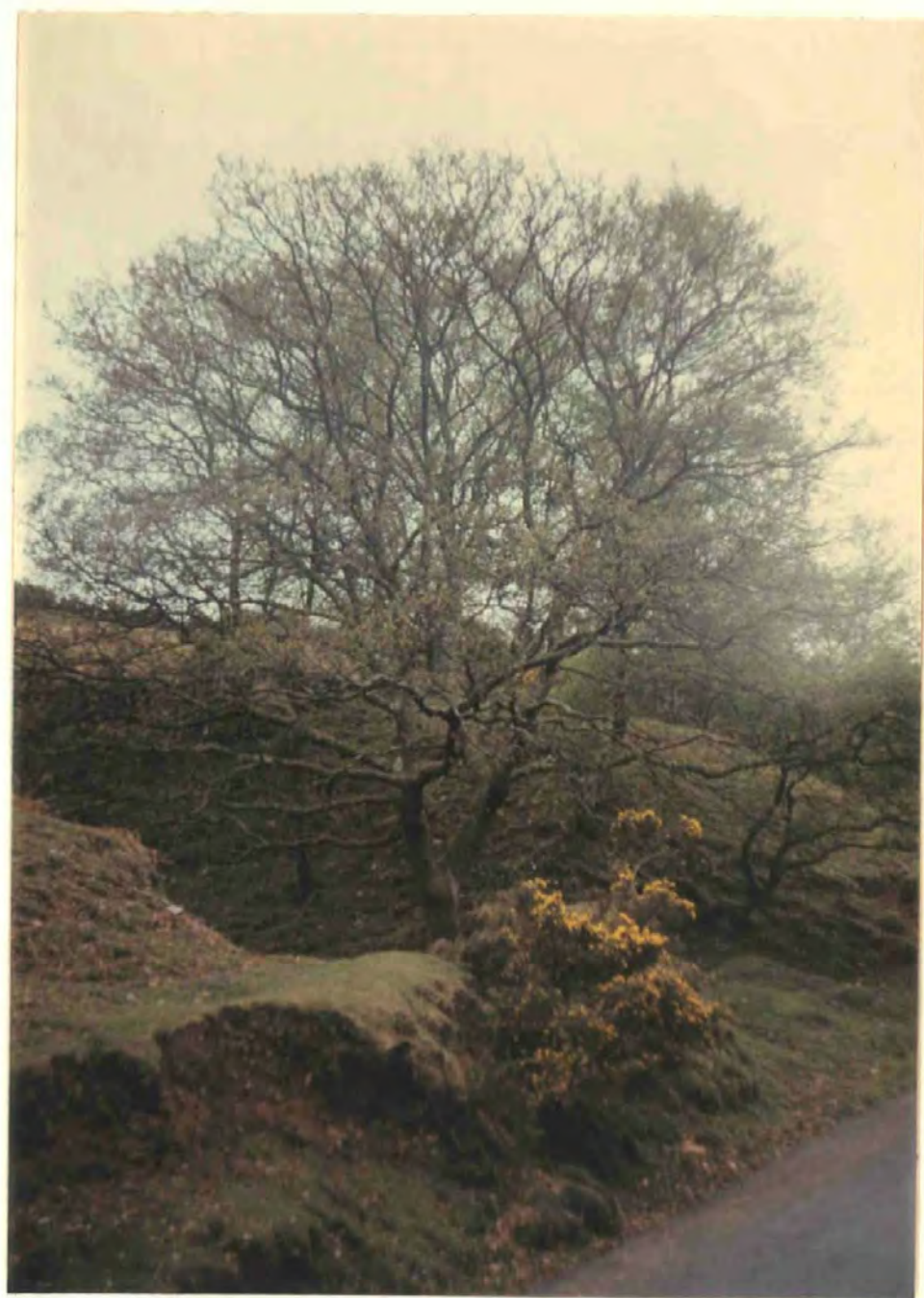
Pictorialised scatter diagrams plotted from the analysis of the leaf morphometrics of the quantitative sample trees are given in Appendix D.

### 3:3:4 Appraisal of the choice of sampling sites

From the site descriptions given in sections 3:3:1:1 to 3:3:3:1, it is evident that the quantitative sites occur at different altitudes. In order to eliminate any possible altitudinal effects on gall

Plate 6. Meavy sample oak tree (hybrid).

(Photographed in November).



distributions, it would be necessary to have sample sites containing the entire range of the indigenous oak taxa. Since this was not possible in this study, it was hoped that any effects on the distributions of galls due to differences in altitude should be minimised, and any effects due to the taxonomic status of the host be maximised, by the careful selection of sites. This was done by choosing sites which were as similar as possible in their morphologies and situations.

Qualitative 'within' site and 'between' site sampling covering the full range of the indigenous oak taxa, was undertaken in order to enable a clearer assessment to be made as to the reasons why the gall distributions differed from one quantitative site to the next.

## CHAPTER 4

### GENERAL BIOLOGY OF CYNIPID GALL WASPS

#### 4:1 Alternation of Generations

The Cynipidae, in common with some other members of the Hymenoptera, display an alternation of generations in their life cycles. Until the time of Hartig (1843) the natural histories of gall insects had received very little attention, and it was Hartig (1843) who first brought attention to the fact that certain gall wasp species appeared to have no males. He surmised from anatomical examination of the insects that they were hermaphrodite, but these observations were soon disproved. It was not until the work of Bassett (1873) who showed how some bisexual spring forms, living in a distinct gall, gave rise to agamic forms living within different structured galls in the autumn, that the picture regarding the alternation of galls became clearer. Riley (1873) also elucidated the subject by showing that Cynips operator Osten Sacken, which produces a bud gall in the spring was in fact the alternate generation gall of C. operatola Riley, which produces a small pip like gall between the acorn and cupule of Quercus tinctoria. However, it was not until the work of Adler (1881) and Adler and Straton (1894) that the life histories of the Cynipidae were finally elucidated. Both a bisexual and an agamic generation often exist in which one generation gives rise to the other, though the genus Cynips appears to have lost the sexual generation entirely, and depends solely on the agamic parthenogenetic generation. Amongst the Cynipidae both the agamic sexual females are diploid whilst the males are invariably haploid. Agamic females produce two types of egg. One of these undergoes meiosis and hence the insects are haploid giving rise to males. The

others which do not undergo meiosis, give rise to sexual generation females. Females of the sexual generation do not resemble their agamic parents, a situation which, before the work of Adler (1881), caused considerable taxonomic confusion. Indeed before the elucidation of the alternation of generations, insects of the sexual and alternate agamic generation were in some cases classified as being of different genera. Such was the case for Neuroterus whose agamic females had previously been classified as being of the genus Spathegaster (Adler and Straton, 1894).

The process whereby agamic females give rise to females of the sexual generation is known as thelotokous parthenogenesis, whilst that giving rise to males is known as arrhenotokous parthenogenesis (Slobodchikoff and Daly, 1971). Doncaster (1910, 1911, 1916) showed that agamic females of N.lenticularis Oliv. (= N.quercusbaccarum L.) may produce either male or female offspring by one of the above pathenogenetic processes, but that an individual agamic female never gave rise to both males and females. In A.operator austorior form austorior Kinsey, it has been shown (Patterson 1928) that the same agamic female can give rise to both male and female offspring, though they normally tend to produce an uneven sex ratio which vastly favours one sex or the other. The reasons for this are not clear but they may be due to differing conditions acting upon the agamic females. Other species of cynipid seem to rely totally on parthenogenesis to maintain the species, the sexual generation being dispensed with. The evolutionary advantages of thelotoky (the development of diploid females from unfertilised eggs) are discussed in Slobodchikoff and Daly (1971).

As is pointed out by Slobodchikoff and Daly (1971) arrhenotoky and the

haplo-diploid system confer a considerable selective advantage on the Hymenoptera. The advantages of diploidy are that it offers protection against the effects of somatic mutation, heterozygosity and recombination as long as the average fitness of the diploid population is greater than that of the haploid one. A disadvantage is that of a greater genetic load, since all males are haploid, recessive lethal mutations do not accumulate in the population. The genetic load in males is reduced to a very low level, hence females possess the advantages of diploidy whilst the males obviate any obvious disadvantages.

#### 4.2 Life cycle

The Cynipidae which possess an alternation of generations may complete their full life cycle from agamic to sexual generations within a single year, as is found in Neuroterus. In A. quercuscalicis which relies solely on the agamic generation in Britain, the life cycle has been found during this work, to take up to 3 years to complete. Amongst the cynipids which display an alternation of generations, the sexual and agamic generations normally exploit different parts of the host tree, for example the oak apple gall B. pallida agamic females arise from galls in the roots, whilst its sexual generation insects arise from galls on buds. As Darlington (1974) points out, when an organism exhibits two methods of reproduction, sexual and agamic, the sexual phase follows a period of plenty and precedes one of scarcity. It is for this reason that most cynipids which have an alternate generation, produce their sexual generation in the spring and their agamic generation in the late summer and early autumn. Agamic females which have over-wintered in galls in protected environments, for example under a layer of leaf litter as in Neuroterus, emerge in the following spring and oviposit eggs which give rise to either males or females. When these sexual generation adults emerge, they mate and the females lay diploid eggs which give rise to the agamic females,



and so the cycle is completed. The life cycle for Neuroterus is diagrammatically represented in Figure 7. In other genera the agamic generation may overwinter for two years before emerging in the second spring to complete the cycle.

The host taxon may differ from the sexual to the agamic generation, as has been shown to be the case with A.kollari (Marsden-Jones, 1953), who demonstrated that A. circulans Mayr. which produces galls in the axillary buds of the Turkey oak Q.cerris L., was in fact the sexual generation of A.kollari which galls buds in Q. robur and Q. petraea.

Amongst those cynipids which appear to have lost their sexual generation is A.quercuscalicis, which induces gnarled galls on acorns. It is stated (Eady and Quinlan, 1963) that A. cerri Beyerinck is the sexual generation of A. quercuscalicis though no galls have been recorded from Britain, but on the continent occur on the catkins of Q.cerris. The galled acorns fall to the ground during acorn fall in the autumn, and the insects may overwinter as either larvae or adults before emergence in spring following one or two winters (Cobb, 1972). In this investigation it has been found that insects may spend up to three winters in the gall prior to emergence. What determines why galls, which were all collected from the same host at the same time, and all kept under the same conditions, should produce emergents after one, two or three winters is unclear. A possible reason why this phenomenon occurs may be related to the acorn production of the host. Oaks do not produce an acorn crop every year, hence if all the wasps emerged in the spring following a good mast year they would be unable to maintain the population as galls could not be induced. Therefore by the emergence of a proportion of the adult wasps each spring, some adults will be able to oviposit in a good mast year and so maintain the population.

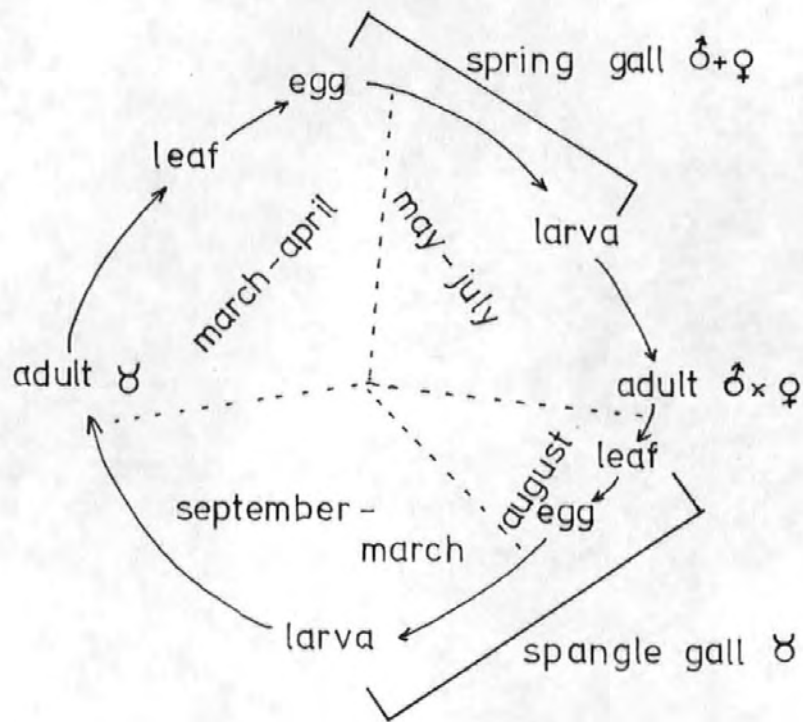


Figure 7. Diagram of the life-cycle of wasps of the genus Neuroterus.

### 4:3 Accounts of the Biology of each gall species recorded

#### 4:3:1 Andricus callidoma (Hartig) (= cirratus Adler).

Both generations of A.callidoma are known to occur in Britain (Eady and Quinlan, 1963). The sexual generation induces galls on catkins in the spring which mature towards the end of May (tufted galls of male catkins). Galls induced by the agamic generation occur in the axillary buds in the late summer (stalk spindle gall). No galls induced by the sexual generation were found during the duration of this work, though several galls of the agamic generation were encountered and collected in order to rear out the occupants. No insects emerged from these galls and nothing further to the details given by Connold (1908), Askew (1961) and Eady and Quinlan (1963) can be offered about their general biology and life cycles.

#### 4:3:2 Andricus curvator (Hartig).

A.curvator possesses a full alternation of generations, with the agamically induced galls occurring in lateral or terminal buds (Eady and Quinlan , 1963) during August and September. These galls (collared bud galls) are not distinctive and can be easily mistaken for buds which have failed to open. Galls induced by the sexual generation (blister galls) occur in the laminae of leaves (see Appendix E , Plate 1 ) in the petioles of leaves and also in small twigs where swelling and distortion of the host tissue takes place. Sexual generation galls found in this survey occurred in all the above positions on the host, but most commonly in the laminae of leaves and almost invariably in the basal section of the leaf lamina. Adults of the sexual generation as well as inquiline and parasites were reared from galls collected during this work; details of these and their locations are given in Table 1 .

Table 1. Legend.Host taxa.

Q.r = Quercus robur.  
 Q.p = Quercus petraea.  
 Int = Hybrid oaks.

Host galls.

A.kol = A.kollari.  
 C.q-f. = Cynips quercusfolii.  
 C.div. = C.divisa.  
 T.meg. = Trigonaspis megaptera.  
 A.q-r. = A.quercusramuli.  
 N.alb. = Neuroterus albipes.  
 A.q-c. = A.quercuscalicis.  
 A.cur. = A.curvator.  
 B.pall. = Biorhiza pallida.  
 A.q-l. = A.quadrilineatus.  
 N.qb. = N.quercusbaccarum.

Emergents.

Causer = Cynipid gall inducer.  
 (para) = Parasites (Hymenoptera:chalcidoidea)  
 (inq) = Inquilines.

Key to Sites.

W.W = Wistmans Wood. C.Br = Caddover Bridge. Cl.W = Cleeve Wood.  
 (SX 613771) (SX 554464)  
 Harf. = Harford. Noss. = Noss Mayo. Sibley = Sibleyback Res.  
 (SX 627603)  
 Newnh. = Newnham Glos. Kilc = Killcreggan, Dunbarton.  
 (SO 674095)  
 Burra = Burrator Res. Pitlo = Pitlochry. Ext.R.W = Exton Station.  
 (SX 568693) (NO 936578)  
 Hen.Cas. = Henbury Castle. Burley = Burley, Hants. Strines, Yorks.  
 (SX 685725) (SZ 226032) (SK 222909)  
 Meavy. Grenof = Grenofen. Yarnier Wood. Piles Copse. Totley, Yorks.  
 (SX 546667) (SX 489708) (SX 780780) (SX 645620) (SK 304788)  
 Holne Wood. Lust'l = Lustleigh. C.Park = Central Park, Plymouth.  
 (SX 712702)

Table 1. Legend (continued).Key to Sites.

Robor =Roborough Down. Cock'fd.=Cockingford.  
(SX 503653)

Salop=Shropshire.W'wick=Warwick.F'bor=Farnborough Station.  
(TQ 868561)

Lydc't=Lydcott Wood.Ausewell Rocks.Edge.P=Edgecumbe Park.  
(SX 734716)

Blaxton Wood. Rose'cr.=Rosecraddoc Manor.Dittis=Dittisham.  
(SX 472637) (SX 538708)

Plym.Br=Plym Bridge.Seaton valley.New Br.=New Bridge.  
(SX 712709)

Hessenf'd.=Hessenford.

Dates.

Date coll =Date of gall sampling.

Date emerg. = Date of emergence of the gall inhabitants.

Table 1. List of the emergents from oak galls.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
Q.r	A.kol	Causer	♂	W.W	22/9/76	23/9/76
"	"	"	"	"	"	25/9/76
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	Torymus cingulatus(para)-	-	C.Br	3/7/75	-
Int	"	Causer	♂	Cl.W	8/7/75	7/9/75
"	"	"	"	"	"	"
"	"	"	"	"	"	8/9/75
Q.r	"	T.nigricornis(para)	-	W.W	22/9/76	-
"	"	"	-	"	"	-
"	"	T.cingulatus(para)	-	Harf.	10/4/75	-
-	"	T.nigricornis(para)	♀+♂	Noss.	15/5/75	24/5/75
"	"	5 Synergus gallaepomiformis(inq)-	-	Noss	15/5/75	-
"	"	2 S.umbraculus (inq)	♀ <sub>15</sub>	Harf.	26/6/75	1/7/75
"	"	3 S.gallaepomiformis(inq)	♀	Sibley.	6/5/75	7/5/75
"	"	3 S.umbraculus(inq)	♀ <sub>15</sub>	Harf.	30/4/75	20-27/5/75
-	"	Eurytoma brunniventris (para)	-	C.Br	3/7/75	-
-	"	7 S.gallaepomiformis (inq)	♀ <sub>15</sub>	Kilc.	1/1/75	6/2/75
-	"	4 S.reinhardi (inq)	♀ <sub>15</sub>	Newnh.	5/4/75	21-27/5/75
"	"	4 S.umbraculus (inq)	♀ <sub>15</sub>	"	"	"
Q.r	"	4 S.gallaepomiformis (inq)	2♀+2♂	Burra.	1/7/75	13-17/7/75
"	"	1 S.umbraculus (inq)	♂	"	"	"
-	"	3 Olynx trilineatus (para)	-	?	-	-
Int	"	2 T.auratus (para)	-	Pitlo.	3/4/75	20/4/75
Q.r	"	Causer	♂	Ext.RW	16/8/76	7/9/77
"	"	"	"	"	"	"
"	"	3 T.nitens(para)	-	"	"	9/2/77
Int	"	2 T.nigricornis(para)-	-	Noss.	15/5/75	2/6/75
Q.r	"	Ceroptres arator(inq)-	-	Newnh.	-	4/5/75
"	"	T.auratus (para)	-	Harf.	10/4/75	-
"	"	Eupelmus urozomus(para)-	-	"	"	-
"	"	Megastigmus stigmatizans (para)	-	Newnh.	-	27/4/75
"	"	Mesopolobus jucundus	-	Harf.	10/4/75	-

Table 1.cont.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
Q.r	A.kol	T.nigricornis(para)	-	Sibley.	5/5/75	20/5/75
Int	"	2 Causers	♂	Hen.Cas.	27/6/75	6/9/75
-	"	T.nigricornis(para)	-	?	28/1/76	5/2/76
Q.r	"	Causer	♂	Ext.RW	16/8/76	14/9/76
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	Harf.	26/6/75	20/9/75
"	"	T.cingulatus(para)	-	Ext.RW	16/8/76	17/9/76
-	"	T.nigricornis(para)	-	Noss	15/5/75	26/6/75
-	"	S.umbraculus(inq)	-	Pitlo.	3/4/75	-
Q.r	"	Causer	♂	W.W	22/9/76	-
"	"	T.nigricornis(para)	-	Ext.RW	16/8/76	17/9/76
Q.p	"	Causer	♂	Burley.	9/12/74	25/4/75
"	"	Causer	"	Burley.	"	23/4/75
-	"	Causer	"	Noss.	15/5/75	1/8/76
-	"	M.jucundus(para)	-	C.Br	3/7/75	-
Q.r	"	T.nigricornis(para)	-	Ext.RW	16/8/76	17/9/76
"	"	Causer	♂	Sibley.	5/5/75	3/9/75
-	C.q-f.	Causer	♂	Yarner	9/12/76	10/12/76
-	"	"	"	C.Br	23/10/75	6/1/76
Q.p	"	T.nigricornis(para)	-	Yarner	11/10/76	march/77
"	"	"	-	"	30/9/76	Feb/77
"	"	"	-	"	11/10/76	Feb/77
Int	C.div.	Causer	♂	Hen.Cas.	27/6/75	-
"	"	E.brunniventris(para)	♂	"	"	-
"	"	"	"	"	"	-
"	"	"	"	"	"	-
"	"	"	"	"	"	-
Q.r	"	T.nigricornis(para)	-	Burra.	Nov/74	2/3/75
"	"	E.brunniventris(para)	♂	"	29/9/75	14/1/76
Q.p	"	Caenacis divisa(para)	-	Strines.	17/10/75	9/2/76
Int	"	E.brunniventris(para)	-	Meavy.	30/7/76	7/9/76
"	"	"	-	"	"	9/9/76
-	"	E.urozomus(para)	-	Grenof.	27/9/76	march/77
Int	"	Causer	♂	Meavy.	30/7/76	7/9/76
Q.p	"	T.nigricornis(para)	-	Yarner.	11/10/76	march/77
"	"	Causer	♂	Strines.	17/10/75	3/2/76



Table 1.continued.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
Q.r	T.meg.	S.albipes	-	Piles	26/6/75	5/7/75
-	A.q-r.	4 Causers	♀	Totley.	6/6/76	11/6/76
-	"	3 Causers	"	"	"	"
-	"	6 Causers	"	"	"	12/6/76
-	"	3 Causers	"	"	"	14/6/76
-	"	1 Causer	"	"	"	15/6/76
Int	N.alb	T.auratus(para)	-	Burra.	1/7/75	12/9/75
Qr	A.q-c.	Causer	♂	Holne.	20/10/74	-
"	"	Causer	"	Lust'l.	7/9/75	-
"	"	Causer	"	C.Park	Nov/76	-
"	"	Causer	"	"	"	-
"	"	Syntomaspis cyanea (para)	-	"	"	Feb/77
"	"	Causer	♂	"	"	-
Q.r	"	Causer	"	Yarner	-	-
Int	A.cur	Causer	-	Holne	27/6/75	2/7/75
Q.r	"	T.auratus(para)	-	Harf.	26/6/75	1/7/75
Int.	"	"	-	C.Park	19/6/75	24/6/75
Q.r	"	Causer	♀	W.W	8/6/76	16/6/76
"	"	"	"	"	"	"
Int	"	"	♂	Robor.	26/5/76	3/6/76
"	"	"	"	"	"	"
Q.r	"	Cecidostiba geganius (para)	-	Cock'fd.	8/7/75	14/7/75
Int	"	T.auratus (para)	-	Holne.	27/6/76	2/7/76
Q.r	"	"	-	Harf.	26/6/75	1/7/75
"	"	Causer	♀	"	13/5/75	27/5/75
"	"	"	♂	"	"	"
Q.p	"	T.auratus(para)	-	Yarner	3/6/76	15/6/76



Table 1. continued.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
-	<u>B. pall.</u>	<i>Syntomaspis apicalis</i>	-	Pitlo.	3/4/75	-
		<i>Olynx skianeuros</i> (para)	-	"	"	-
Q.r	"	2 <i>Hobbia stenonota</i> (para)	-	Burley.	12/7/75	8/8/75
"	"	<i>T. auratus</i> (para)	-	Salop.	9/12/74	?/6/75
		<i>S. apicalis</i> (para)	-	"	"	-
"	"	2 <i>H. stenonota</i> (para)	-	Burley	12/7/75	14/7/75
-	"	<i>T. auratus</i> (para)	-	F'bor.	1/6/76	22/6/76
		1 Causer	♀	"	"	21/6/76
-	"	<i>S. apicalis</i> (para)	-	Pitlo.	3/4/75	3/9/75
-	"	<i>O. skianeuros</i> (para)	-	W'wick.	10/1/75	-
		<i>T. auratus</i> (para)	-	"	"	-
-	"	4 Causers	♂s	F'bor.	1/6/76	23/6/76
		<i>T. auratus</i> (para)	-	"	"	22/6/76
Q.r	"	<i>E. brunniventris</i> (para)	-	Burley.	12/7/75	-
-	"	3 <i>T. auratus</i> (para)	-	F'bor.	1/6/76	21/6/76
		1 <i>S. apicalis</i> (para)	-	-	-	8/3/77
Q.p	"	<i>T. cingulatus</i> (para)	-	Totley.	6/7/76	-
-	"	<i>Synergus reinhardi</i> (inq)	-	W'wick.	-	-
-	"	5 <i>Cecidostiba leucopeza</i> (para)	-	Pitlo.	3/4/75	-
		3 <i>C. leucopeza</i> (para)	-	} - 1 gall		
		1 <i>T. auratus</i> (para)	-			
		23 <i>T. nigricornis</i> (para)	-			
?	"	78 Causers	♂s	Yarner.	9/6/76	22/6/76
		18 <i>T. auratus</i> (para)	-	"	"	"
-	"	64 Causers	♂s	F' Bor.	1/6/76	14/6/76
-	"	109 Causers	"	F'bor.	"	15/6/76
-	"	38 <i>O. skianeuros</i> (para)	-	F'bor.	"	-
-	"	25 Causers	♂s	F'bor.	"	18/6/76
		13 <i>T. auratus</i> (para)	-	"	"	19/6/76
Q.r	"	19 Causers	♂s	Newnh.	6/6/76	18/6/76
		3 <i>T. auratus</i> (para)	-	"	"	18/6/76
-	"	3 Causers	♀s	F'bor.	1/6/76	20/6/76
		8 <i>T. auratus</i> (para)	-	"	"	23/6/76
-	"	21 <i>T. auratus</i> (para)	-	F'bor.	"	21/6/76
-	"	51 Causers	♀s	F'bor.	"	15-16/6/76
		10 <i>T. auratus</i> (para)	-	"	"	18/6/76
-	"	2 Causers	♂s	F'bor.	"	20/6/76
		1 <i>T. auratus</i> (para)	-	"	"	22/6/76

Table 1. continued.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
-	<u>B.pall.</u>	<i>Cecidostiba semifascia</i> (para)	-	Pitlo.	3/4/75	-
-	"	5 Causers	♀ <sub>1s</sub>	F'bor.	1/6/76	15-16/6/76
-	"	1 <i>T.auratus</i> (para)	-	"	"	22/6/76
Q.r	"	1 <i>T.auratus</i> (para)	-	Burley.	12/7/75	14/7/75
-	"	6 Causers	♀ <sub>1s</sub>	F'bor.	1/6/76	18/6/76
-	"	2 <i>T.auratus</i> (para)	-	"	"	20/6/76
-	"	6 Causers	♀ <sub>1s</sub>	F'bor.	"	19/6/76
-	"	5 <i>T.auratus</i> (para)	-	"	"	22/6/76
Int	<u>A.q-l.</u>	Causer	♂	Meavy.	26/5/76	31/5/76
"	"	Causer	"	Meavy.	"	"
"	"	<i>Caenacis divisa</i> (para)	-	Meavy	1/7/75	14/7/75
"	"	<i>Mesopolobus tibialis</i> (para)	-	Meavy	"	15/7/75
"	"	1 Causer	♂	Meavy.	2/7/75	-
"	"	1 Causer	-	Meavy.	"	-
"	"	1 Causer	"	Meavy.	"	-
Int	"	1 <i>Mesopolobus jucundus</i> (para)	-	Cl.W	8/7/75	1/8/75
"	"	1 <i>M.jucundus</i> (para)	-	Cl.W	"	4/8/75
Q.r	"	1 Causer	♂	Tavy Cl.	23/5/76	4/6/76
Int	"	1 Causer	"	Meavy	1/7/75	-
"	"	1 <i>M.xanthocerus</i> (para)	-	Meavy.	"	-
"	"	1 <i>M.xanthocerus</i> (para)	-	Meavy.	"	-
"	"	1 <i>Tetrastichus aethiops</i>	-	Meavy.	"	-
"	"	1 <i>M.tibialis</i> (para)	(para)	Meavy.	"	-
Q.r	<u>N.qb.</u>	<i>M.jucundus</i> (para)	-	Piles.	26/6/75	-
-	"	1 Causer	♀	Noss.	15/5/75	28/5/75
-	"	4 Causers	♀ <sub>1s</sub>	Lyde't.	5/5/75	12/5/75
-	"	1 Causer	♂	Noss.	16/5/75	28/5/75
-	"	"	"	"	"	10/5/75
-	"	"	"	"	-	"
-	"	"	"	"	-	"
-	"	"	"	"	-	"
Q.p	"	1 Causer	"	Ausewell.	7/6/76	10/6/76

Table 1. continued.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
Q.r	N.qb	1 Causer	♂	Meavy.	26/5/76	all by 31/5/76
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	♀	"	"	"
Q.p	"	1 Causer	♂	Edge.P	12/5/75	19/5/75
"	"	"	"	"	"	"
"	"	"	"	"	"	"
Q.p	"	1 T.auratus (para)	-	Blaxton.	3/6/76	25/6/76
Q.r	"	1 Synergus nervosus (inq)	-	Yarner.	22/11/74	27/3/75
Int	"	1 Olynx orsames (para)	-	Cl.W	8/7/75	1/8/75
"	"	1 M.tibialis (para)	-	Holne.	26/6/75	4/7/75
Q.p	"	1 M.jucundus (para)	♂	Holne.	29/6/75	14/7/75
"	"	"	"	Holne.	"	"
"	"	"	"	Holne.	"	"
"	"	"	"	Holne.	"	"
"	"	"	"	Holne.	"	"
"	"	"	♀	Holne.	"	"
"	"	1 T.aethiops (para)	-	Holne.	"	"
Q.p	"	M.jucundus (para)	♂	Holne.	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	"	"	"	"
"	"	"	♀	"	"	"
"	"	"	"	"	"	"
Q.r	"	1 Causer	♂	Rose' cr.	5/5/75	-
"	"	1 Causer	"	"	"	-
Q.r	"	1 Causer	"	Dittis.	3/6/76	11/6/76

Table 1. continued.

Host taxa	Host gall	Emergents	Sex	Site	Date coll.	Date emerg.
Q.r	N.qb.	Lysiphe lebus sp. (Braconidae).	-	Piles.	26/6/75	-
"	"	1 Causer	♀	Meavy.	26/5/76	10/6/76
"	"	1 Causer	♂	Noss.	4/5/75	10/5/75
"	"	1 M.jucundus (para)	-	Piles.	6/6/75	20/7/75
-	"	1 T.auratus (para)	-	Plym.Br.	11/5/75	5/6/75
-	"	1 T.auratus (para)	-	Seaton.	5/5/75	-
-	"	1 T.auratus (para)	-	New Br.	26/7/75	-
Q.p	"	1 T.auratus (para)	-	Yarner.	30/5/75	15/6/75
Q.r	"	1 T.auratus (para)	-	Burra.	1/7/75	19/7/75
"	"	1 M.jucundus (para)	-	Burra.	"	20/7/75
Q.p	"	1 T.auratus (para)	-	New Br.	27/6/75	-
"	"	1 T.auratus (para)	-	New Br.	"	-
-	"	Causers (6 Galls)	♂'s	Noss.	15/5/75	24-28/5/75
Q.r	"	Causers (2 Galls)	"	?	1/5/75	9/5/75
-	"	1 Causer	♀	Burley.	10/1/75?	-
Q.p	"	1 Causer	♂	Noss.	1/5/75	9/5/75
Q.r	"	1 Synergus gallae- pomiformis(inq)	-	Lust'l.	8/7/75	16/7/75
Q.p	"	Causers (8 Galls)	♀'s	Hessenf'd.	5/5/75	18/5/75
Q.r	"	1 Causer	"	Burley.	9/4/75	28/4/75
"	"	Causers (4 Galls)	"	Seaton.	5/5/75	-
"	"	1 Causer	♂	Seaton.	"	-

4:3:3 Andricus fecundator (Hartig) (= pilosus Adler)

Both generations of A.fecundator were found during this work; the sexual generation induces galls on catkins (hairy catkin galls) whilst the agamic generation induces galls in buds which mature in August and September (artichoke galls, see appendix E , Plate II ). Galls of the agamic generation are in two parts; there is the outer gall which resembles a partially opened bud which encases a hard shelled inner gall in which the larva develops. The adult may leave the gall in the following spring or delay its emergence for 2-3 years (Darlington, 1974), and proceed to oviposit in male catkins which then give rise to galls of the sexual generation. The outer galls normally remain attached to the trees and can be readily identified from their artichoke appearance.

Large numbers of agamic galls were encountered during this work, and at every site there was an imbalance of dispersion with a few trees being heavily infected and others having no galls. Reasons for such an imbalance are not clear but they do <sup>not</sup> appear to be connected with date of leaf burst, as at each of the sites leaf burst from tree to tree takes place over only one or two days. No emergents from either generation of gall were reared, although approximately 100 galls of each generation were collected. The timing of the collection of these galls seems to be very critical for successful rearing.

4:3:4 Andricus inflator (Hartig) (= globuli Hartig)

During this survey only the sexual generation gall was found, which occurs in apical buds where it causes considerable swelling and coalescence of tissue (appendix E , Plate III ). The sexual generation matures during September and the galls remain attached to the host tree during the winter. The agamic generation gall which occurs in lateral and terminal buds and is globular in shape (Eady

and Quinlan , 1963), matures during October and the galls falls from the bud prior to overwintering. No examples of the agamic generation galls were found during this work, and the rearing of occupants of 22 sexual generation galls was unsuccessful.

Darlington (1968) states that galls of the sexual generation if removed in the spring from the host tree give good results for the rearing out of the gall occupants, so it would seem that timing of collection is critical as the collection during this work was undertaken in February and early March.

#### 4:3:5 Andricus kollari (Hartig)

For many years only one generation of this species was known, the agamic generation which causes the 'marble' gall of buds (appendix E ,Plate IV ). Marsden-Jones (1953) however, showed conclusively that the galls attributed to A.circulans Mayr., which occur in the buds of Q.cerris were the sexual generation of A.kollari, as had been earlier postulated by Beijerinck (1902) but which he was unable to demonstrate. Marsden-Jones (1953) stated that rarely will the agamic females of A.kollari oviposit in buds of Q.robur but thought that this would occur under natural conditions. In his experiments no bud galls of the sexual generation were induced in Q.robur. In September 1975 I set up five bags each containing an agamic female of A.kollari on a host of Q.robur at Roborough Down (see section 3:3:2:1). One female was observed inserting her ovipositor in an axillary bud, the other four females showed little interest in the buds and spent most of their time on the inside surfaces of the bags. The bags were inspected on the 29th September 1975 and the buds inspected for any signs of gall development. All the females, except the one which had been observed ovipositing, were dead, the surviving female living for a total of 36 days, a period nearly three times longer than the 13.2 days of adult life quoted by Marsden-Jones (1953).

In the spring of 1976 the bagged twigs were again inspected for signs of gall development, but no recognisable gall structures were found (twigs had been left bagged throughout the winter). However a bud in the bag in which the agamic female had been seen to oviposit, though not resembling a gall did contain a larva which had hollowed out the centre of the bud and prevented bud development. The larva was collected but failed to pupate and identification was impossible.

Due to the apparent failure of Q.robur to host galls of the sexual generation of A.kollari and the failure of the agamic females to induce other agamic galls on Q.robur. it would indicate that the sexual generation galls on buds of Q.cerris are obligatory to the life cycle of A.kollari. If this is the case many aspects concerning the life cycle of A.kollari are unclear. For example, many of the sites where galls of the agamic generation of A.kollari occur, are in isolated localities and are often many miles from the nearest specimens of Q.cerris which host the sexual generation. How the sexual generation wasps cover the distances to isolated oaks of Q.robur and Q.petraea in order to oviposit is unclear, though winds may play a major part in their dispersal, as the flying capability of cynipids in general when observed in the Laboratory appear weak and could not alone account for the quite substantial distances that in many cases have to be covered from Q.cerris to Q.robur or Q.petraea. Indeed wind-borne dispersal of insects over considerable distances is well known (Johnson, 1969). I have often observed high numbers of agamic galls of A.kollari occurring on isolated oaks in windswept locales, higher numbers than I have found on oaks in more sheltered situations, which suggests a role for wind in the dispersal of the adults. It may be that the sexual generation of A.kollari is in the process of being lost, though I can offer no evidence to support this. Marsden-Jones (1953) states that the spread

of the marble gall of A.kollari in Britain was made possible by the introduction of Q.cerris in 1735, implying that A.kollari is dependent on Q.cerris as host for its sexual generation.

Galls of the agamic generation mature towards the end of summer and adults emerge in August and September of the year of gall induction, or overwinter in the galls (which remain attached to the host trees) prior to emergence in August or September of the succeeding year. Due to the ease in recognising the agamic galls of A.kollari and the fact that they remain attached to the host trees, it is easy to estimate how many survive predation by chalcid wasps and insectivorous birds such as tits (Parus spp.). The emergence holes of the gall causers are quite distinct from those caused by chalcid parasites and inquilines. The emergence holes caused by the adults are large (1 - 2mm,) in comparison with those caused by parasites and inquilines (< 1 mm.). Bird damage to the gall structures caused by their pecking away at the gall to expose the developing larvae is also very distinctive, since portions of the gall are torn away exposing the central gall chamber.

Mortality figures for two sites, one at Roborough Down (see section 3;3:2:1) which were based on a sample of 60 galls monitored during this survey from August 1975 to January 1976, and the other from a sample of 16 galls collected at Exton Railway station G.R. SX 981864 on the 16th August 1976, are given in Tables 2 a, and

2 b. The survivals of adult A.kollari from the Exton sample are higher than those from Roborough Down (but are based on a smaller sample). However if the galls collected from Exton had been left on the trees during the winter, as was the case at Roborough Down, it is possible that of the 9 galls containing visible larvae a proportion would have been taken by tits, which would have given figures closer to those obtained from the survey at Roborough Down. Lists of emergents and sites where A.kollari was found are given in Table 1.



Status of Gall.	Numbers.	Percent.
Galls with viable larvae	0	0
Aborted galls	6	10
Parasitised galls	8	13.3
Galls attacked by birds	14	23.4
Galls attacked by fungi	6	10
Galls evacuated by causers	26	43.3
Totals	60	100.0

Table 2a. Mortality figures for a sample of 60 galls of the agamic generation of Andricus kollari, from a survey at Roborough Down (August 1975-January 1976).

Status of Gall.	Numbers.	Percent.
Galls with viable larvae	9	56.25
Aborted galls	0	0
Parasitised galls	3	18.75
Galls attacked by birds	0	0
Galls attacked by fungi	1	6.25
Galls evacuated by causers	3	18.75
Totals	16	100.0

Table 2b .Mortality figures for a sample of 16 galls of the agamic generation of A.kollari, from a survey made at Exton Railway Station (August 16th. 1976).

4:3:6 Andricus ostreus (Hartig)

Both generations are known to occur in Britain (Askew, 1961: Eady and Quinlan, 1963) but only galls of the agamic generation were found in this study. The agamic galls are hard smooth structures, globular in shape and are found attached to the midribs and larger veins of leaves. The galls mature in autumn. The sexual generation galls are induced in buds during April and May. They vary from yellow to pale brown in colour and often have leaf scales attached to their sides and apices (Eady and Quinlan, 1963).

4:3:7 Andricus quadrilineatus (Hartig)

During this work only galls of the agamic generation were found; the sexual generation is unknown and may not exist. Eady and Quinlan (1963) in their key to the Cynipinae make no mention of the sexual form. The agamic galls occur on both catkins and leaves in May and June. During this work agamic galls were found on only a few trees (all Q. robur), but they were often very numerous when they occurred. Galls on the laminae of leaves invariably stunt the lamina growth around the leaf margin. Many galls may occur on a single catkin and though small in size (3-4mm) they are very distinctive red coloured structures with four ridges radiating out from the apex of the gall to the base.

4:3:8 Andricus quercuscalicis (Burgsdorff)

The biology of this species is covered in detail in section 4.4 as a special study was made of it.

4:3:9 Andricus quercusramuli (L.)

Both generations are known to occur in Britain, the sexual generation gall occurring in catkins and the agamic generation galls occurring in lateral buds (Eady and Quinlan, 1963). The agamic gall is obscure, being more than half concealed in bud scales, and I

have found no specimens which I could positively identify as being induced by A. quercusramuli since there were no emergents. I have found several galls caused by the sexual generation, and have successfully reared both adult gall causers and parasites from them (see Table 1 ).

Galls of the sexual generation are large pilose structures occurring on catkins in the spring, and mature during May and June (see appendix E , Plate V. ). Eady and Quinlan (1963) state that galls of A. quercusramuli occur on both Q. robur and Q. petraea though during this work I have only found ~~them~~ occurring on Q. robur.

#### 4:3:10 Andricus quercusradicis (Fabricius)

A. quercusradicis undergoes a full alternation of generations, with the agamically induced galls occurring on the roots or stem bases of young saplings (Eady and Quinlan, 1963). I found no examples of the agamic galls, most certainly as a result of my having worked on mature oaks. Galls of the sexual generation occur in leaf petioles and small twigs in which small swellings of the host tissue are induced. I found only a few specimens of these galls and was unsuccessful in rearing any occupants.

#### 4:3:11 Andricus testaceipes (Hartig)

The agamic and sexual generation galls of A. testaceipes were encountered during this survey. However galls of the agamic generation which are red conical structures occurring on the bark of the host tree, were only found once on the trunk of Q. robur. Galls of the sexual generation cause a swelling of the midrib in leaves and are green, maturing by the end of August. The gall structure on occasions induces the midrib to bend so preventing the leaf from lying in a flat plane. No occupants from either generation of gall were reared.

4:3:12 Biorhiza pallida (Olivier)

B.pallida is known to undergo an alternation of generations, the sexual generation galls occurring on buds during May and June, whilst the agamic generation occurs on roots maturing during October of the second year (Eady and Quinlan, 1963). Only galls of the sexual generation were found during this work. They are large globular structures with a pink/white colouration resembling small apples, hence their common name of Oak apples (appendix E , Plate VI ).

The gall structure is plurilocular and plurilarval and hosts large numbers of inquilines and parasites (for lists of emergents collected during this work see Table 1 ).

Though the galls were induced by developing wasps of the sexual generation I found that adult emergents from any individual gall to be always of the same sex, either male or female, and in none of the galls used for rearing were both males and females reared from the same gall (see Table 3 ). This suggests that an individual agamic female has the facility to produce only male or female eggs, although the mechanisms which determine this are not known.

The sexual generation galls start developing in May and June and mature during July and August, when the adults emerge. Since each gall gives rise to only one sex, on emergence a mate has to be found to fertilise the eggs, prior to ovipositing in roots of oaks. After the emergence of the adults the oak apple galls often remain attached to the host tree, becoming discoloured, turning brown and eventually decomposing. Examples of the sexual generation galls have been found during this work on both Q.robur and Q.petraea as well as on their hybrids.

Gall number	Number of adult causers emergents	Sex	
		Male	Female
1	1	0	1
2	4	4	0
3	41	41	0
4	37	0	37
5	64	64	0
6	109	109	0
7	25	25	0
8	19	19	0
9	3	0	3
10	51	0	51
11	2	2	0
12	5	0	5
13	6	0	6
14	6	0	6
Totals	373	263	110

Table 3 .The emergents from a sample of 14 galls of the sexual generation of Biorhiza pallida indicating the separation in the sexes between galls.(Galls collected and reared during June 1976).

4:3:13 Cynips spp.

Four species of Cynips, C.divisa (Hartig), C.disticha (Hartig), C.longiventris (Hartig) and C.quercusfolii (L.) were found, and since they have similar life cycles they are discussed together. All four species undergo an alternation of generations, the sexual generation galls occurring in buds during April and May and mature during August. Emergents oviposit in the midribs or larger veins of leaves, from which develop galls induced by the agamic generation. Only the distinctive agamic generation galls were found. C.divisa (appendix E , Plate VII ) and C.disticha are often gregarious, while galls of C.longiventris and C.quercusfolii (appendix E , Plates VIII, IX ) are usually solitary, although I have found up to three individuals on a single leaf. The agamic galls of the Cynips spp. found are unilocular and unilarval with the exception of C.disticha which is unilarval but bilocular.

I found that in any particular population of oak one or two trees are often very heavily infested with C.divisa whilst the other trees are totally devoid of these galls, a situation which exists for a number of different cynipid galls. Reasons why this may arise are discussed in section 7.0.

4:3:14 Neuroterus spp.

In Britain four species of Neuroterus occur:- N.albipes (Schenck), N.numismalis (Fourcroy), N.quercusbaccarum (L.) and N.tricolor (Hartig). Of these by far the most common and ubiquitous species found during this work was N.quercusbaccarum. All four species of Neuroterus undergo an alternation of generations, each species producing the sexual generation in the spring and the agamic generation in the autumn.

The sexual generation galls of N.quercusbaccarum (appendix E , Plate V ) are similar in shape and size to those of N.tricolor

and both occur on leaves, though N. quercusbaccarum was found more commonly on catkins. Galls of these two species can be readily separated by their colour; N. quercusbaccarum are white or pale green with areas tinged with red, whilst N. tricolor have no red colouration and are pilose. Sexual generation galls of N. numismalis are biconvex protruding from both surfaces of the leaf lamina and are regular in shape. The sexual generation galls of N. albipes are small ovoid structures arising from large veins and occasionally from the midribs of leaves. Leaf lamina development from the gall to the edge of the leaf seems to be arrested by the presence of the gall, so producing misshapen leaves.

The occupants of the sexual generation galls emerge during June and July, mate and oviposit in the laminae of developed leaves, with the exception of N. tricolor which oviposit in lammas growth (Askew, 1962). Agamic galls begin to develop in July and August and reach maturity by September and October, when small circular galls (spangle galls) may be seen on the abaxial surface of the leaf lamina. The agamic generation galls of each species are distinct and can be readily identified (appendix E , Plates X, XI ). In the early autumn, just prior to leaf fall, the peduncles that attach the galls to the leaves abscise and the galls drop to the ground. The developing larvae then overwinter within the galls protected by leaf litter which accumulates after gall detachment. During the following spring the agamic females emerge and proceed to oviposit in buds or very young leaves, with the possible exception of N. tricolor which may oviposit in expanded leaves (Askew, 1963). In addition agamic females of N. quercusbaccarum also oviposit in developing male catkins, and so complete the alternation of generations.

During this study both the sexual and agamic generation galls of N.tricolor were rarely found, though the other three species were common. Details of emergents of gall causers, inquilines and parasites are given in Table 1 .

#### 4:3:15 Trigonaspis megaptera (Panzer)

Both the sexual and agamic generation galls of T.megaptera were found, the former being much more common. The sexual generation galls develop in spring (Eady and Quinlan, 1963) during April and May, from lateral and terminal buds. When mature they are roughly spherical in shape and have a white/yellow colouration often with red/pink tinges. The adult insects emerge in May and June and the fertilised eggs are oviposited in small veins along the abaxial surfaces of leaves, and occasionally along the midrib. The galls are often gregarious. The agamic galls are reniform and are small, normally less than 1mm x 2mm. They remain attached to the leaves rather than fall to the ground independently, as occurs with spangle galls of Neuroterus spp., and <sup>the insects</sup> overwinter in the gall. The agamic females emerge the following spring and oviposit in buds so completing the cycle.



4:4            ANDRICUS QUERCUSCALICIS    BURGS DORFF4:4:1    Gall structure

It has been stated (Claridge, 1962) that the galls caused by the agamic generation of A. quercuscalicis, 'Knopper' galls, occur on the cupules of acorns of the British oak species. Although the gall may absorb the cupule to some considerable extent, I have found that the gall originates from the acorn itself and then grows around the cupule encapsulating it. A single acorn may have a number of galls growing from it, as many as five have been found developing from a single acorn (Cobb, 1971), and although acorns with as many as four galls developing from them were found during this work, the majority of acorns had only one gall each.

The structure of the knopper gall is in two parts:- (a) there is a thick woody outer gall which is highly convoluted and roughly conical in shape. At the apex of the gall structure there is an opening which leads into an enclosed chamber at the bottom of which occurs (b) a smooth inner gall which contains the developing larva (Figure 8 ). While the gall is developing during July to September it has a pliable consistency and is brilliant green in colour (Plate 7 ). The outer gall at this time is covered in a sugary exudate of honeydew, the function of which is unclear though it may act as a protective layer in trapping potential parasites. Bequaert (1924) listed many cynipid galls from both Europe and America as being honeydew producers.

4:4:2    The origins of A. quercuscalicis in Britain

The first confirmed report of the presence of A. quercuscalicis in mainland Britain is generally taken as that made by Claridge (1962) who found a number of galls on Q. robur in Northamptonshire during the autumn of 1961. Connold (1908) mentions the occurrence of galls of

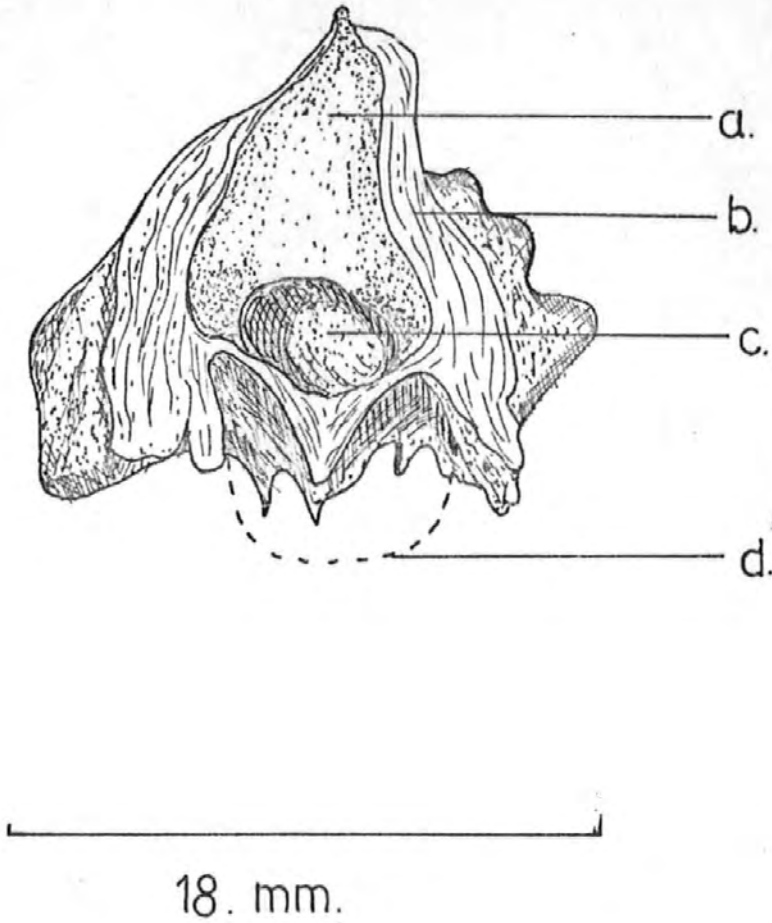


Figure 8. Drawing of cross section through an agamic gall Andricus quercuscalicis (Knopper gall).

- (a) Inner cavity of gall.
- (b) Woody case of gall.
- (c) Inner gall containing developing wasp.
- (d) Position of acorn cupule.

Plate 7. knopper galls of the agamic generation  
of A. quercuscalicis developing on acorns  
of Q. robur.



A. quercuscalicis in Jersey in 1902, where he stated that they predominate on Q. robur but also occur on Q. petraea. If this is really the case it is the only record of A. quercuscalicis occurring on Q. petraea.

There is some evidence (Cobb, 1972) that galls of A. quercuscalicis were also present in Cromer, Norfolk in the 1920s and at Charmouth in Dorset in 1935. A certain amount of confusion therefore exists as to the date that A. quercuscalicis first appeared on oaks in this country. The large numbers of reports of the occurrence of galls from sites in eight English counties since that of Claridge (1962) gives weight to the argument that it is likely that A. quercuscalicis has been present in England, in small numbers at least, for longer than the original 1961 report would indicate. What is certain is that galls of A. quercuscalicis have become well established since the report of Claridge (1962), and during the course of this study were recorded from a number of widely distributed areas. These records are listed in Table 1 .

#### 4:4:3 The life cycle of A. quercuscalicis

The galls of A. quercuscalicis on the acorns of British oaks are caused by agamic females (Eady and Quinlan, 1963). Eggs are laid in the buds of female flowers during early spring and after the emergence of the larvae from the eggs, gall development is initiated on the acorns. By the autumn, August-October, the galls have reached maturity. Overwintering has been found during this work to take place usually as larvae or pupae, and on three occasions as fully developed adults. It has been shown (Cobb 1972) that the gall causers may remain in the gall for two winters prior to emergence in the following spring. I have found that under Laboratory conditions of dryness and warmth, insects as larvae, pupae, or adults have been known to overwinter for three consecutive years and still emerge as viable adults. The reason

for the varying lengths in the life cycle, 1 to 3 years, is possibly an important adaptation to overcome the possibility of a non-mast year for local oaks. The factors which control which galls give rise to adult insects in which year are not understood, but it seems more likely that some physiological cue from within the insect comes into operation, than some external environmental cue. This is because there was a variation in the emergence years of the wasps from several different sites, although the galls were collected from a particular site on the same day, and handled and stored under the same conditions in the Laboratory.

The sexual generation of A. quercuscalicis is unknown in Britain, though it is stated (Eady and Quinlan 1963) as occurring on the catkins of Q. cerris in the spring and early summer in continental Europe. Due to the widespread occurrence of agamic 'Knopper' galls which I have only found occurring on Q. robur, it seems unlikely that A. quercuscalicis is dependent upon its sexual generation for its survival and probably has the capacity for prolonged periods of agamic reproduction, since in many instances Q. robur hosts <sup>of</sup> A. quercuscalicis are largely isolated from hosts of its sexual generation, Q. cerris.

Alternatively since the sexual generation gall is inconspicuous on the catkins of Q. cerris, it may be easily overlooked. Certainly after extensive searches on both Q. cerris and Q. robur I have not found any sexual generation galls, and I have not come across any literature confirming its presence in the British Isles.

#### 4:4:4 The economic importance of Andricus quercuscalicis

Due to the now widespread occurrence of the 'Knopper' gall throughout certain counties in England, an investigation into any possible effects that the galls' presence might have on the natural regeneration of oaks, was initiated.

It has been stated (Watt 1919) that up to 80% of acorns are consumed by birds, mice and voles or attacked by fungi before they have had a chance to germinate. Of the 20% that remain some will abort, leaving only a relatively small proportion of the original number to germinate successfully. With such a large mortality of acorns due to the cases mentioned, it was thought that the presence of a new threat to acorn viability could possibly threaten natural oak regeneration. During this work I have found oak hosts bearing anything from a single gall to having the entire acorn crop galled by A. quercuscalicis, with a high density of galling on affected oaks being the more common situation. Heavily galled hosts therefore appear to be very susceptible to regeneration failure. In order to estimate the affect that the galls have on the germination of acorns, some experiments were instigated. 50 normal and a 100 galled acorns were collected from each of two sites in Devon during October 1976. Site (1) was Yarner Wood N.N.R (grid reference SX780780) in the Bovey valley, and site (2) was at Holne (grid reference SX730705) in the valley of the Dart. The galled acorns were sorted into two groups depending upon the degree of galling:- (1) partially galled acorns, which were defined as those with more than 50% of the acorn clearly visible and (2) totally galled acorns, defined as those which had less than 10% of the acorn visible. Once the galls were sorted they were stored until November 15th 1976 when the germination experiments were set up. 50 replicates of each category from both the sites were planted in plastic beakers containing Levingtons potting compost, giving totals of a 100 ungalled acorns (controls), a 100 partially galled acorns and a 100 totally galled. Numbers of germinating acorns were counted up until June 13th 1977.

From the results (see Table 4) it is clear that there is a large drop in the viability of the galled acorns. For the Yarner wood and Holne samples combined the germination in the controls was 60%,

	No.acorns planted	No.acorns germinated	%germination
YARNER			
Partially galled	50	13	26
Totally galled	50	4	8
Controls	50	31	62
HOLNE			
Partially galled	50	9	18
Totally galled	50	2	4
Controls	50	29	58

Table 4. Results of the germination experiments using acorns galled by A. quercuscalicis from two sites:- Yarner Wood N.N.R and Holne.  
(Partially galled=more than 50% of the acorn visible.  
Totally galled = less than 10% of the acorn visible).



for the partially galled 22%, whilst only 6% of the totally galled group germinated. This loss of viability could therefore considerably reduce the likelihood of successful natural regeneration, in isolated highly infected sites. Brookes (1976) working on the mineral nutrition and development of Q.robur and Q.petraea obtained a figure of 27.3% for seedling survival at 4 months for acorns collected from Yarner wood. This figure is much smaller than that obtained for the controls in this work (62% survival for acorns from Yarner wood and 58% survival for acorns from Holne), though the range of figures he obtained from five sites (7.4% - 85.7% survival) embraces the figures obtained here. Acorn viability, if free from insect or fungal attack, is largely dependent upon having a large fresh weight and a good nutrient content (Brookes 1976).

In continental Europe the natural mortality of A.quercuscalicis is attributable to the attacks of chalcid parasites on the gall causing larvae. Askew is stated (Claridge 1963) as having seen both inquiline and parasitic species, common in Britain, in Knopper galls from France. Cobb (1971) found the remains of a hymenopterous parasite in a gall of A.quercuscalicis but was unable to identify it. I have reared an individual of Syntomaspis cyanea (Hymenoptera: Chalcidoidea) from an agamic gall of A.quercuscalicis collected from a Q.robur host from Central Park, Plymouth during November 1976. The gall was kept in a gauze covered jar in the Laboratory prior to the emergence of the chalcid during February 1977. It seems that at least some of the galls are being parasitised by chalcid species common to Britain, though I have not found any inquilines.

It is clear from this work that the numbers of parasites of A.quercuscalicis in Britain are small, possible reasons for this being due to the structure of the gall itself.

It is clear from this work that in mainland Britain the numbers of inquilines and parasites are low; reasons for this may be

related to the structure of the gall offering good protection to the gall causing larvae. However from the observations of Askew (Claridge 1963) it is more probable that by their infrequent occurrence and their relative rarity, galls of A. quercuscalicis have avoided a high degree of inquiline colonisation and parasite attack, although the gnarled gall structure with its sticky secretions must also play an important part in the prevention of attack by other insects.

CHAPTER 5RESULTS OF SAMPLING5:1 Introduction

As described in Chapter 2, sampling for the distributions of cynipid galls was undertaken both qualitatively and quantitatively. Both sampling regimes covered the full range of the indigenous oak taxa viz:- Q.petraea, Q.robur and Q.x rosacea.

The qualitative sampling programme recorded the occurrence of gall species and their numbers, along three transects. The first transect, a 'geographic' transect, covered a range of altitudes from a high level Q.robur site at Wistmans wood, along the Walkham and Tavy valley system (Figure 5 ) to a low level Q.petraea site at Warleigh wood (see section 3:2:1:11). The other two transects were across Yarner wood NNR (see section 3:2:2 ) covering a limited range of altitudes, but representing an intensive sampling regime of a single wood, with all indigenous oak taxa present.

The quantitative sampling was undertaken at six sites to determine the 'within-leaf', 'within-canopy' and 'inter-tree' distributions of galls. Comparisons between sites and hosts of differing taxa could therefore be made to determine whether hosts exhibited any preferential galling.

5:2 Results of Qualitative sampling5:2:1 Transect along the Walkham and Tavy valleys

From table 5, it is clear that the Q.robur specimens sampled along the transect hosted more species of cynipid galls, and in greater numbers, than hosts of Q.petraea. When Q.petraea specimens have a high percentage of galled leaves, this is normally due to an abundance of only a few species of gall. Conversely when Q.robur specimens have a high percentage of galled leaves, this is due to high numbers of several species of gall. The results of sampling along the Tavy/Walkham

transect clearly illustrate this trend.

In table 5 it can be seen that Q.robur hosts more species of cynipid galls and in larger numbers than Q.petraea, with hybrid oak specimens hosting species and numbers in quantities somewhere between that found on Q.petraea and Q.robur.

Table 6 lists the species which were present at each of the sampling sites along the transect. From this it can be seen that the most ubiquitous species encountered was N.quercusbaccarum which was present at all the sites, followed by A.kollari which occurred at seven of the sites, and T.megaptera (six sites) and A.curvator (five sites). The most abundant species encountered was also N.quercusbaccarum followed by N.numismalis, N.albipes and C.disticha and A.curvator. Galls of C.longiventris, A.quadrilineatus and C.quercusfolii were by far the rarest in occurrence.

These results indicate that differences occur in the numbers of species and degree of galling between differing host taxa. However whether these differences are due entirely to the taxonomic status of the host (presumably due to differing physiologies) or due to environmental factors (effects of altitude and exposure) cannot be deduced from these results alone. In order to minimise the environmental effects and to maximise any host effects upon the gall distributions, two 'within-wood' transects were sampled across Yarner wood N.N.R.

#### 5:2:2 Sampling results; Yarner Wood N.N.R. transects.

Two transects were sampled across Yarner wood (see section 3:2:2 ) each covering the range of the indigenous oak taxa; a sketch map of the reserve is given in Figure 6.

Table 7 shows the degree of galling of sample trees along the South-North transect, and table 8 for the sample trees along the West-East transect. On comparing Tables 7, 8 with Table 5 for

Site	Host taxon	% leaves galled	No.gall species
Wistmans wood	Q.robur	3.4	7
Heckwood	Q.robur	7.0	8
Ward Bridge	Q.robur	4.7	6
Dittisham	Q.robur	1.3	2
Bedford Bridge	Int.	2.3	1
Grenofen weir	Int.	6.8	2
Double waters	Int.	1.3	4
Denham Bridge	Int.	0.3	4
Lopwell Dam	Q.petraea	1.5	2
Blaxton wood	Q.petraea	1.7	3
Warleigh wood	Q.petraea	0.5	2

Table 5 .Gall occurrence along the Walkham/Tavy  
valley transect,combined years 1976-1977.

Table 6. List of the species occurring at sites along the Walkham/Tavy valley transect.

Site	Gall species	Total No.
Wistmans wood	A. curvator	
( <u>Q. robur</u> )	N. quercusbaccarum	
	T. megaptera	
	A. kollari	
	C. quercusfolii	
	A. quadrilineatus	
	A. ostreus	7
Heckwood	A. kollari	
( <u>Q. robur</u> )	A. fecundator	
	N. albipes	
	N. quercusbaccarum	
	N. numismalis	
	T. megaptera	
	A. ostreus	
	C. longiventris	8
Ward Bridge	A. kollari	
( <u>Q. robur</u> )	A. curvator	
	N. quercusbaccarum	
	T. megaptera	
	N. numismalis	
	A. quercuscalicis	6
Dittisham	A. curvator	
( <u>Q. robur</u> )	N. quercusbaccarum	2
Bedford Bridge	N. quercusbaccarum	1
Grenofen Weir (hybrid).	C. disticha	
(hybrid)	N. quercusbaccarum	2
Double Waters	A. kollari	
(hybrid)	N. quercusbaccarum	
	A. quadrilineatus	
	C. disticha	4
Denham Bridge	N. quercusbaccarum	
(hybrid)	C. longiventris	
	C. disticha	
	A. kollari	4
Lopwell Dam	N. quercusbaccarum	
( <u>Q. petraea</u> )	A. kollari	2
Blaxton Wood	A. curvator	
( <u>Q. petraea</u> )	N. quercusbaccarum	
	T. megaptera	3
Warleigh Wood	A. curvator	
( <u>Q. petraea</u> )	N. quercusbaccarum	2

Taxon	Transect point	Spring galls present	No. leaves galled/ 300 leaf sample	Autumn galls present	No. leaves galled/ 500 leaf sample
	TG29	-	-	-	-
	TG28	-	-	-	-
<u>Q. robur</u>	TG27	-	-	-	-
<u>Q. robur</u>	TG26	N.q-baccarum	1	17N.q-baccarum	5
	TG25	2 A.callidoma	-	-	-
	TG24	2 N.q-baccarum	1	5N.q-baccarum	1
	TG23	2 B.pallida	-	1N.q-baccarum 1A.ostreus	1
	TG22	-	-	-	-
Hybrid	TG21	-	-	-	-
	TG20	1 N.q-baccarum	1	1 C.disticha	1
	TG19	8 N.q-baccarum 1 B.pallida	2	-	-
<u>Q. petraea</u>	TG18	-	-	-	-
	TG17	-	-	-	-
	TG16	-	-	63N.q-baccarum	6
Hybrid	TG15	-	-	-	-
	TG14	1 B.pallida	-	-	-
	TG13	1 N.q-baccarum	1	-	-
	TG12	-	-	-	-
<u>Q. petraea</u>	TG11	-	-	9N.q-baccarum 1A.ostreus	5
	TG10	-	-	7N.q-baccarum 1A.ostreus	2
	TG9	-	-	7N.q-baccarum	2
<u>Q. petraea</u>	TG8	-	-	8.N.q-baccarum 1A.ostreus	5
	TG7	7 N.q-baccarum 1 A.curvator	3	60N.q-baccarum	6
	TG6	4 N.q-baccarum	4	90N.q-baccarum	6
Hybrid	TG5	6 N.q-baccarum	3	500N.q-baccarum 16N.albipes 2C.disticha 2A.kollari	15

Table 7. Combined monthly data for Yarner Wood South-North transect 1976. Spring data based on 300 leaf sample, Autumn data based on 500 leaf sample. (N.q-baccarum = Neuroterus quercusbaccarum).

Taxon	Transect point	Spring galls present	No. leaves galled 200 leaf sample	Autumn galls present	No. leaves galled/200
( <u>Q. petraea</u> )	TN4	-	-	-	-
	TM3	-	-	-	-
(hybrid)	TL6	3 A. curvator	2	7 N. q-baccarum	1
		4 N. q-baccarum	1		
	Tk4	1 T. megaptera	-	-	-
	TJ3	-	-	-	-
	TH3	1 B. pallida	-	-	-
	TG4	1 B. pallida	-	-	-
(hybrid)	TF2	1 T. megaptera	-	9 N. q-baccarum	2
		1 A. curvator			
	TE3	-	-	-	-
	TD3	-	-	-	-
(hybrid)	TC4	1 N. q-baccarum	1	-	-
		1 T. megaptera			
( <u>Q. petraea</u> )	TB6	-	-	6 N. q-baccarum	1

Table 8. Combined monthly data for Yarner Wood East - West transect for 1976. Data based on a random sample of 100 leaves/tree each month June - September.

Legend.

A. curvator = Andricus curvator.

B. pallida = Biorhiza pallida.

N. q-baccarum = Neuroterus quercusbaccarum.

T. megaptera = Trigonaspis megaptera.

=sexual generation gall.

=agamic generation gall.



the Walkham/Tavy transect it can be seen that similarities occur, both in the degree to which trees of the same taxonomic status are galled, and in relation to the number of gall species which occur.

Affects of altitude and exposure are largely eliminated between the trees at Yarner, and since the results obtained follow the same trends as those found in the Walkham/Tavy transect, it appears that the differences in the degree of galling between hosts of differing taxonomic status, may be more closely related to the suitability of the oaks' physiology to host galls (Q.robur being more suitable than Q.petraea with Q.x rosacea being in an intermediate position) than to any environmental conditions imposed on the oaks.

Several workers (Askew 1962 , Frankie personal communication, Frankie et al 1977 ) mention that oaks in exposed situations tend to host greater numbers of galls than those in more sheltered positions. In particular Frankie et al ( 1977) has shown that isolated oaks newly planted in the urban environment often host greater numbers of galls due to an imbalance of associated insects:- thus gall wasps reach the isolated oaks in advance of parasites, and therefore enjoy a high population for one or two years, until parasitic wasps arrive and act as a density-dependent regulatory factor. Hence a cycle of initially high numbers of galls followed by a subsequent reduction due to parasitism exists. Whether the same situation exists for naturally occurring, isolated mature oaks, is not clear. Over the three year period during which this work was undertaken, galls were relatively abundant at all the sample sites during 1975 and 1976, but during 1977 gall populations fell dramatically, which was probably less due to parasitism than to climatic conditions discussed later (section 7 ).

Another factor which may affect the degree to which galling occurs is the date of leaf burst. Askew (1962) states that

N.numismalis has a tendency to be found in greater numbers on late opening trees. N.quercusbaccarum & shows a similar tendency but is less marked. N.albipes & appears to be independent of the date of leaf burst. Askew (1962) believes that the date of leaf burst may account for the positive association he found between the agamic generations of N.quercusbaccarum and N.numismalis; however, he conceded that a large variation in numbers, of any one species of gall, also occurs for trees having the same date of leaf burst, and it is therefore likely that some other property (probably physiological) of the tree also influences galling.

The results obtained for the transects across Yarner show large variations in the degree of infestation between trees of the same and differing taxonomic status, despite the trees coming into leaf within a few days of each other.

The trend is however towards Q.robur hosting more species of cynipid galls and in larger numbers than Q.petraea. The importance of a possible physiological property of certain oaks to be more suitable to host galls is further borne out by the finds that several gall species occurred solely on Q.robur hosts (Table 1 ). These findings differ from those of Connold (1908) and Eady and Quinlan (1963) who list these species as occurring on both Q.robur and Q.petraea hosts, though this could be due to their incorrect identification of the oak hosts.

#### 5:2:2:1 Conclusion

Greater numbers of gall species, and larger numbers of galls, are found on Q.robur, even when hosts of Q.robur and Q.petraea have similar dates of leaf burst, and are subjected to the same environmental conditions. Thus some physiological property of Q.robur must make it a more suitable host for cynipid galls than Q.petraea. The intermediate galling of Q.petraea x robur hybrids, lends further

support to the contention (Cousens 1963, Rushton 1972, Wigston 1974, 1975) that hybridisation between these two species is the result of introgression.

### 5:3:0 Quantitative Sampling Results

#### 5:3:1 Introduction

The sample sites chosen for a quantitative study of the distributions of cynipid oak galls are described in Chapter 3. An explanation of the sampling technique employed is given in section 2:3:0.

The results of three differing sampling regimes are given:

- (1) the 'within-leaf' gall distributions,
- (2) 'within-tree' spatial (canopy) distributions and
- (3) 'between-tree' distributions.

In addition the sampling technique devised provided an additional distribution category (4):- the linear distribution along a sample unit consisting of a twig of ten leaves (see section 2:3:0).

#### 5:3:2 Within-leaf Distributions

All leaves bearing galls of Neuroterus spp. found during the sampling of the quantitative sites were divided into three sections along the length of the lamina, and the positions and numbers of each gall species occurring in each section was recorded. The results obtained for each of the three years 1975, 1976, 1977 are given in figures 9 , 10 , and 11 . The combined results for the three years are given in figure 12 .

The results for 1975 show that the agamic galls of N.tricolor, N.numismalis and N.quercusbaccarum tended to predominate in the apical sections of the leaves, whilst N.albipes predominated towards the middle of the leaves. The results for 1976 (figure 10 ) differ from those of 1975 in that N.albipes was found in greater numbers

Figure 9 .Within-leaf distributions of ♂  
Neuroterus galls 1975.

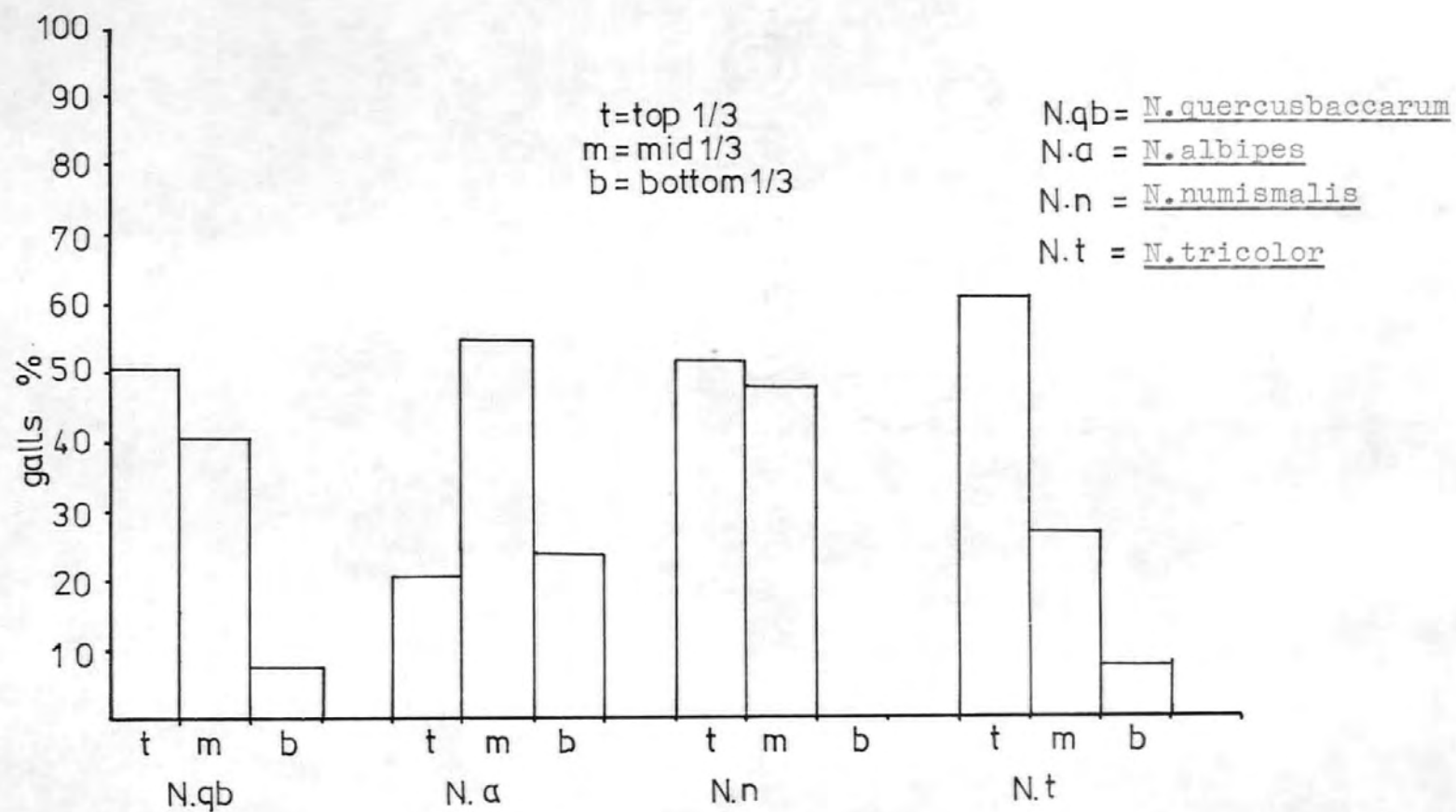
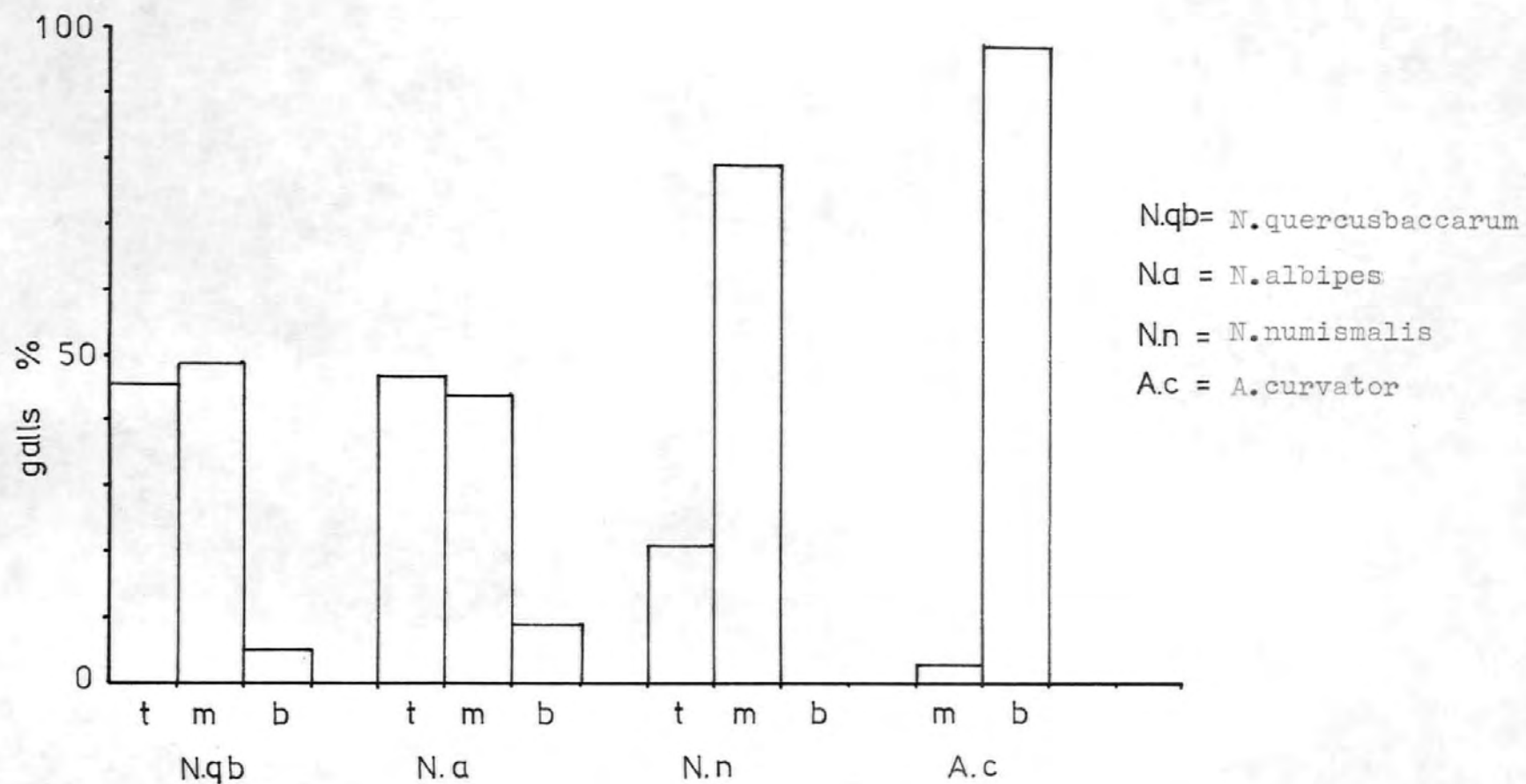


Figure 10 .Within-leaf distributions of ♂ galls  
Neuroterus spp. and ♂ ♀ galls of  
A.curvator 1976. (Notation as Fig.9).



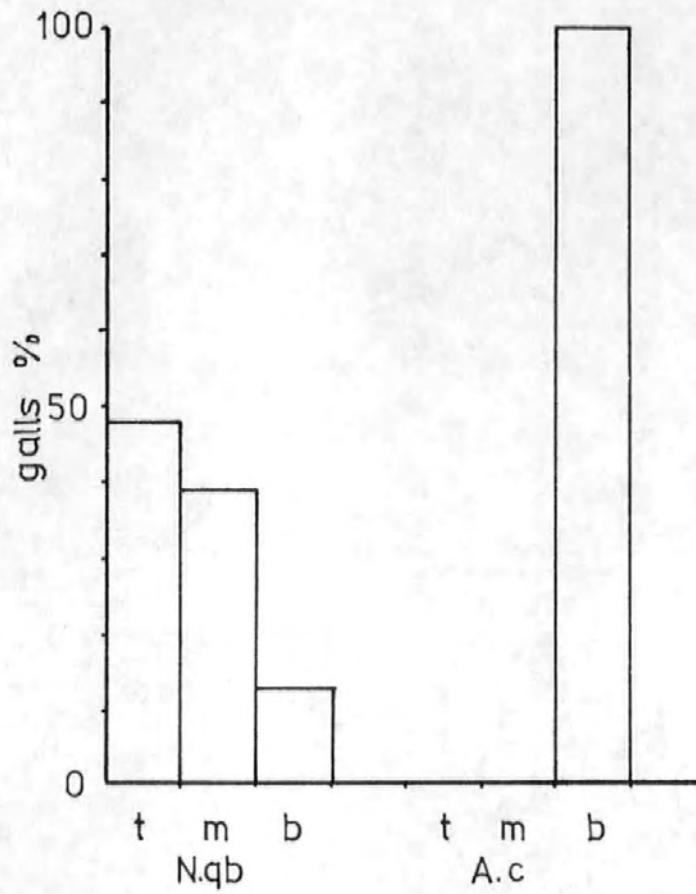
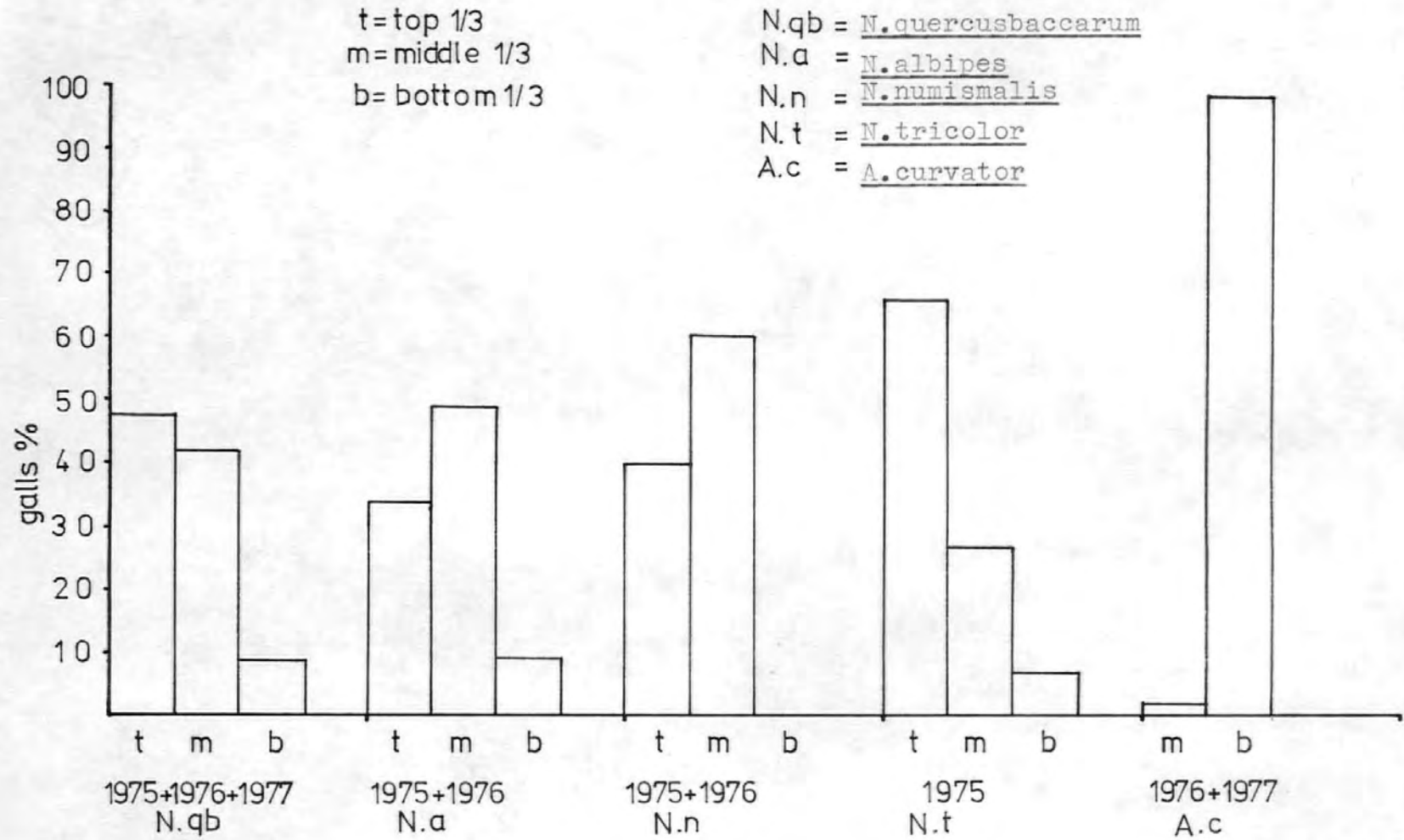


Figure 11. Within-leaf distributions of *N. quercus baccarum* galls (♂) and *A. curvator* galls (♂ ♀) 1977. (Notation as Fig.9).

Figure 12 .Within-leaf distributions of Neuroterus spp. ♂  
galls and ♂ ♀ galls of A.curvator, combined  
years data.



in the apical section, and N. quercusbaccarum and N. numismalis were found in greater numbers in the mid-leaf section, although the overall differences were small for N. quercusbaccarum and considerably larger for N. numismalis. In none of the years when N. numismalis was recorded were any of its galls found in the basal section of the leaves. In 1977 N. quercusbaccarum was again found to predominate in the apical section, and the results obtained were very similar to those of 1975 (compare figure 9 with figure 11). No data were obtained for N. albipes in 1977.

In addition to the spangle galls of Neuroterus spp. records were kept of the sexual generation galls of A. curvator which causes blister galls in the lamina of leaves (section 4:3:2). From figure 12 for the combined results for 1976 and 1977 it is clear that almost 100% of these galls occur in the basal section of the leaves. From figure 12 it is evident that N. quercusbaccarum and N. albipes have a wide range of distributions over the surfaces of leaves, while N. numismalis and A. curvator in particular have much narrower ranges of distribution.

The frequencies of gall occurrence on the leaves were calculated for the commoner gall species encountered during 1976 and 1977 (tables 9, 10). The combined frequencies for 1976 and 1977 are given in table 11. From these frequency data the variances and their means were calculated, allowing an estimate to be made of the degree of aggregation of the galls from their variance/mean ratios (Southwood 1966). The variance/mean ratios of the gall species for 1976 and 1977 are given in tables 12, 13. From these it is clear that all the gall species have ratios much greater than unity indicating that they are highly aggregated. Neuroterus spp. in particular have very large variance/mean ratios for their agamic



Number of galls/leaf	Frequency					
	1	2	3	4	5	6
0	8660	9157	9158	9160	9174	9158
1	190	3	9	3	3	5
2	83	5	8	11	0	4
3	64	1	0	3	1	1
4	36	4	0	0	0	0
5	29	0	0	0	0	5
6	16	1	0	0	0	2
7	22	7	1	0	0	0
8	18	0	0	0	0	2
9	11	0	0	0	0	0
10	8	0	1	0	0	0
11	7	0	0	0	0	1
12	2	0	1	0	0	0
13	2	0	0	0	0	0
14	1	0	0	0	0	0
15	6	0	0	0	0	0
16	4	0	0	0	0	0
17	2	0	0	0	0	0
18	1	0	0	0	0	0
19	0	0	0	0	0	0
20	2	0	0	0	0	0
21	4	0	0	0	0	0
22	1	0	0	0	0	0
29	2	0	0	0	0	0
31	2	0	0	0	0	0
35	2	0	0	0	0	0
40	1	0	0	0	0	0
42	1	0	0	0	0	0
56	1	0	0	0	0	0
75	1	0	0	0	0	0

Table 9. Frequencies of autumn generation galls  
1976, occurring on leaves.

Legend.

1 = <i>N. quercusbaccarum</i>	4 = <i>A. curvator</i>
2 = <i>N. albipes</i>	5 = <i>C. divisa</i>
3 = <i>N. numismalis</i>	6 = <i>C. disticha</i>

Table 10. Frequencies of autumn generation galls  
1977, occurring on leaves.  
(\* = species of gall not encountered  
during 1977).

Legend.

1=N. quercusbaccarum

2=N. albipes

3=N. numismalis

4=A. curvator

5=C. divisa

6=C. disticha

Number of galls/leaf	Frequency					
	1	2*	3	4	5*	6*
0	1722	1827	1816	1812	1827	1827
1	13		-	8		
2	11		-	6		
3	9		1	-		
4	8		3	-		
5	6		-	1		
6	5		1	-		
7	7		2	-		
8	2		-	-		
9	9		1	-		
10	1		-	-		
11	1		-	-		
12	4		-	-		
13	4		-	-		
14	1		-	-		
15	1		-	-		
16	5		-	-		
17	1		-	-		
18	2		-	-		
19	1		-	-		
20	-		-	-		
21	2		-	-		
22	-		-	-		
23	2		-	-		
24	-		-	-		
25	1		-	-		
26	-		1	-		
27	1		-	-		
<u>29</u>	1		-	-		
<u>30</u>	1		-	-		
<u>35</u>	1		-	-		
<u>36</u>	1		-	-		
<u>37</u>	2		-	-		
<u>40</u>	1		-	-		
<u>41</u>	1		-	-		
<u>43</u>	-		1	-		
<u>50</u>	-		1	-		
<u>75</u>	1		-	-		

Table 10.

Number of galls/leaf	Frequency						
	1	2	3	4	5	6	7
0	10377	11245	11303	11295	11291	11291	11274
1	203	29	2	8	4	3	9
2	94	20	1	2	4	6	7
3	73	7	-	1	2	1	1
4	44	4	-	-	1	3	3
5	35	1	-	-	-	-	-
6	21	-	-	-	1	1	1
7	29	-	-	-	-	1	3
8	20	-	-	-	2	-	-
9	20	-	-	-	-	-	-
10	9	-	-	-	-	-	1
11	8	-	-	-	1	-	-
12	6	-	-	-	-	-	-
13	6	-	-	-	-	-	-
14	2	-	-	-	-	-	-
15	7	-	-	-	-	-	-
16	9	-	-	-	-	-	-
17	3	-	-	-	-	-	-
18	3	-	-	-	-	-	-
19	1	-	-	-	-	-	-
20	2	-	-	-	-	-	-
21	6	-	-	-	-	-	-
22	1	-	-	-	-	-	-
23	2	-	-	-	-	-	-
24	-	-	-	-	-	-	-
25	1	-	-	-	-	-	-
26	-	-	-	-	-	-	1
27	1	-	-	-	-	-	-
28	-	-	-	-	-	-	-
29	3	-	-	-	-	-	-
30	1	-	-	-	-	-	-
31	1	-	-	-	-	-	-
32	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-
34	-	-	-	-	-	-	-
35	3	-	-	-	-	-	-
36	1	-	-	-	-	-	-
37	2	-	-	-	-	-	-
40	2	-	-	-	-	-	-
41	1	-	-	-	-	-	-
42	1	-	-	-	-	-	-
43	-	-	-	-	-	-	1
50	-	-	-	-	-	-	1
56	1	-	-	-	-	-	-
75	1	-	-	-	-	-	-

Table 11. Frequencies of autumn generation leaf galls,  
1976 and 1977 combined data.

Legend.

1=N. quercusbaccarum

5=C. disticha

2=A. curvator

6=N. albipes

3=C. divisa

7=N. numismalis

4=A. ostreus

<u>Species</u>	<u>Variance/mean ratio</u>
N.quercusbaccarum	13.87
N.albipes	5.48
N.numismalis	6.18
A.curvator	2.36
C.disticha	5.94
C.divisa	2.01

Table 12.Variance to mean ratios for the agamic  
generation galls 1976.

<u>Species</u>	<u>Variance/mean ratio</u>
N.quercusbaccarum	18.76
N.albipes	*
N.numismalis	32.5
A.curvator	2.31
C.disticha	*
C.divisa	*

Table 13.Variance to mean ratios for the agamic  
generation galls 1977.(\* no records for  
1977).

generation, indicative of high levels of aggregation. Since Neuroterus spp. utilise similar resources and have similar requirements for space, high aggregations of galls would tend to impose conditions where competition would result, a situation which is discussed in further detail in sections 5:3:3:, 5:3:5 and 6:3.

### 5:3:3 Discussion

Apart from A.curvator which is almost entirely restricted to the basal regions of the leaves, the apical and middle sections of the leaves are selected most often as sites for oviposition.

The two numerically commonest species of Neuroterus, N.quercusbaccarum and N.numismalis, predominate in different sections of the leaves. N.quercusbaccarum predominates in the apical section, and is also found in the middle and basal sections, while N.numismalis predominates in the mid-leaf area and was solely restricted to this and the apical leaf area. Galls of N.albipes predominated in the mid-leaf region, though they were occasionally found occurring towards the apices and bases of the leaves. Fewer galls of N.albipes were encountered than N.quercusbaccarum and N.numismalis, and the galls most often occurred in the mid-lamina region close to the mid-vein. N.numismalis galls tended to develop close to the margins of the leaves, particularly those found in the apical region. N.quercusbaccarum galls were found in all positions on the leaves, and did not appear to occupy any favoured sites.

Hough (1953C) working on the within-leaf distributions of the common spangle gall (N.quercusbaccarum) found that the apical region of the leaves hosted the greatest ratio of galls per unit area. He explained these findings as being due to female wasps, of the sexual generation, selecting areas of the leaves which are expanding at the maximum rate, as sites for oviposition; Hough (1953C) and Ashby (1948, 1948a) have shown that the maximum rate of growth occurs towards the apices of leaves. Hough (1953C) explained why

some trees were heavily infested with galls and others having minimal or no infestation in terms of leaf burst; trees whose leaves were not at the ideal developmental stage for oviposition therefore do not support heavy infestations.

Since N. quercusbaccarum has an earlier flight period (Askew 1962) than N. numismalis it has a greater choice of egg laying sites, explaining its predominance in the apical regions of the leaves. The flight periods of all Neuroterus spp. overlap to some extent, with N. numismalis being the last species seeking sites for oviposition. It appears likely that N. albipes selects mid-leaf sites as a means of avoiding competition with N. quercusbaccarum which was numerically the commonest species encountered. Competition between N. albipes and N. numismalis in the mid-leaf areas may to some extent be alleviated by N. albipes occurring towards the centre of the lamina while N. numismalis occurs more towards the leaf margins, and because N. albipes has the longest flight period which begins before that of N. quercusbaccarum and ends mid-way through that of N. numismalis.

Askew (1962) working on the within-leaf distributions of the agamic galls of Neuroterus spp. found that N. numismalis galls predominated in the apices of leaves, N. quercusbaccarum predominated in the mid-leaf area and N. albipes tended towards the bases. Hough (1953c) working on the within-leaf distributions of N. quercusbaccarum, found that these galls predominated at the apices of the leaves and that numbers progressively decreased towards the leaf bases. The results presented here for N. quercusbaccarum are in agreement with those of Hough (1953c), and differ from those of Askew (1962). These differences may be explained by the fact that Askew (1962) worked on the distributions of galls on the leaves of young oaks, whereas the work of Hough (1953c) and that presented here was based on leaves from mature oaks. Askew (1962) points out that during his study the mature oaks came into leaf two weeks

before the young trees, and it seems possible that the difference between these results may be due to the availability of suitable oviposition sites during the flight periods. This could explain the predominance of N.numismalis galls in the leaf apices of young oaks recorded by Askew (1962), since having the latest flight period the leaves of young oaks would be more suitable for oviposition later, than the leaves on mature trees. Conversely, N.quercusbaccarum with its earlier flight period would find sites suitable for oviposition earlier, and these would tend to be on mature oaks since they are in leaf earlier. Such an explanation would account for the much greater numbers of N.quercusbaccarum encountered on mature oaks, than of N.albipes and N.numismalis.

The mechanism by which gall wasps select suitable sites for oviposition is unknown, though the ability to select leaves of different stages of development has been shown in the aphid Aphis fabae Scob. (Kennedy et al. 1950, Ibbotson and Kennedy 1950). Hough (1953) postulated that the selection of suitable leaves is probably related to the translocation of complex nitrogenous substances in the phloem of young and senescent leaves. If this is the case and there is a difference in physiology between Q.robur and Q.petraea, this would help to explain the greater occurrence of galling in Q.robur than in Q.petraea.

Rosenthal et al. (1971) who worked on the inter-tree distributions of galls on Q.lobata Nee., postulated that gall formation may be affected by concentrations of auxins, from within the plant, acting on the plant cells which make up the gall, as well as by the insect within it. If this is so it would mean that the sexual generation females could detect the differences in auxins concentrations within the leaf, when selecting suitable sites in which to oviposit.



It seems evident from the work of several authors (Burdick 1967, Marsden-Jones 1953) on the oviposition behaviour of cynipid wasps, that the wasps are careful in their selection of sites, and do not oviposit at random. It is evident that some wasp species will only oviposit in certain of closely related oak taxa. Sites into which eggs have already been laid but which show no evidence of gall development, may be detectable by fecund females, and hence they may be able to avoid competition with other fecund females.

The work of Jankiewicz et al. (1970) on the translocation of  $^{14}\text{C}$  labelled assimilates to galls of C. quercusfolii found that galls were powerful physiological sinks for assimilates and mineral nutrients. Thus, it would seem likely that as well as competition for egg-laying sites, and for space for the galls to develop, there is also competition for the nutrients required for the gall development on which the larvae depend.

#### 5:3:4 Within-Tree Distribution

Askew (1962) working on the distributions of Neuroterus spp. galls on small oaks averaging 10 feet high, showed that there was both a vertical and horizontal separation in the distributions of these galls. He found that N. numismalis tended to predominate towards the tops of the trees and towards the ends of the branches; N. quercusbaccarum predominated in the middle position both vertically and horizontally, while N. albipes predominated towards the bottom of the tree, close to the bole.

During the course of this work the distribution of galls on mature oaks was investigated; as well as the vertical and horizontal distributions, the aspect of the galls on the oaks was also recorded to determine if there was any preferential galling on the sides facing or sheltered from the prevailing winds.

Results for the height distributions of the sexual generation galls of N. quercusbaccarum for 1976, occurring at all aspects, distances from the bole (horizontal distribution) and sample sites are given in table 14. From this it can be seen that the greatest percentage of leaves galled by N. quercusbaccarum (5.46% of leaves) occurs at between heights of 6-8 metres. The results for the horizontal distributions of the sexual generation galls are given in table 15, for N. quercusbaccarum, for all sites and aspects. From these it is clear that the galls tend to predominate close to the bole, and their distribution tails off towards the periphery of the crown. (Due to the scarcity of sexual generation galls of other Neuroterus spp. this information was only recorded for N. quercusbaccarum).

The distributions of the agamic, spangle galls of the three most common species of Neuroterus encountered during this work, were also investigated. From table 16 it is clear that the agamic galls of all Neuroterus spp. predominate at heights of 2.0 metres, and that N. quercusbaccarum was by far the commonest species recorded. The horizontal distributions of the galls are given in table 17; from which it is apparent that all three species of Neuroterus (N. quercusbaccarum, N. albipes and N. numismalis) predominate towards the end of the branches away from the bole. Such a result is probably due to the morphology of the oaks, whose structure is such that the foliage tends in the main to be around the periphery of the crown, with little leaf development within the crown. Wasps seeking site to lay their eggs will therefore be attracted to these areas where leaf growth is most pronounced.

This situation in mature oaks with large crown, differs greatly from that found by Askew (1962) with small oaks. In the case of small sapling oaks, leaves are produced along the whole length of the branches, a situation which does not exist in mature oaks. The horizontal and vertical distributions of galls found on mature

Height (metres)	% leaves galled	Mean No. galls/leaf	St.error
0 - 2	1.065	0.0128	0.0045
2 - 4	1.482	0.0222	0.0046
4 - 6	3.798	0.0422	0.0094
6 - 8	5.455	0.0545	0.0217
8 -10	2.001	0.02	0.02

Table 14 .The vertical distribution of ♂ ♀ galls of N.quercusbaccarum 1976.Data from all aspects, distances and sites.

Distance (metres)	% leaves galled	Mean No. galls/leaf	St.error
0 - 2	2.863	0.0344	0.0066
2 - 4	2.2	0.0326	0.0072
4 - 6	0.745	0.0075	0.003
6 - 8	0.202	0.002	0.002
8 -10	1.471	0.0147	0.0142

Table 15 .The horizontal distribution of ♂ ♀ galls of N.quercusbaccarum 1976.Data from all aspects,sites and heights.

	Height (metres)	No.leaves sampled	%leaves galled	No.galls	Mean No. galls/leaf	St.error
N. quercus baccarum	0 - 2	1375	9.309	541	0.394	0.053
	2 - 4	5861	5.801	1483	0.253	0.024
	4 - 6	1729	2.082	130	0.075	0.034
	6 - 8	214	6.5	121	0.565	0.226
	8 - 10	0	0	0	0	
N. numismalis	0 - 2	1375	1.16	108	0.079	
	2 - 4	5861	0.26	108	0.018	
	4 - 6	1729	0	0	0	
	6 - 8	214	0	0	0	
N. albipes	0 - 2	1375	0.58	27	0.02	
	2 - 4	5861	0.085	8	0.0014	
	4 - 6	1729	0.058	7	0.004	
	6 - 8	214	0	0	0	

Table 16. The vertical distribution of Neuroterus spp.  
spangle ( 8 ) galls 1976. Data from all  
aspects, distances and sites.

	Distance (metres)	No.leaves sampled	%leaves galled	No.galls	Mean No. galls/leaf	St.error
N. quercusbaccarum	0 - 2	3353	3.042	328	0.098	0.014
	2 - 4	2797	4.97	389	0.139	0.017
	4 - 6	1749	6.518	562	0.3213	0.054
	6 - 8	1215	12.017	872	0.718	0.102
	8 -10	65	27.69	125	1.923	0.714
N. numismalis	0 - 2	3353	0	0	0	
	2 - 4	2797	0	0	0	
	4 - 6	1749	0.343	64	0.037	
	6 - 8	1215	2.06	152	0.125	
	8 -10	65	0	0	0	
N. albipes	0 - 2	3353	0	0	0	
	2 - 4	2797	0	0	0	
	4 - 6	1749	0.114	8	0.005	
	6 - 8	1215	0.99	34	0.028	
	8 -10	65	0	0	0	

Table 17 .The horizontal distribution of Neuroterus spp.  
spangle galls ( ♂ ) 1976.Data from all aspects  
heights and sites.

oaks are therefore indicative of the morphologies of the oaks rather than as a result of inter-specific competition. Competition and site selection almost certainly determines the within-leaf, and within-sample distributions, as discussed in sections 5:3:2 and 5:3:6.

The affect of the aspect on the distributions of galls was also investigated, in order to determine whether the windward surfaces of the oaks were galled more frequently than other surfaces of the oaks. The wind can have at least two effects on exposed trees. The sides facing the prevailing winds take the full force of the wind, and also whilst the tree acts as a wind break it creates eddies around itself, so drawing movements of air back upon itself from a direction opposite to that of the prevailing wind. Since the wind appears to be the major mechanism for the dispersal of cynipid wasps, the distributions over the crowns of oaks may be related to the prevailing winds and the ways they act upon the oak host.

As well as recording the vertical and horizontal distributions of the galls, the aspects at which they occurred was also recorded in 20° segments around the crown. Table 18 summarises the results for the agamic galls of N.quercusbaccarum for 1976, which combine the data for all heights and distances from all the quantitative samples sites. It can be seen that the North-Westerly and North-Easterly aspects had smaller percentages of galled leaves than aspects from the South-East, through South to South-West. When the data for N.quercusbaccarum for 1977 are combined with that of 1976 (Table 19) it can be seen that the leaves occurring in the West aspect, through South to East, were much more heavily infested than occurred in aspects to the North of the East-West 'divide'. Since the prevailing winds in the area of study are from the South-West, it could be deduced that high densities of galling would occur in the region of 225°.

Aspect	No.leaves sampled	% leaves galled	No.galls	Mean No. galls/leaf	St.error
0-20	768	5.33	170	0.2214	0.036
20-40	473	4.44	131	0.277	0.088
40-60	355	3.66	56	0.1577	0.068
60-80	570	4.21	74	0.129	0.033
80-100	367	7.09	68	0.185	0.047
100-120	461	7.81	231	0.501	0.189
120-140	676	6.21	169	0.25	0.072
140-160	583	8.748	226	0.387	0.095
160-180	634	3.15	61	0.096	0.031
180-200	571	5.6	155	0.271	0.062
200-220	565	8.67	244	0.432	0.09
220-240	478	3.97	79	0.165	0.078
240-260	469	5.54	114	0.243	0.064
260-280	399	9.52	196	0.49	0.103
280-300	374	6.42	71	0.189	0.047
300-320	347	1.44	65	0.187	0.162
320-340	514	4.67	73	0.142	0.035
340-360	585	4.79	93	0.16	0.05
Totals	9189		2209		

Table 18 .The distributions of the common spangle gall  
N. quercus baccarum (8) 1976, in terms of aspect.  
 Data from all quantitative sites, for all  
 heights and distances.

Aspect (0°)	No.leaves sampled	% leaves galled	No.galls	Mean no. galls/leaf
0- 20	908	4.85	211	0.232
20- 40	605	4.63	239	0.395
40- 60	463	3.89	119	0.257
60- 80	678	3.69	83	0.122
80-100	451	7.98	210	0.466
100-120	578	6.92	307	0.531
120-140	843	6.29	252	0.299
140-160	702	8.12	267	0.38
160-180	783	3.96	179	0.229
180-200	671	5.37	172	0.256
200-220	713	7.85	295	0.414
220-240	654	5.2	155	0.237
240-260	571	5.43	277	0.485
260-280	477	9.02	276	0.579
280-300	472	6.14	91	0.193
300-320	608	1.48	98	0.161
320-340	622	3.86	73	0.117
340-360	685	4.82	139	0.203

Table 19. Distributions of the common spangle gall(8)  
N.quercusbaccarum in terms of aspect,  
combined data for 1976 and 1977. Data from  
all quantitative sample sites, and for all  
heights and distances.



In the areas of the canopy occupying<sup>123</sup> the aspects from  $300^{\circ}$ , through North to  $80^{\circ}$ , there is a noticeable fall in the percentage of leaves galled (mean 3.89% leaves galled, compared with 6.6% for aspects  $180^{\circ}$ - $270^{\circ}$ , and a mean of 6.7% for aspects  $90^{\circ}$ - $180^{\circ}$ ).

It is probable therefore that the wind affects the distribution of galls within the canopies of mature oaks, in so far as aspect is concerned, though the positions within the leaves is due to other causes discussed elsewhere (see sections 5:3:3, 5:3:6).

#### 5:3:5 Inter-tree distributions

Inter-tree distributions, for the quantitative sample sites, were investigated to determine the effects of exposure on the gall infestation of oak hosts. At each of the three wooded quantitative sample sites, Piles copse (Q.robur), Wistmans wood (Q.robur) and Ausewell rocks (Q.petraea), two trees were sampled; one within the wood canopy and the other in an exposed position at the edge of the wood. The trees at the other quantitative sample sites were all in exposed situations. The differences in galling between the exposed and sheltered trees were summarised in table 20, spring generation 1976 and table 21 autumn generation 1976. From table 20 it is clear, with the exception of Ausewell rocks, that oaks in exposed situations hosted more gall species and had a greater number of their leaves galled, than the oaks in more sheltered situations. A similar situation also existed for the autumn generation galls 1976 (table 21), which with the exception of Piles copse, showed that the exposed hosts harboured larger numbers and more species of gall than sheltered hosts. The reasons for the differences in galling densities between exposed and sheltered oaks is almost certainly related to wind exposure. The wind acts as the major agent of dispersal of the

Site	Status	Number of species open	wood	% of leaves open	galled wood
Ausewell	Q.p	2	4	11.6	1.7
Piles	Q.r	3	2	3.89	0.54
Wistmans	Q.r	3	2	2.33	1.08
Meavy	Int.	5	-	7.89	-
Roborough	Int.	4	-	1.73	-
Harford 1	Q.r	3	-	0.22	-
Harford 2	Q.r	0	-	0	-

Table 20. Comparison of the number of species and the percentage of leaves galled, from six sites spring generation 1976.

Site	Status	Number of species open	wood	% of leaves open	galled wood
Ausewell	Q.p	3	3	5.34	1.3
Piles	Q.r	5	4	0.38	10.7
Wistmans	Q.r	5	3	5.8	4.6
Meavy	Int.	10	-	7.0	-
Roborough	Int.	4	-	0.52	-
Harford 1	Q.r	4	-	5.4	-
Harford 2	Q.r	1	-	0.24	-

Table 21. Comparison of the number of species and the percentage of leaves galled, from six sites autumn generation 1976.

(Q.p = Q.petraea; Q.r = Q.robur; Int. = Oaks of hybrid status Q.x rosacae).

adult wasps, and its effects on the distribution of galls is further discussed in section 5:3:4.

It is apparent from the data from the qualitative sample sites (sections 5:2:1, 5:2:2) than Q.robur hosts more gall species and in greater numbers than Q.petraea. Hybrid oaks are more difficult to categorise in terms of their gall compositions, and show no clear patterns. The hybrid sample oak at Roborough hosted few gall species in low numbers for both the generations in 1976, while the sample tree at Meavy hosted more species of gall than were found on any tree of either Q.robur or Q.petraea.

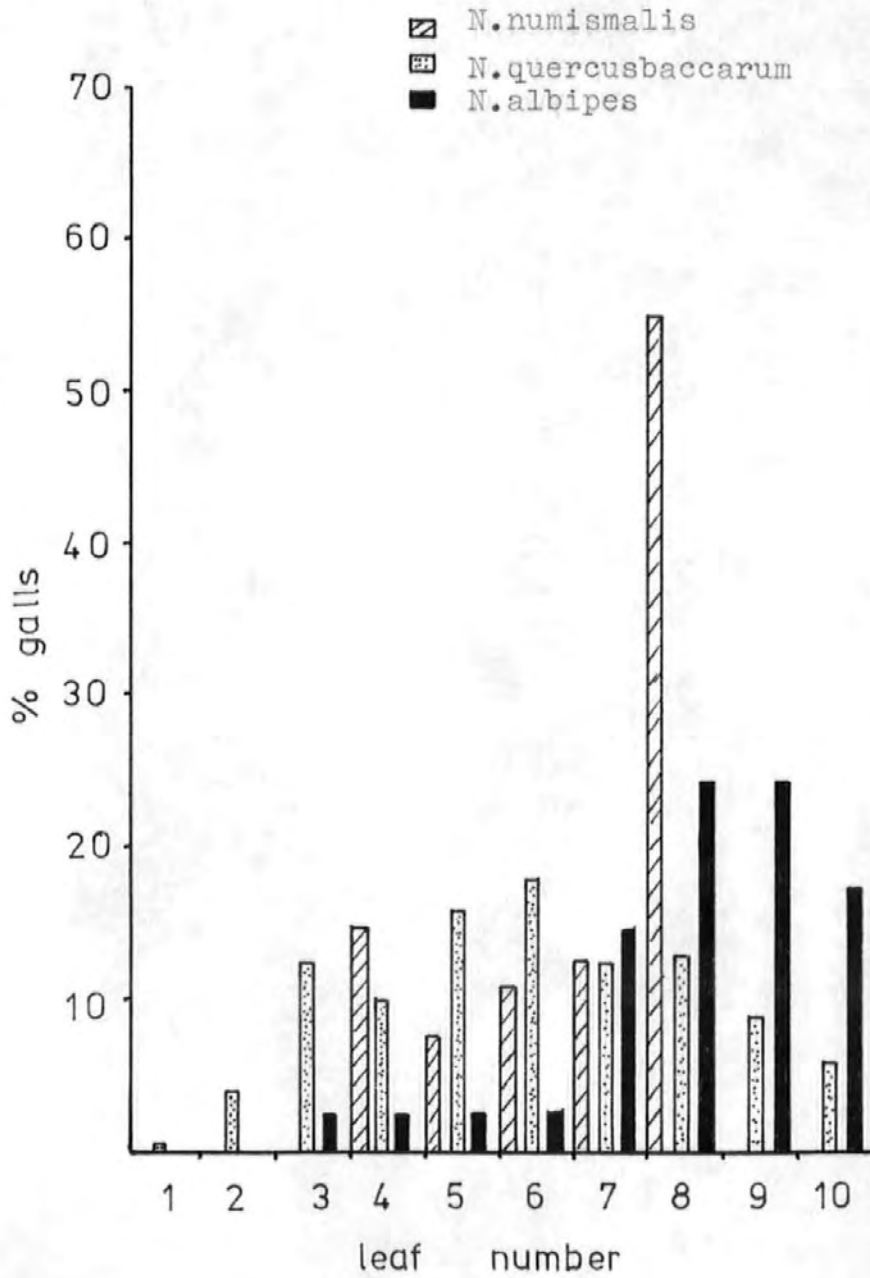
Many factors contribute to the gall distributions on oaks, the degree of exposure of the host to wind and the date of leaf burst, but it is clear that Q.petraea hosts are less suitable to act as hosts to cynipid oak gall wasps, than Q.robur.

#### 5:3:6 Results for the Within-Sample Distributions

The method of sampling the quantitative sites utilised the collections of leaf clusters, each having up to 10 leaves in each (section 2:3:0). Each leaf in a sample unit was assigned a number from 1 (basal leaf) to 10 (apical leaf). The species of galls, their numbers, and positions, on each of the leaves were recorded, giving information on the distributions within the sample units (leaf clusters), as well as on the distributions within the leaves themselves (sections 5:3:2, 5:3:3).

The within-sample distributions of agamic galls of N.quercusbaccarum, N.albipes and N.numismalis are given in figure 13. It is clear that the distribution of N.quercusbaccarum covers the range of the sample unit, peaking at leaf number 6. The distribution for N.albipes is offset, and peaks at leaves 8 and 9 with no galls occurring on the basal leaves 1 and 2. While leaves 3, 4, 5 and 6

Figure 13. The distributions of  $\delta$  Neuroterus spp. galls within the sample units, 1976.



host only a very small percentage of the galls (20% of galls occurring on these 4 leaves). The galls of N.numismalis peak at leaf 7 where 53% of them occurred. Leaves 1 and 2 (basal leaves) and 8, 9 and 10 (apical leaves) were totally devoid of galls caused by N.numismalis. During leaf burst the basal leaves of the cluster open first and the apical leaves last. If these distributions and the separation between the species which occurs is related to leaf burst, it would seem apparent that N.quercusbaccarum, which occurred on all the leaves, has a longer flight period than either N.albipes or N.numismalis (or is able to utilise leaves at different stages of development) because it peaks in activity at a time when leaves 5 and 6 are most suitable for ovipositing in. Similarly the flight period for N.numismalis would appear to be much shorter and later than that of N.quercusbaccarum, with oviposition activity taking place when leaves 3-7 are available and peaking when leaf 7 is available. N.albipes would have a flight period with a duration somewhere between that of N.quercusbaccarum and N.numismalis, since galls were found on leaves 3-10, with their numbers peaking towards the apical leaves (8 and 9). Askew (1962) worked on the timing of the life cycles of Neuroterus spp., and from his data, apart from N.tricolor which is not discussed here, N.numismalis sexual females have the latest flight period, and were observed by him ovipositing during the first half of June, N.quercusbaccarum from the end of May to the beginning of June, and N.albipes from the middle of May to the beginning of June. The flight periods of all three species overlap to a degree, though N.albipes with the earliest and longest flight period would appear to have the greatest choice of oviposition sites, followed by N.quercusbaccarum and N.numismalis. From the results it can be deduced that N.quercusbaccarum is more a generalist in its choice of sites, whilst N.numismalis with its late flight period has had to become more of a specialist (determined by the remaining available sites after N.quercusbaccarum and N.albipes have oviposited).

CHAPTER 6.6:0 Community Ecology of the Oak-Gall complex.6:1 Introduction

Using the raw data from the work on gall distributions (sections 5:2, 5:3.) analysis was undertaken to discover if there are any associations between the taxonomic status of the oaks and their gall complements. Factors influencing competition and niche partitioning between species were also investigated, together with other population regulatory mechanisms. The study of gall distributions (section 5:3:2) showed that there is niche separation between the leaf-galling Neuroterus spp.. This separation may be controlled by such mechanisms as differing adult flight periods, differing dates of leaf burst, differing rates of dispersal of adult wasps and possibly by competition for space between ovipositing females. In order to investigate these aspects the data on the distributions were analysed to examine the extent of interspecific interactions, including association and competition.

6:2 Association Analysis

Association analysis was carried out between habitats (sites), gall species on the trees, and gall species on individual leaves. Matrices for sites x sites (in terms of gall species) and species x species were drawn up from the basic data in the form of presence or absence (Figures 14, 15). Using the data contained in these matrices association coefficients were calculated from 2 x 2 contingency tables of the form:

		O.T.U. X		
		+	-	
O.T.U. Y	+	a	b	a+b
	-	c	d	c+d
		a+c	b+d	n

[illegible]

Raw data matrix of sampling sites x sampling sites in terms of numbers of species in common, combined data for years 1976 and 1977.

A=A. robur  
B=A. petraea  
C=A. intermedia  
D=A. callidoma  
E=A. curvator  
F=A. fecundator  
G=A. inflator  
H=A. kollari  
I=A. ostreus  
J=A. quadrilineatus  
a=A. quercuscalicis  
l=A. quercusradicis  
n=A. quercusarumuli  
N=B. pallida  
O=C. disticha  
P=C. divisa  
Q=C. longiventris  
R=C. quercusfolii  
S=N. albigipes  
T=N. numismalis  
U=N. quercusbaccharum  
V=N. tricolor  
W=T. megaptera

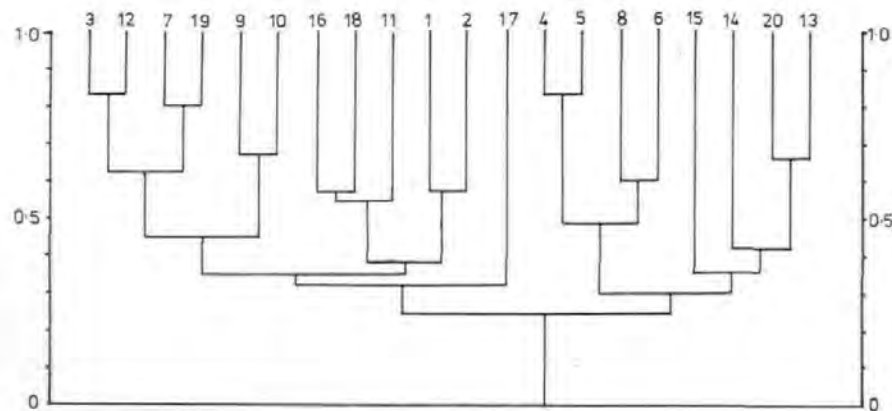
- 1=Burrator  
2=Speech House(Dean)  
3=Lymptone  
4=Roborough  
5=heavy  
6=Harford 1  
7=Harford 2  
8=Piles 1  
9=Piles 2  
10=Histmans 1  
11=Histmans 2  
12=Ausewell 1  
13=Ausewell 2  
14=Heckwood  
15=Ward Bridge  
16=Dittisham  
17=Bedford Bridge  
18=Grenofen  
19=Double waters  
20=Denham bridge  
21=Lopwell dam  
22=Blaxton wood  
23=Warleigh wood  
  
24-47 =South-North transect  
across Yarnar wood.  
48-58 =West-East transect  
across Yarnar wood.

Figure 15. Raw data matrix gall species x sites, for gall presence or absence.



(5+4)A	.49	.325	.405
(4+12)B	.38	.195	
(7+10)C	.285	.13	
(4+10)D	.17	.285	
(13+20)E	.275	.15	
(3+0)F			.358
(6+3)F	.25	.25	
(16+18)G	.315	.325	
(1+2)H			
(0+11)G <sup>1</sup>			
(F+A)F <sup>1</sup>			
(D+C <sup>1</sup> )C <sup>1</sup>			
(B+14)B <sup>1</sup>			
(I+C <sup>1</sup> )C <sup>1</sup>			
(E <sup>1</sup> +15)E <sup>1</sup>			
(G <sup>1</sup> +16)G <sup>1</sup>			
(Q <sup>1</sup> +17)Q <sup>1</sup>			
(P <sup>1</sup> +18)P <sup>1</sup>			
(U <sup>1</sup> +19)U <sup>1</sup>			

A	B	C	D	E	G'	F	G	H	G'	F'	C''	E'	G''	E''	G'''	G'''
.480																
.478	.618															
.41	.41															
.338	.328	.39														
.434			.38													
.508			.443	.359												
.494			.203	.263	.135											
.295			.358	.233	.408	.278										
.305			.378	.213	.281	.25	.32									
.368			.292	.224	.414	.19		.375								
			.307	.301	.205			.278	.279							
			.37					.330	.353	.256						
								.153	.201	.290	.289					
										.279	.342	.177				
										.29	.271		.239			
										.268					.235	
										.274					.212	



1. Highborough Down.
2. Heavey.
3. Harford 1.
4. Harford 2.
5. Piles copse (open).
6. Piles copse (wood).
7. Wistmans wood (open).
8. Wistmans wood (wood).
9. Auswell rocks (wood).
10. Auswell rocks (open).
11. Heckwood.
12. Ward bridge.
13. Dittisham.
14. Bedford bridge.
15. Grenofen weir.
16. Double waters.
17. Lenham bridge.
18. Lopwell dam.
19. Maxton wood.
20. Warleigh wood.

Where O.T.U's (Operational taxonomic unit) are gall species.

- " c is the number of occurrences of species X alone.
- " b is the number of occurrences of species Y alone.
- " a is the number of joint occurrences of species X and Y.
- " d is the number of non-occurrences of both X and Y.
- " n is the total number of samples.

The coefficient of association chosen is that of Jaccard (1908) which ignores the consideration of mismatches (d in the contingency table) which are considered as having no relevance in this context since the lack of galls cannot indicate the presence of interactions between galls. Sneath and Sokal (1973) give Jaccard's coefficient as

$$S_J = \frac{a}{a+b+c}$$

As the value for  $S_J$  tends towards 1.0 from 0, the greater is the degree of association between the species under consideration. Values of  $S_J$  which are greater than 0.5 are indicative of positive associations. Jaccard's coefficient was used in preference to that of Czekanowski (1932), which also ignores conjoint absences and is given as

$$\frac{2a}{2a + b + c}$$

This was because of the likelihood of many conjoint presences making Jaccards coefficient more attractive, because it gives a wider spread of values at the upper end of the range than Czekanowski's coefficient.

#### 6:2:1 Association between Habitats (sites)

The community matrix of Jaccards coefficients for sites is given in figure 16. From this a new matrix can be generated by use of single link clustering techniques (Everitt 1974, Sokal and Sneath 1963) whereby sites with the highest level of association are combined, and substituted in the matrix as a 'single site' A,B, whose associations

with the remaining sites are, by convention, the average association with each of site A and site B

$$\left[ \alpha_{c,AB} = \frac{\alpha_{cA} + \alpha_{cB}}{2} \right]$$

Where  $\alpha_{cA}$  is the coefficient of interaction, which in this case is given by Jaccard's coefficient.

This procedure is repeated until only a single value remains in the generated matrix. From this a dendrogram is constructed to show pictorially the clustering of entities (sites or gall species).

#### 6:2:1:1 Results of Association Analysis

The highest level of association occurred between sites 4 (Harford 2) and 5 (Piles copse, open situation) and between sites 3 (Harford 1) and 12 (Ward Bridge), both having a value of  $S_J = 0.83$  (figure 16). Lower values of association are seen to occur between sites 7 (Wistmans wood, open situation) and 19 (Blaxton wood) with a value  $S_J = 0.8$ .

From the dendrogram (figure 16) it can be seen that the cluster at C' (sites 3,12,7 and 19) are all Q.robur sites in exposed situations, with the exception of 19 (Blaxton wood) which is a sheltered Q.petraea site. The D cluster (sites 9 and 10) is comprised of Ausewell rocks open and exposed sites, which are both Q.petraea. The D cluster clusters with C' at C'' with a value of  $S_J = 0.443$ .

Another strong association exists between sites 6 and 8 (Piles copse, sheltered situation and Wistmans wood, sheltered situation) which cluster with a value of  $S_J = 0.6$  at F. These sites, both Q.robur in sheltered positions, are topographically very similar (sections 3:3:1:1, 3:3:1:2), being typical Dartmoor oakwoods on west-facing valley sides.

Sites 1 and 2 (Meavy and Roborough Down) of intermediate taxonomic status also display a strong association clustering at H with a value  $S_J = 0.57$ . The H cluster links with G' (sites 16, 18 and 11) at

G'' with a value  $S_J = 0.375$ .

Site 17 (Denham bridge) has a low level of association with other sites, and clusters with G''' with a value  $S_J = 0.319$ . This was described in section 3:2:1:8 as being atypical of the site in that it was a small oak surrounded by large mature standards.

Although a few apparent anomalies of association between the sites occur, it is evident that trees of the same taxonomic status existing in similar topographies tend to be highly associated, in terms of gall species. Therefore it is both the taxonomic status of the host tree and its degree of exposure which influences, and possibly determines, gall occurrences.

#### 6:2:2 Associations between gall species

Community matrices and dendrograms, for spring and autumn-generation galls, were constructed from data gathered from both the 'qualitative' Walkham/Tavy valley transect and the eight 'quantitative' sampling sites. All the data were treated qualitatively for this analysis. The community matrix in terms of Jaccard's coefficients and its corresponding community dendrogram for spring generation galls are given in figure 17. From this it can be seen that the highest degree of association exists between species 5 (N.albipes) and species 6 (N.numismalis) with a value of  $S_J = 0.667$ . The B cluster between species 1 (A.curvator) and 7 (N.quercusbaccarum) with a value of  $S_J = 0.455$  displays the next highest degree of association.

The A''' cluster containing species 1,3,4,5,6 and 7 (A.curvator, A.quadrilineatus, A.quercusramuli, N. albipes, N. numismalis and N. quercusbaccarum) consists of leaf galls with the exception of A.quercusramuli which galls catkins. The association between A.quercusramuli, N.albipes and N.numismalis is at a low level ( $S_J = 0.275$ ) and is of no significance. Species 8 (T.megaptera) and 2 (A.fecundator) also have very low values for  $S_J$  and are not associated; they are bud galls and occupy totally different

1	2	3	4	5	6	7	8	
1.0	0.084	0.215	0.0	0.072	0.084	0.455	0.125	1
	1.0	0.0	0.0	0.0	0.0	0.05	0.0	2
		1.0	0.2	0.143	0.167	0.25	0.0	3
			1.0	0.05	0.5	0.05	0.0	4
				1.0	0.667	0.096	0.0	5
					1.0	0.1	0.0	6
						1.0	0.131	7
							1.0	8

$(5+6)=A$  0.078 0.0 0.155 0.275  
 $(1+7)=B$  0.067 0.233 0.025  
 $(A+4)=A'$  0.0 0.178  
 $(A'+3)=A''$  0.0  
 $(A''+B)=A'''$  0.034  
 $(A''' + 8)=A''''$  0.017  
 $(A''''+2)=A'''''$

0.098 0.0 A B A' A'' A'''  
 0.128 0.088  
 0.0 0.057  
 0.0 0.145  
 0.064

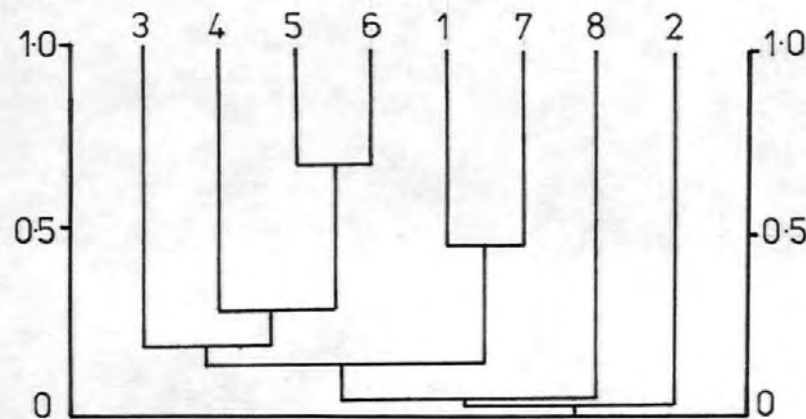


Figure 17. Community matrix and dendrogram, for 8 species of gall, spring generation 1976.

Legend.

1. Andricus curvator.
2. A. fecundator.
3. A. quadrilineatus.
4. A. quercusramuli.
5. Neuroterus albipes.
6. N. numismalis.
7. N. quercusbaccarum.
8. Trigonaspis megaptera.

parts of the host from the other gall species, and must be mutually excluded from one another.

The community-matrix and the corresponding dendrogram for the autumn-generation galls for 1976 are given in figure 18. The highest degree of association exists between species 14(A.kollari) and 3 (N.quercusbaccarum) and between species 1(A.fecundator) and 4 (A.ostreus) both with a value of  $S_J = 0.34$ . Although they are the most highly associated it is not highly significant due to an imbalance in the numbers of specimens found during the sampling. A.kollari is a bud gall whereas N.quercusbaccarum occurs on leaves, therefore the association is at the level of occurrence or distribution, not at the level of interaction. A similar situation also exists between A.fecundator (bud gall) and A.ostreus (leaf gall).

Although these associations are not at an interactive level, they are meaningful at the distributional level of association. They may be indicative of a preference for a specific host taxon or morphology, or may even be related to altitudinal or other topographical effects.

#### 6:2:3 Within-leaf associations

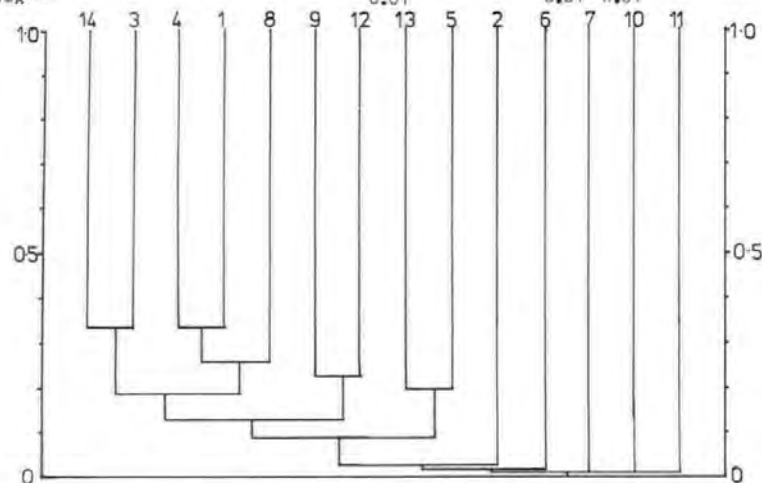
A final community-matrix and dendrogram were constructed using the data on the joint occurrences of gall species on individual leaves, for the years 1976 and 1977 combined (figure 19). It can be seen that a very high degree of association exists between species 1 (N.quercusbaccarum) and 7 (C.quercusfolii) with a value of  $S_J = 0.998$ . This is a product of the rarity of galls of C.quercusfolii combined with an abundance of galls of N.quercusbaccarum found during the sampling, rather than a genuine association.

The A" cluster which consists of species 1(N.quercusbaccarum), 7(C.quercusfolii), 4(A.ostreus) and 6(C.disticha) show relatively high degrees of association. The reasons for this are similar to those given above for the high association found between C.quercusfolii and N.quercusbaccarum, namely an imbalance of the numbers

1	2	3	4	5	6	7	8	9	10	11	12	13	14
1.0	0.15	0.25	0.34	0.0	0.0	0.0	0.3	0.1	0.15	0.0	0.08	0.23	0.05
	1.0	0.08	0.2	0.0	0.0	0.0	0.15	0.0	0.0	0.0	0.0	0.0	0.03
		1.0	0.2	0.07	0.0	0.0	0.17	0.2	0.0	0.07	0.17	0.29	0.34
			1.0	0.0	0.0	0.09	0.22	0.0	0.1	0.0	0.14	0.08	0.32
				1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.05
					1.0	0.0	0.0	0.0	0.0	0.0	0.17	0.0	0.03
						1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03
							1.0	0.23	0.15	0.0	0.08	0.1	0.14
								1.0	0.0	0.0	0.23	0.15	0.1
									1.0	0.0	0.0	0.0	0.03
										1.0	0.0	0.0	0.05
											1.0	0.1	0.17
												1.0	0.1
													1.0

Figure 18 .Community matrix and dendrogram for 14 gall species, autumn generation 1976.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	A	B	A'	C	D	A''	A'''	A''''	A'''''
(4+1)=A	0.18	0.23		0.0	0.0	0.05	0.26	0.25	0.13	0.0	0.11	0.16	0.19	1.0								
(4+3)=B	0.0			0.06	0.02	0.02	0.16	0.15	0.02	0.06	0.17	0.2	0.0	0.21	1.0							
(A+B)=A'	0.17			0.0	0.0	0.03		0.14	0.14	0.0	0.1	0.13				0.19	1.0					
(9+12)=C	0.0			0.0	0.09	0.0			0.0	0.0		0.13				0.16	0.12	1.0				
(13+5)=D	0.0				0.0	0.0			0.0	0.0						0.13	0.07	0.07	1.0			
(A'+B)=A''	0.12				0.01	0.03			0.08	0.03								0.14	0.1	1.0		
(A''+C)=A'''	0.06				0.05	0.02			0.04	0.02								0.09		1.0		
(A''' +D)=A''''	0.03				0.03	0.01			0.02	0.01											1.0	
(A''''+2)=A'''''					0.02	0.01			0.01	0.01												1.0
(A''''' +6)=A''''''						0.01			0.01	0.01												1.0



Legend.

1. A.fecundator.
2. A.inflator.
3. A.kollari.
4. A.ostreus.
5. A.quercuscalicis.
6. A.quercusradicis.
7. B.pallida.
8. C.disticha.
9. C.divisa.
10. C.longiventris.
11. C.quercusfolii.
12. N.albipes.
13. N.numismalis.
14. N.quercusbaccarum.

	1	2	3	4	5	6	7	8	9		
<i>N. quercusbaccarum</i>	x	0.977	0.9507	0.9836	0.9243	0.9755	-	-	0.9983		
<i>N. albipes</i>		x	-	-	-	-	-	-	-		
<i>N. numismalis</i>			x	-	-	-	-	-	-		
<i>A. ostreus</i>				x	-	0.4615	-	-	-		
<i>A. curvator</i>					x	-	-	-	-		
<i>C. disticha</i>						x	-	-	-		
<i>C. longiventris</i>							x	-	-		
<i>C. divisa</i>								x	-		
<i>C. quercusfolia</i>									x		
(1+9)A	-	0.4855	0.4754	0.4918	0.4622	0.4878	-	-	-	A	A
(A+4)A'	-	0.2443	0.2377	-	0.2311	0.4747	-	-	-	-	-
(A'+6)A''	-	0.1221	0.1188	-	0.1155	-	-	-	-	-	-
(A''+2)A'''	-	-	0.0594	-	0.0577	-	-	-	-	-	-
(A''' +3)A''''	-	-	-	-	0.0288	-	-	-	-	-	-
(A''''+5)A'''''	-	-	-	-	-	-	-	-	-	-	-

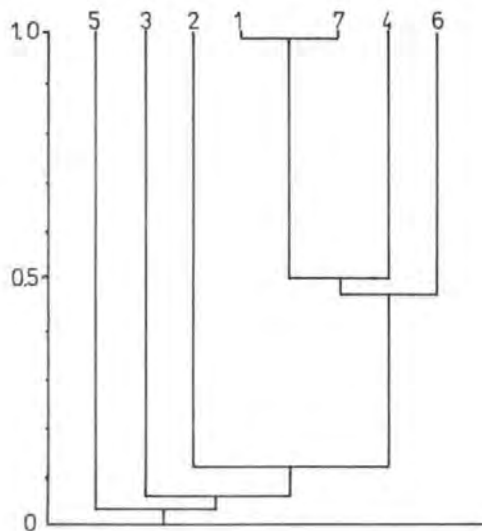


Figure 19 .Community matrix ( $S_j$ 's) and community dendrogram for associations on individual leaves, autumn generations 1976/1977.

Legend.  
 Species1=*N. quercusbaccarum*  
 2=*N. albipes*  
 3=*N. numismalis*  
 4=*A. ostreus*  
 5=*A. curvator*  
 6=*C. disticha*  
 9=*C. quercusfolia*



of individuals of the species found during the sampling. The degree of association between A.ostreus and C.disticha with N.quercusbaccarum is slightly lower in this case than that between C.quercusfolii and N.quercusbaccarum, due to the greater numbers of galls of A.ostreus and C.disticha found, and because they were occasionally found on leaves devoid of N.quercusbaccarum. The degrees of association between species 5 (A.curvator), 3 (N.numismalis) and 2 (N.albipes) are at a low level, which is indicative of the rarity of joint occurrences of these species on a single leaf. As already described in section 4:3:3 niche partitioning occurs between these species and N.quercusbaccarum; the species have different flight periods and utilise leaves at different stages of development.

The association analysis of gall species (section 6:2:2) indicate positive interactions between some species which might be competing, or avoiding competition through niche partitioning. This is investigated in the following section.

### 6.3 Competition analysis

I have shown (section 5:3:5) that at each of the sample sites (with the exception of Piles copse), exposed oaks were more heavily infested than oaks within the wood canopy (Table 21). In addition the exposed oaks supported greater numbers of gall species (Table 21) and hence a greater degree of competition may occur on these trees prior to the establishment of density dependent regulatory factors. It has been established (section 5:2) that Q.robur hosts a greater number of gall species, in greater densities, than either Q.petraea or hybrid hosts (table 5).

Isolated oaks appear to be acting as ecological 'islands', leading to a rapid increase in the population of colonising gall-causers. These are then sustained at high levels until the regulatory effects of parasites become significant.

Yeaton and Cody (1974) working on island song-sparrow populations found that island breeding densities exceeded those of comparable mainland sites, although the total number of species was smaller on islands. They concluded that the greater densities on islands were

1	2	3	4	5	6	7	8	9	10	11		CE
1.00.011		0.014	0.024	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1	1.05
5.4	1.0	0.124	0.062	0.0	0.0	0.0	0.004	0.0	0.0	0.0	2	6.59
2.31	0.045	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	3.355
1.3	0.007	0.0	1.0	0.0	0.0	0.0	0.004	0.0	0.0	0.0	4	2.311
0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	5	1.0
0.388	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	6	1.388
0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	7	1.0
0.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	8	2.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	9	1.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	10	1.0
6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	11	7.4
SE16.79	1.063	1.137	2.086	1.0	1.0	1.0	1.008	1.0	1.0	1.0		

Fig. 20 .Community matrix for the community interaction coefficients( $a_{ij}$ ) for autumn generation galls 1975.(N=number of individual leaves).  
SE=species effect,CE=community effect.

Legend.

Species1=N. quercusbaccarum,2=N. albipes,3=N. numismalis,4=N. tricolor,5=A. ostreus,  
6=C. divisa,7=C. disticha,8=C. longiventris,9=C. quercusfolii,10=A. curvator,  
11=A. quercusradicis.

	1	2	3	4	5	CE
1	1.0	0.011	0.0479	0.0	0.0	1.06
2	0.011	1.0	0.0	0.0	0.0	1.011
3	1.6	0.0	1.0	0.0	0.0	2.6
4	0.0	0.0	0.0	1.0	0.0	1.0
5	0.0	0.0	0.0	0.0	1.0	1.0
SE	2.611	1.011	1.048	1.0	1.0	

Figure 21 .Community matrix of the community interaction coefficients( $a_{ij}$ ) for spring generation galls 1976.  
SE=species effect,CE=community effect.

Legend.

Species 1=N. quercusbaccarum  
 2=A. curvator  
 3=N. albipes  
 4=N. numismalis  
 5=A. quadrilineatus

1	2	3	4	5	6	7	8	9	CE
1.0	0.004	0.0	0.0	0.0	0.0	0.004	0.0	0.0	1 1.01
0.89	1.0	0.0	0.0	0.013	0.0	0.0	0.0	0.0	2 1.903
0.003	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	3 1.003
0.027	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4 1.027
0.86	0.095	0.0	0.0	1.0	0.0	0.19	0.0	0.0	5 2.145
0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	6 1.0
0.34	0.0	0.0	0.0	0.011	0.0	1.0	0.0	0.0	7 1.351
0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	8 1.0
1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	9 2.0
SE 3.94	1.1	1.0	1.0	1.024	1.0	1.023	1.0	1.0	

Figure 22 .Community matrix for the community interaction coefficients( $a_{ij}$ ) for autumn generation galls 1976.(N=number of individual leaves).  
SE=Species effect,CE=community effect.

Legend.

Species 1=N.quercusbaccarum.

2=N.albipes.

3=N.numismalis.

4=A.curvator.

5=A.ostreus.

6=C.divisa.

7=C.disticha.

8=C.longiventris.

9=C.quercusfolii.

1	2	3	4	5	6	7	8		CE
1.0	0.012	0.001	0.0	0.001	0.0	0.024	0.0	1	1.04
2.26	1.0	0.0	0.0	0.073	0.0	0.0	0.0	2	3.33
0.122	0.0	1.0	0.0	0.0	0.0	0.0	0.0	3	1.122
0.273	0.0	0.0	1.0	0.0	0.0	0.0	0.0	4	1.273
4.143	1.179	0.0	0.0	1.0	0.0	0.072	0.0	5	6.393
0.5	0.0	0.0	0.0	0.0	1.0	1.0	0.0	6	2.5
1.043	0.0	0.0	0.0	0.0	0.006	1.0	0.0	7	2.049
2.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	8	3.0
SE	11.34	2.191	1.0	1.0	1.075	1.01	2.095	1.0	

Fig. 22a .Community matrix for the community interaction coefficients( $a_{ij}$ ) for autumn generation galls 1976.(N =the number of sample units-10 leaves).  
SE=species effect,CE=community effect.

Legend.

Species 1=N.quercusbaccarum.

2=N.albipes.

3=N.numismalis.

4=A.curvator.

5=A.ostreus.

6=C.divisa.

7=C.disticha.

8=C.quercusfolii.

probably due to the absence of competition from other species normally present on the mainland; a phenomenon known as 'competitive release'.

Using the gall distribution data, competitive interactions and niche-partitioning were investigated for species of gall occupying the same trophic position (i.e. leaf galls). Such interactions would tend to be indirect due to the fixed nature of galls when competing for a contested resource.

Community matrices were constructed (Figs: 20, 21, 22(a)) where the element  $a_{ij}$  is the probability ( $P_{ij}$ ) of an individual of species  $j$  encountering an individual of species  $i$ , relative to the probability ( $P_{jj}$ ) of encountering an individual of the same species where:

$$P_{jj} = 1/N^2 \sum_{k=1}^N n_{jk}^2$$

is the probability of an intraspecific encounter; and

$$P_{ij} = 1/N^2 \sum_{k=1}^N n_{ik} n_{jk}$$

is the probability of interspecific encounter,

$$a_{ij} = P_{ij}/P_{jj}$$

is the community interaction coefficient.

$N$  = the number of samples.

$n_{ik}$  is the probability of gall species  $i$  occurring in sample  $k$ .  $a_{ij}$  has been used as a measure of niche breadth, since  $1/P_{ij}$  represents the diversity of samples in which species  $j$  occurs (Post and Riechert 1977).

The community matrix for the autumn generation 1975 is given in figure 20, the spring generation 1976 in figure 21, and the autumn generation 1976 in figures 22(a). If a row of the matrix is summed for a particular species:-

$$CE_i = \sum_{j \neq i} a_{ij} = \sum_{j \neq i} \frac{\sum_k n_{ik} n_{jk}}{\sum_k n_{jk}^2}$$

the effect of all other species on that species (the community effect) may be determined. A large community effect upon a species indicates

that it encounters the other species more frequently than by chance, relative to their population size, and represents the influence that other species of the community exert on any given species.

The species effect on all the other species ( $SE_i$ ) is determined by summing the columns of the matrix for a particular species:-

$$SE_i = \sum_{j \neq i} a_{ji} = \sum_{j \neq i} \frac{\sum_k n_{ik} n_{jk}}{\sum_k n^2_{ik}}$$

A 'generalist' would have a large effect upon the community, and be a successful competitor, while species with low values for SE and high values for CE are successful avoiders of competition through niche partitioning.

From the community matrix for the autumn of 1976 (Figure 22) it is clear that N. quercusbaccarum has a large species effect, and a low community effect, indicating its generalist mode. All the other species recorded, with the exception of C. disticha, have larger community effects than species effects, and hence display a degree of niche partitioning. The community matrix for the autumn generation 1975 (Figure 20) shows that N. quercusbaccarum has a large species effect (16.8) and a low community effect (1.05). All the other species have values for CE which are greater than those for SE, indicating that N. albipes, N. numismalis and A. quercusradicis avoid competition through niche partitioning.

The community matrix for the spring generation 1976 (Figure 21) shows low values for CE and SE for all the species recorded. In this case niche partitioning is less pronounced and is probably due to a reduction in the demand for suitable sites by N. quercusbaccarum, since this species is able to utilise catkins as well as leaves for gall development. These results for the sexual (spring) generation galls, support the trends that were found for the agamic gall distributions, but due to the small numbers that occurred relative to the autumn generation galls, not a great deal of weight has been attached to them.

## CHAPTER 7

### 7.0 Concluding Discussion

The distribution of cynipid-oak galls within and between populations of the indigenous oak species and their hybrids are complex and affected by several factors, both intrinsic and extrinsic. It is evident from the qualitative transect surveys and the quantitative site sampling carried out in this survey, that there is some preferential galling of the two indigenous oak species. Q. robur hosts are more susceptible to infestation by gall-causing species than Q. petraea hosts, both in the numbers of different gall species and in the density of galling of a single species. Oaks of introgressed hybrid status show less clear trends which are difficult to categorise. Individual hybrid oak-hosts have gall compositions which range in both numbers and species from levels below those found for Q. petraea hosts to levels higher than were found for hosts of Q. robur. If there is some physiological property of Q. robur hosts which make it more suitable for gall infestation than hosts of Q. petraea, hosts of hybrid status may act as hosts to galls, combining the gall interaction properties from both Q. robur and Q. petraea.

The nature of these physiological properties are not known, and their elucidation offers scope for further work.

In addition to the effects that any differences in physiologies between the hosts may have, it is apparent from this investigation that other non-physiological effects also affect the distributions of cynipid galls.

The date of leaf burst and its coincidence with the flight periods of fecund adult wasps has been stated to be a factor which effects gall distributions (Askew 1962). The timing of leaf-burst is related to the taxon of the oak as well as being influenced by topographical and climatic effects. The date of leaf-burst, although an important



factory, may not always be critical; since during this investigation adult wasps were found to live for a period of several weeks under natural conditions and could, therefore, avail themselves of leaf-burst over a period of time. From this work and that of others (Marsden-Jones 1953) it is evident that there is a certain amount of selection for egg-laying sites carried out by the wasps themselves. Marsden-Jones (1953) showed that adults of A.kollari are capable of distinguishing between different host taxa. During this work bagged releases of A.kollari agamic females were made on hybrid oaks in which the wasps showed no ovipository behaviour.

In addition to the selection of a suitable host taxon, Hough (1953b) suggests that gall wasps may be capable of selecting sites of rapid tissue expansion in which to oviposit, by being able to detect increases in the auxin levels in the host tissue. Much more work needs to be done on the egg-laying and site selection behaviour of cynipid oak-gall wasps, although the evidence available suggests that the adult wasps may be active in their choice of host taxon.

It is apparent from this investigation that all the gall species which occur on Q.petraea, also occur on oaks of hybrid status and on Q.robur. However several gall species seem to be solely restricted to aff.Q.robur hosts. The reasons for this may be physiological, Q.robur having some favourable property which Q.petraea lacks, or they may be physical such as the thickness of the cuticle. An interesting observation here concerns the sexual generation galls of N.tricolor which occurs on the abaxial surfaces of leaves. These galls are covered in hairs which are very similar to the large stellate hairs that occur on the under surfaces of Q.petraea leaves in the axils of the main veins (Wigston 1975). These hairs are also present when the galls occur on the glabrous leaves of Q.robur, suggesting that although Q.robur normally has glabrous leaves it has the genes for the expression of stellate hairs. The detailed nature of gall pubescence compared with

normal leaf pubescence requires further evaluation.

The greater preference to Q.robur as a host for gall species was further borne out by association analysis of the sample sites. It is clear from the results of this that sites with the same taxonomic status are more closely associated, in terms of gall species supported, than sites of differing status.

Within-site gall distributions on hosts of the same taxon, are often very different. Such differences in gall distributions can be related to the degree of exposure of the host trees. Since wind is the major agent of dispersal of the adult wasps (Hough 1951, Johnson 1969) it could be expected that exposed oaks would show higher degrees of infestation than oaks in sheltered positions. This prediction is supported by the current work which, with one exception, has shown that at all the sample sites exposed trees were more heavily infested than sheltered oaks within the canopy.

Analysis of the within-tree gall distribution frequencies from the quantitative sample sites has shown that gall species are highly aggregated. Distributions of the different gall species may be separated both spatially and temporally and hence many species avoid conditions which might lead to competition.

In addition wind direction seems to determine to some extent the within-tree distributions of galls. Aspects of the host which face the prevailing winds show higher densities of galls than those aspects away from the prevailing winds.

Another factor which might influence the distribution of galls on oaks may be the canopy structure of the trees themselves. Large, tall oaks with no low branching are often totally devoid of galls. This may be related to the weak flight capacities of the adult wasps and to characteristics of the wind which maximises its strength at certain heights from the ground.

Further evidence for the preferential distributions of galls between the two indigenous oak taxa, and the active selection of oak hosts by adult cynipid wasps is available from the work on the alternation of generations (Cameron 1889, Adler 1894, Marsden-Jones 1953).

Marsden-Jones (1953) showed conclusively that Q.cerris is the host of the sexual generation galls of A.kollari and that Q.robur is host to the agamic generation galls. The sexual generation galls of A.kollari have never been found on Q.robur and the agamic "marble" galls have never been found on Q.cerris. It also seems probable in the absence of a suitable Q.cerris host that agamic females of A.kollari can reproduce without the sexual generation for several years, and in some instances may even have lost the power of sexual reproduction altogether.

Another gall causer which may reproduce entirely agamically, having dispensed with its sexual generation, is A.quercuscalicis. There is some confusion in the literature as to when this species first occurred in Britain. The report of Claridge (1962) is generally taken as being the first record of these galls in Britain though Cobb (1972) presents some evidence of their occurrence in Norfolk and Dorset in the 1930's. The abundance of these "knopper" galls from year to year seems to be rather sporadic, galling up to 100% of the acorns on a host one year, subsequently dying away. Galled acorns can contain viable larvae for at least 4 winters before emerging as adult wasps. This long period of viability within the gall is probably an adaptation to overcome the problem of a non-mast year. What triggers the emergence of some wasps after 1,2,3 or 4 winters, when kept under the same conditions is not known, and offers opportunity for further investigation.

A.quercuscalicis is often a very successful gall-causing agent, and could offer a serious threat to the natural regeneration of oaks by greatly reducing acorn viability. However within a woodland only a few trees are affected (albeit very heavily) whilst neighbouring oaks are often totally free from infestation. During this investigation

the first named parasite to be found in Britain of A. quercuscalicis was dissected from a gall obtained from Central Park, Plymouth (Syntomaspis cyanea Hym: Chalcidoidea). Claridge (1962) states that on the continent A. quercuscalicis is attacked by several chalcids present in Britain, although no parasites were known to attack A. quercuscalicis in Britain. Perhaps the discovery of S. cyanea (Hym: Chalcidoidea) is an indication of a new niche, provided by the recent colonisation of the British Isles by A. quercuscalicis.

Apart from the potential effect of A. quercuscalicis on the natural regeneration capacity of Q. robur, galls do not appear to have any obvious deleterious effects on oaks, although they must divert energy away from the oak's growth. Bud galls such as A. fecundator, A. kollari and B. pallida may have some influence on the growth patterns of oaks by rendering apical buds unviable, but such effects are hard to quantify. The oak-gall complex is a highly evolved system which offers advantages to both the host by isolating the wasps and to the insects by providing them with an adequate food supply and a degree of protection from parasitic attack. Indeed the work of Jankiewicz et al (1970) on C. quercusfolii indicates that gall formation is advantageous to the oaks by increasing the rate at which nutrients are recycled from the leaf litter back to the trees biomass, since galls act as mineral sinks for various photosynthetic assimilates which are readily released.

In conclusion no definitive reason can be offered here for the patterns of cynipid oak-gall distributions that were found during this investigation. It is evident however that the taxonomic status of the oak influences the species composition of galls to which it acts as host, the physiology of Q. robur being more suitable for gall induction than that of Q. petraea. The adult gall wasps also seem to determine their own distributions to an extent by their behaviour in the selection of suitable host trees and sites within the host for

egg-laying. Secondary factors affecting gall distributions are related to climatic and topographical conditions. The wind acts as a major agent in the dispersal of adult wasps and their successful colonisation of a potential host is dependent on several factors including the date of leaf-burst and the taxonomic status of the host. Host physiology, adult behaviour patterns, climatic conditions and the degree of exposure of the host tree all act to influence the distributions of galls on oaks.

Gall populations at the sites investigated during this work dropped to extremely low levels during the 1977 season. It was evident from the work on gall parasites that this large drop in gall numbers was not due to parasitic pressures. The most likely reason is to do with the climatic conditions of 1976, which was very hot and dry and brought about an early leaf fall. As a result the cynipid larvae within the galls may not have reached a critical stage of development prior to falling to the ground and once on the ground high mortalities as a result of dehydration of the galls would probably have occurred.

Further work on the oak-gall complex offers scope for several fields of investigation. The fixed nature of galls makes them an ideal subject for work on the population dynamics of predator-prey systems and further evidence of host specificity of galls could provide a rapid and accurate method of elucidating the taxon of the host oak, which would be beneficial to foresters and conservationists alike.

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APPENDICES.

Appendix A. Algol programme for statistical analysis.

Appendix B. Pictorialised scatter diagrams for sample  
trees along the Walkham/Tavy valley transect.

Appendix C. Pictorialised scatter diagrams for sample  
trees along the Yarner Wood transects.

Appendix D. Pictorialised scatter diagrams for the  
quantitative sample sites.

Appendix E. Photographs of galls.

APPENDIX A.

1. Computer programme for statistical analysis of  
gall distributions.
2. Computer data card, showing form of data input.

12/21/25  
STATEMENT

11/11/77

COMPILED BY XALE MX. 50

```

0      'LIST' (LP,10)
0      'WORK' (ED,ICLF=DEFAULT)
0      'PROGRAM' (NEIR)
0      'INPUT' 1,2=CR0
0      'OUTPUT' 3=LP0,01
0      'OUTPUT' 4=TP0
0      'TRACE' 2
0      'BEGIN'
1      'INTEGER' T,CN,HT,LS,SW,MAXL,TQSSQ,T,MAXQFREQ;
1      'INTEGER' LGLO;
2      'REAL' M0,VAR0;
3      'REAL' PCLGLO;
4      'REAL' ASP,IT,DIST;
5      'INTEGER' LPS;
6      SELECT INPUT (2);
8      SELECT OUTPUT (3);
9      PAPERTRM0;
10     NEWLINE(3);
11     COPY TEXT ('(';')');
12     NEWLINE(5);
13     CN:=1;
14     NUC:=READ;
15     LS:=MAXL:=TQ:=MAXQFREQ:=0;
16     TQSSQ:=0;
17     LGLO:=0;
18     'BEGIN'
18     'REAL' 'ARRAY' 'MPL' [1:10],VPLN [1:10];
18     'INTEGER' 'ARRAY' 'LT' [1:10],QPL [1:10];
19     QFREQ [0:200],QPLSSQ [1:10],QPL [1:10];
19     'FOR' I:=0 'STEP' 1 'UNTIL' 200 'DO' QFREQ [I]=0;
22     'FOR' I:=1 'STEP' 1 'UNTIL' 10 'DO' 'BEGIN'
23     LT [I]=QPL [I]=QPLSSQ [I]=0;
25     'END';
26     NEXTC;
26     SW:=READ;
27     ASP:=READ;
28     HT:=READ;
29     DIST:=READ;
30     LPS:=READ;
31     'COMMENT' NEIR)TERMS QUERCUSACCARUM;
31     'FOR' I:=1 'STEP' 1 'UNTIL' LPS 'DO' 'BEGIN'
32     QPL [I]=READ;
34     'IF' QPL [I]>0 'THEN' LGLO:=LGLO + 1;
35     TQ:=TQ + QPL [I];
36     TQSSQ:=TQSSQ + QPL [I]*2;
37     LT [I]=LT [I] + 1;
38     QPLN [I]=QPL [I] + QPL [I];
39     QPLSSQ [I]=QPLSSQ [I] + QPL [I]*2;
40     QFREQ [QPL [I]]=QFREQ [QPL [I]] + 1;
41     'IF' QPL [I]>MAXQFREQ 'THEN' MAXQFREQ:=QPL [I];
42     'END';
43     CN:=CN + 1;
44     LS:=LS + LPS;
45     'IF' MAXL < LPS 'THEN' MAXL:=LPS;
46     'IF' CN>NUC 'THEN' 'GOTO' OVER 'ELSE' 'GOTO' NEXTC;
47     OVER;
47     SPACE(5);

```



```

48 WRITE TEXT ('(LEAF%')');
49 SPACE(4);
50 WRITE TEXT ('(LEAF%')');
51 SPACE(4);
52 WRITE TEXT ('(VARIANCE%')');
53 SPACE(4);
54 WRITE TEXT ('(IN.%OF%LEAVES%SAMPLED%')');
55 NEWLINE(2);
56 'FOR' I:=1 'STEP' 1 'UNTIL' IAXL 'DO'
57 'BEGIN'
58 QPLN[I]:=QPLN[I]/LT[I];
59 VQPLN[I]:=(QPLN[I]-((QPLN[I]+2)/LT[I]))/(LT[I]-1);
60 PRINT(I,4,0);
61 PRINT(QPLN[I],9,5);
62 PRINT(VQPLN[I],6,5);
63 PRINT(LT[I],4,0);
64 NEWLINE(2);
65 'END';
66 NEWLINE(1);
67 M:=TQ/LS;
68 VAR4:=(TSS)-((T+2)/LS)/(LS-1);
69 WRITE TEXT ('(TOTAL%NO%GALLS%=%')');
70 PRINT(TQ,6,0);
71 NEWLINE(2);
72 WRITE TEXT ('(MEAN%=%')');
73 PRINT(M,5,4);
74 NEWLINE(2);
75 WRITE TEXT ('(VARIANCE%=%')');
76 PRINT(VAR4,5,4);
77 NEWLINE(2);
78 PRINT(LS,5,0);
79 WRITE TEXT ('(LEAVES%SAMPLED%')');
80 NEWLINE(3);
81 PRINT (LGL,5,0);
82 WRITE TEXT ('(LEAVES%GALLED%')');
83 NEWLINE(3);
84 PCLGL:=(LGL)*100/LS;
85 PRINT (PCLGL,5,4);
86 SPACE(4);
87 WRITE TEXT ('(PERCENT%LEAVES%GALLED%')');
88 NEWLINE(3);
89 WRITE TEXT ('(GALLS/LEAF%XX%NO.%OF%LEAVES%')');
90 NEWLINE(2);
91 'FOR' I:=0 'STEP' 1 'UNTIL' MAXQFREQ 'DO'
92 'BEGIN'
93 PRINT(I,5,0);
94 PRINT(QFREQ[I],10,0);
95 NEWLINE(1);
96 'END';
97 'END';
98 'END';

```

NO OF SUCKETS USED 25

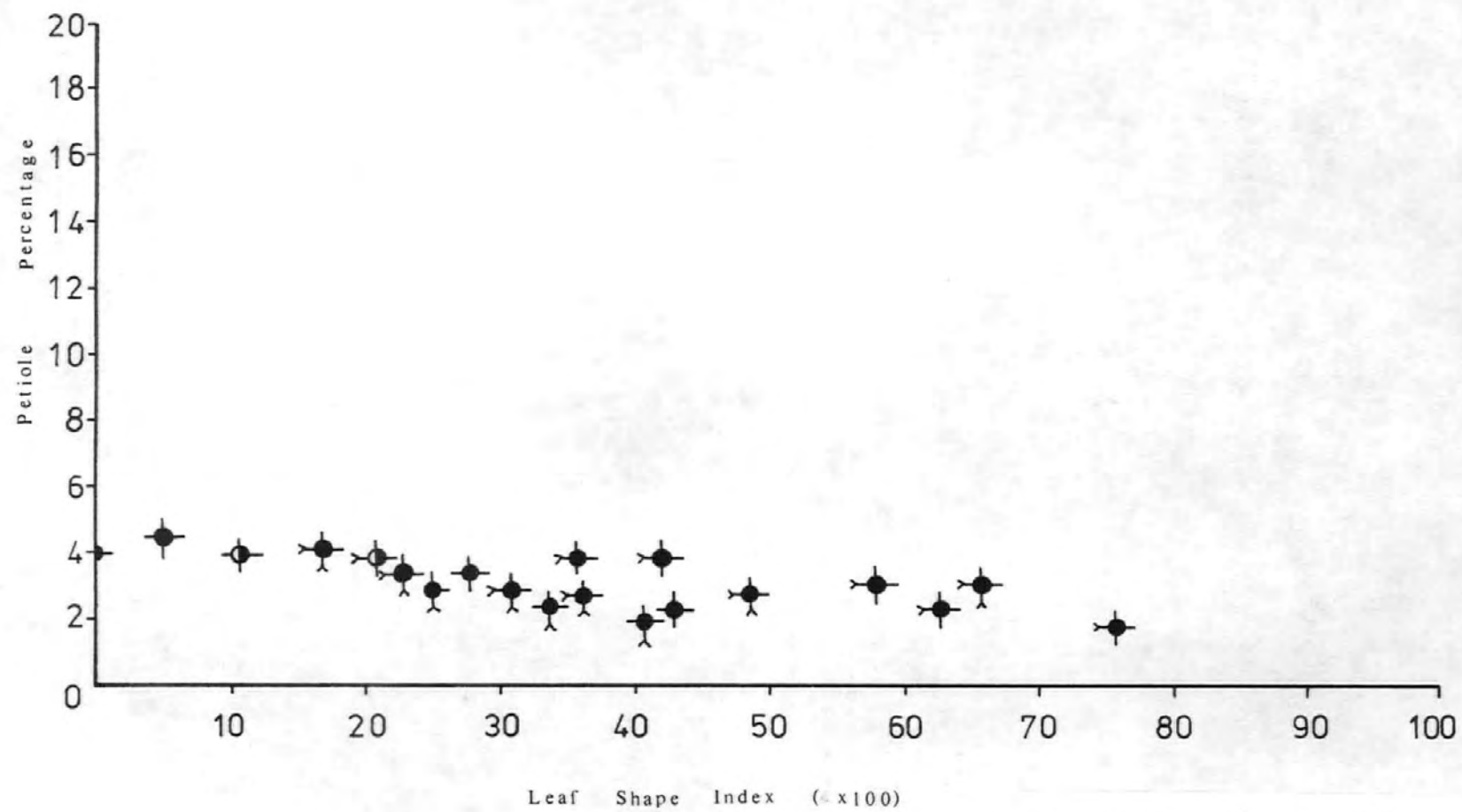
COMPILED #NEUR FC

DOCUMENT CUE LISTING , NRIEJUR : LP10 ON 11/11/77 AT 12.21

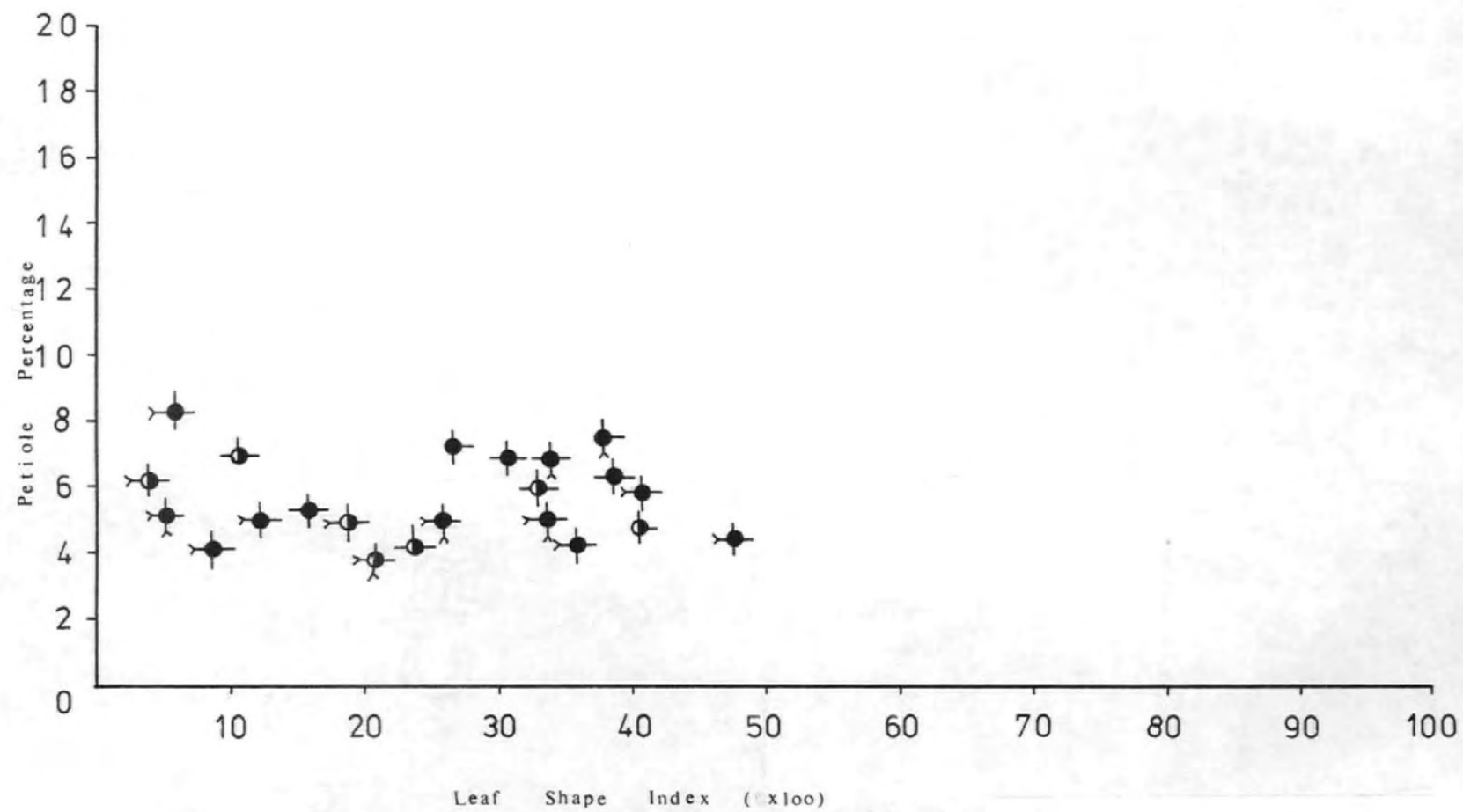


APPENDIX B.

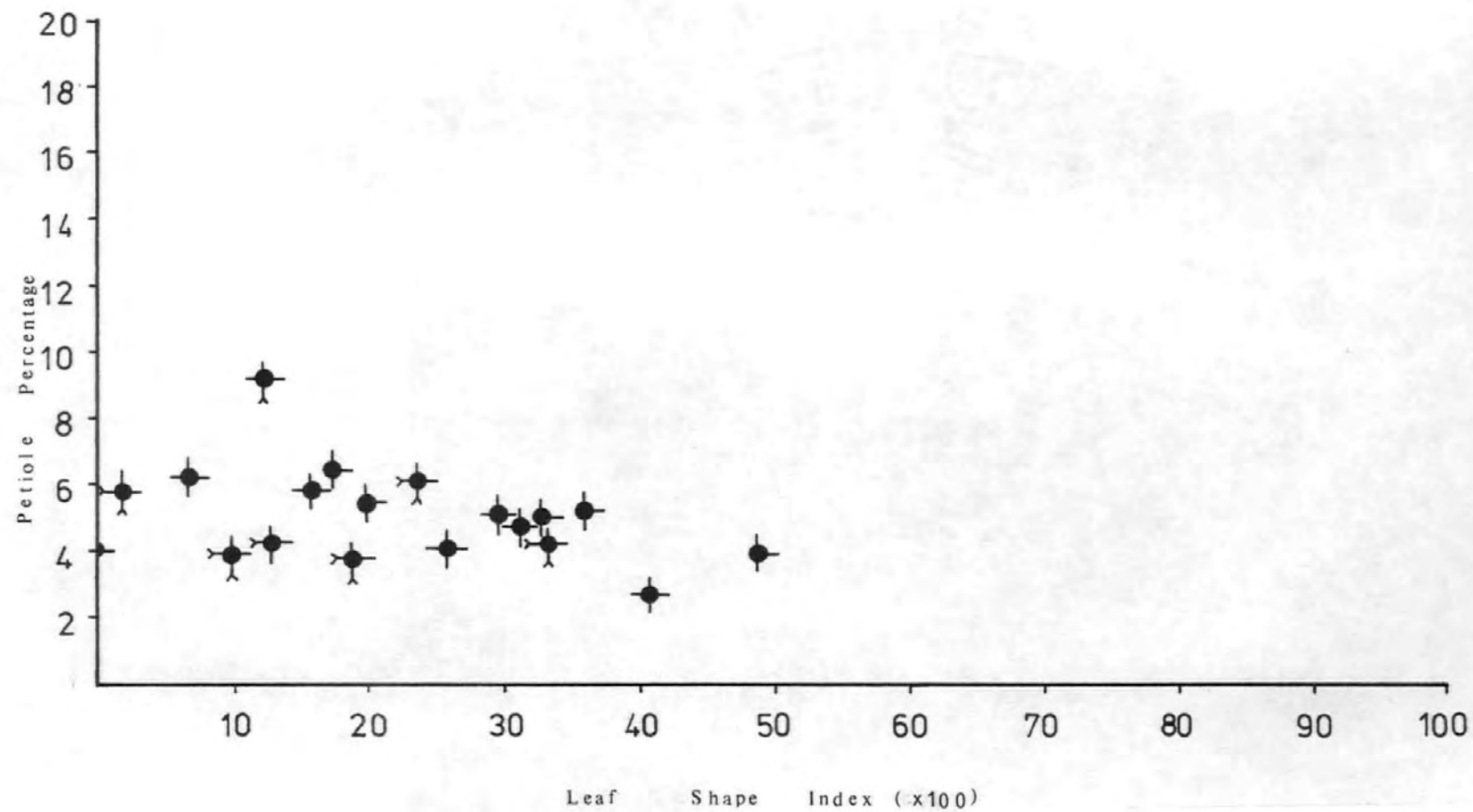
1. Pictorialised scatter diagram (PSD) for Heckwood.
2. PSD for Ward Bridge.
3. PSD for Dittisham.
4. PSD for Bedford Bridge.
5. PSD for Grenofen Weir.
6. PSD for Double Waters.
7. PSD for Denham Bridge.
8. PSD for Lopwell Dam.
9. PSD for Blaxton Wood.
10. PSD for Warleigh Wood Nature Reserve.



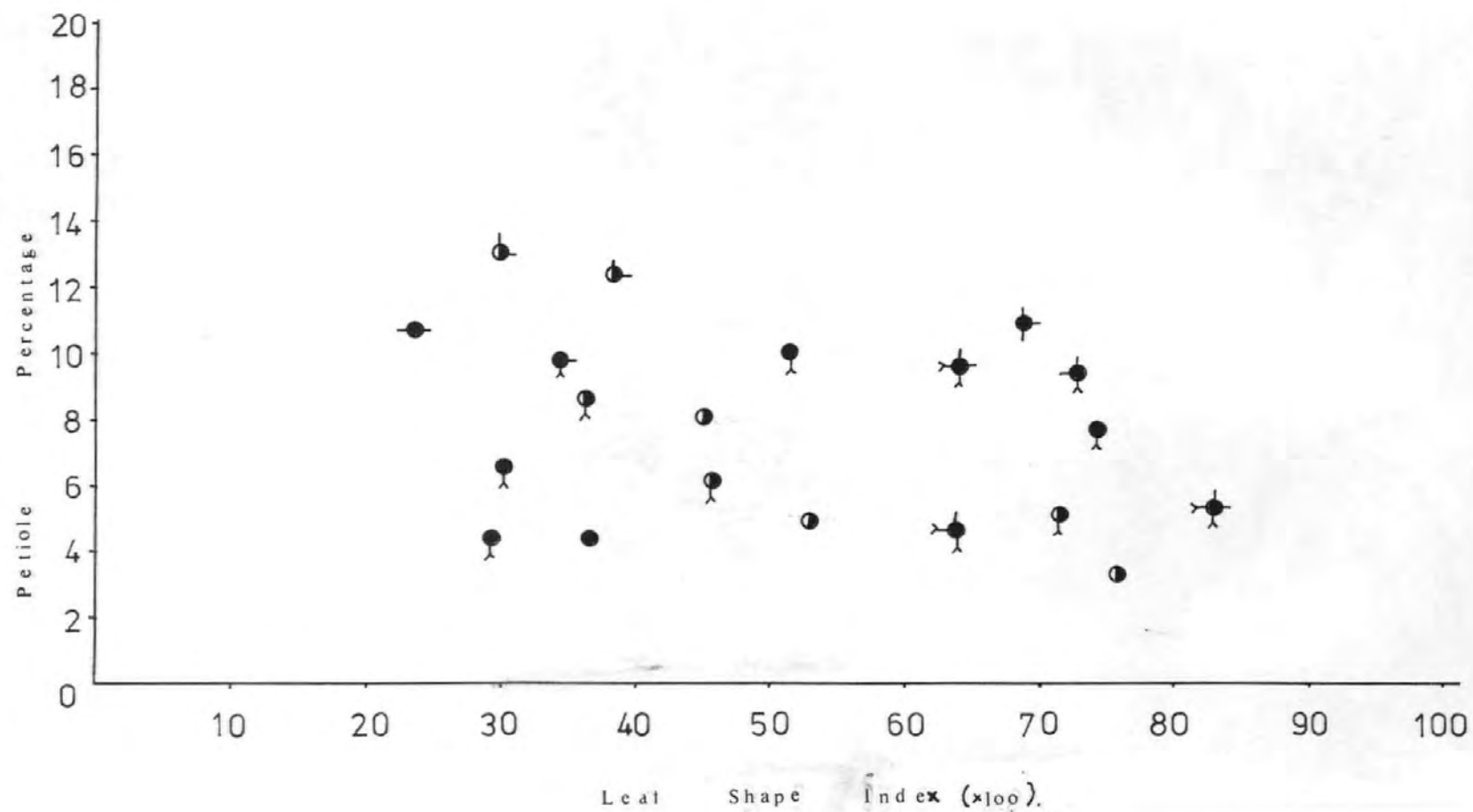
1. Heckwood (Q. robur).



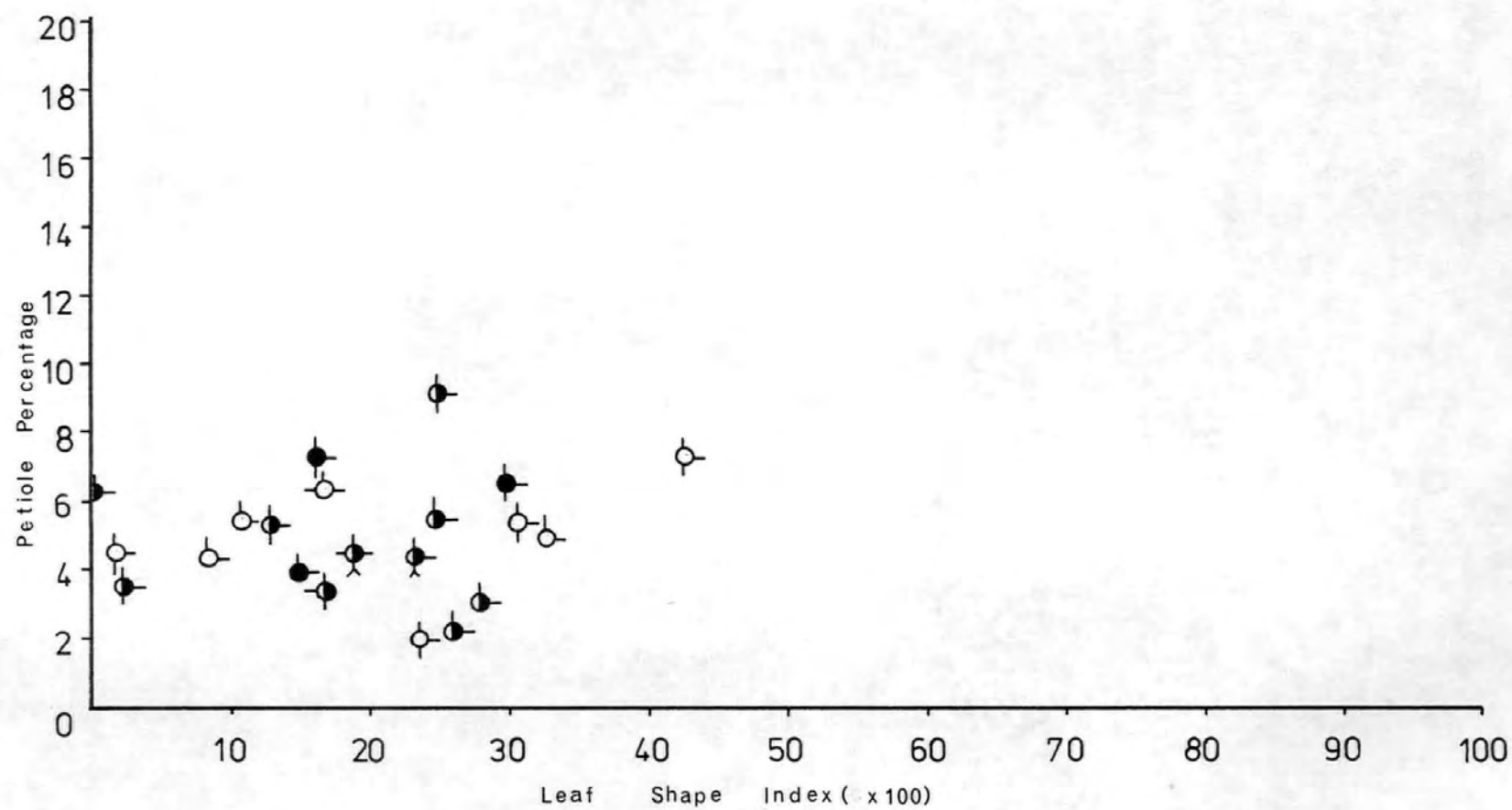
2. Ward Bridge (Q. robur).



3. Dittisham (3. robur).

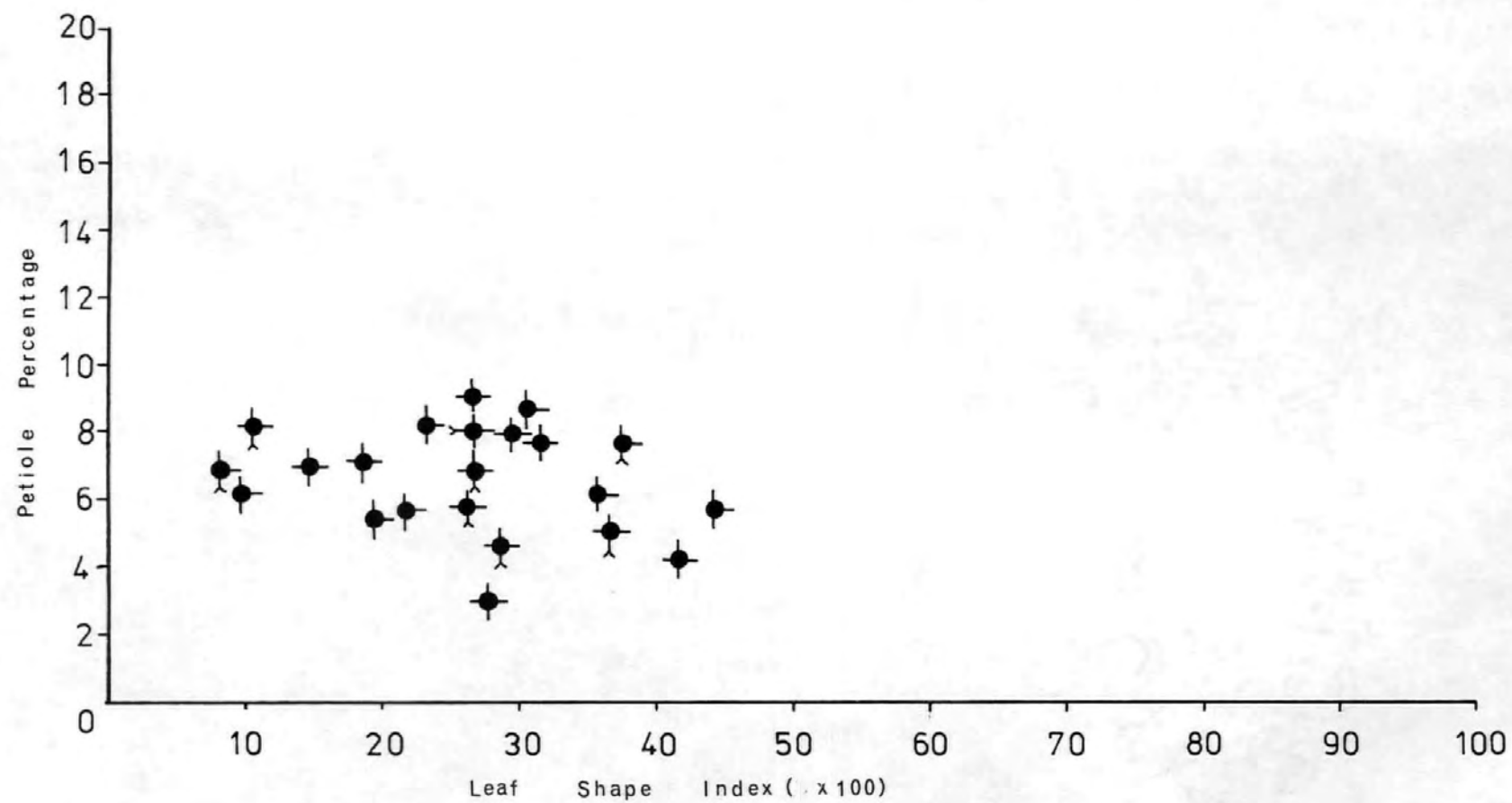


*L. Bedford Bridge* (hybrid).

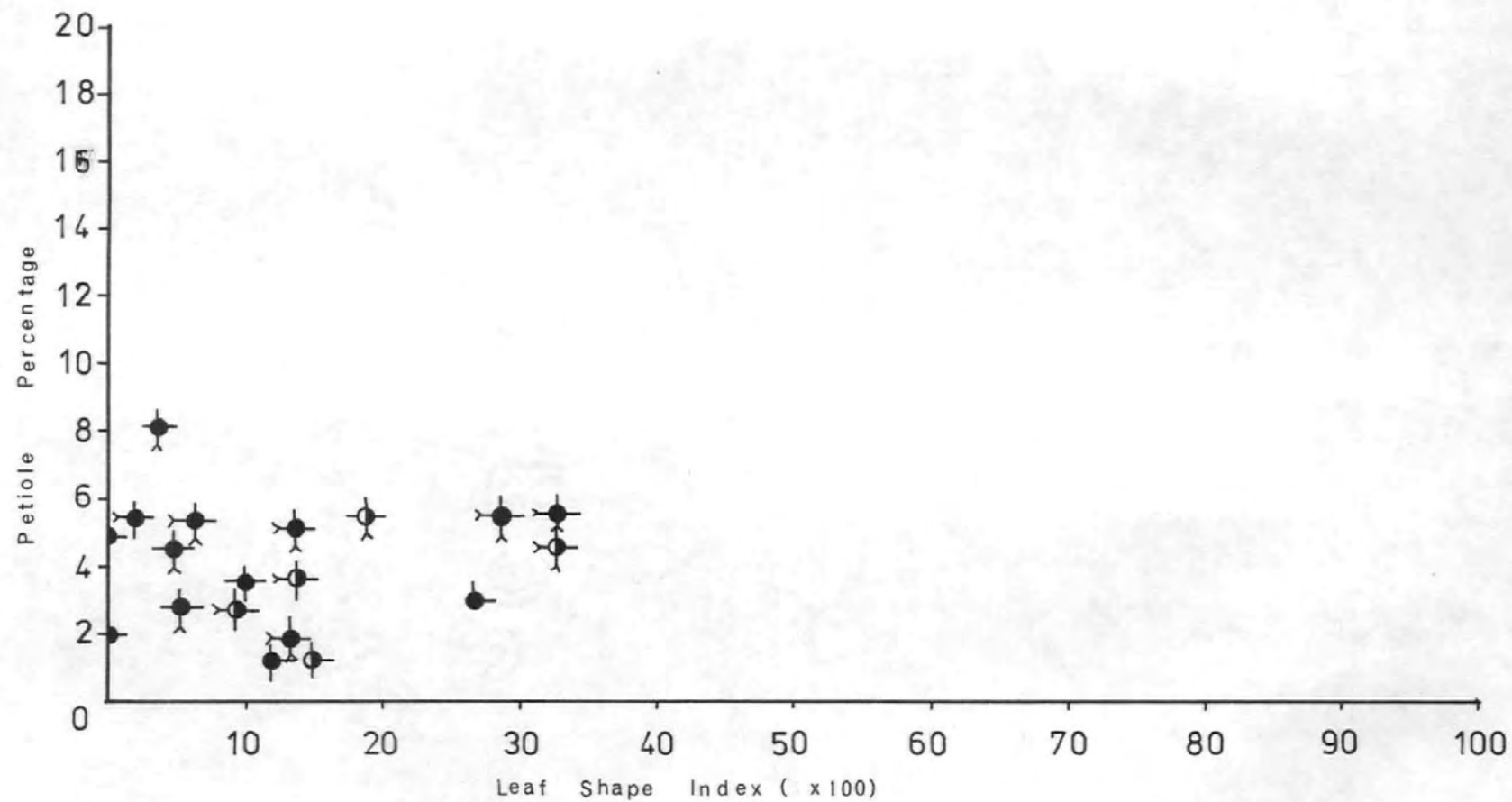


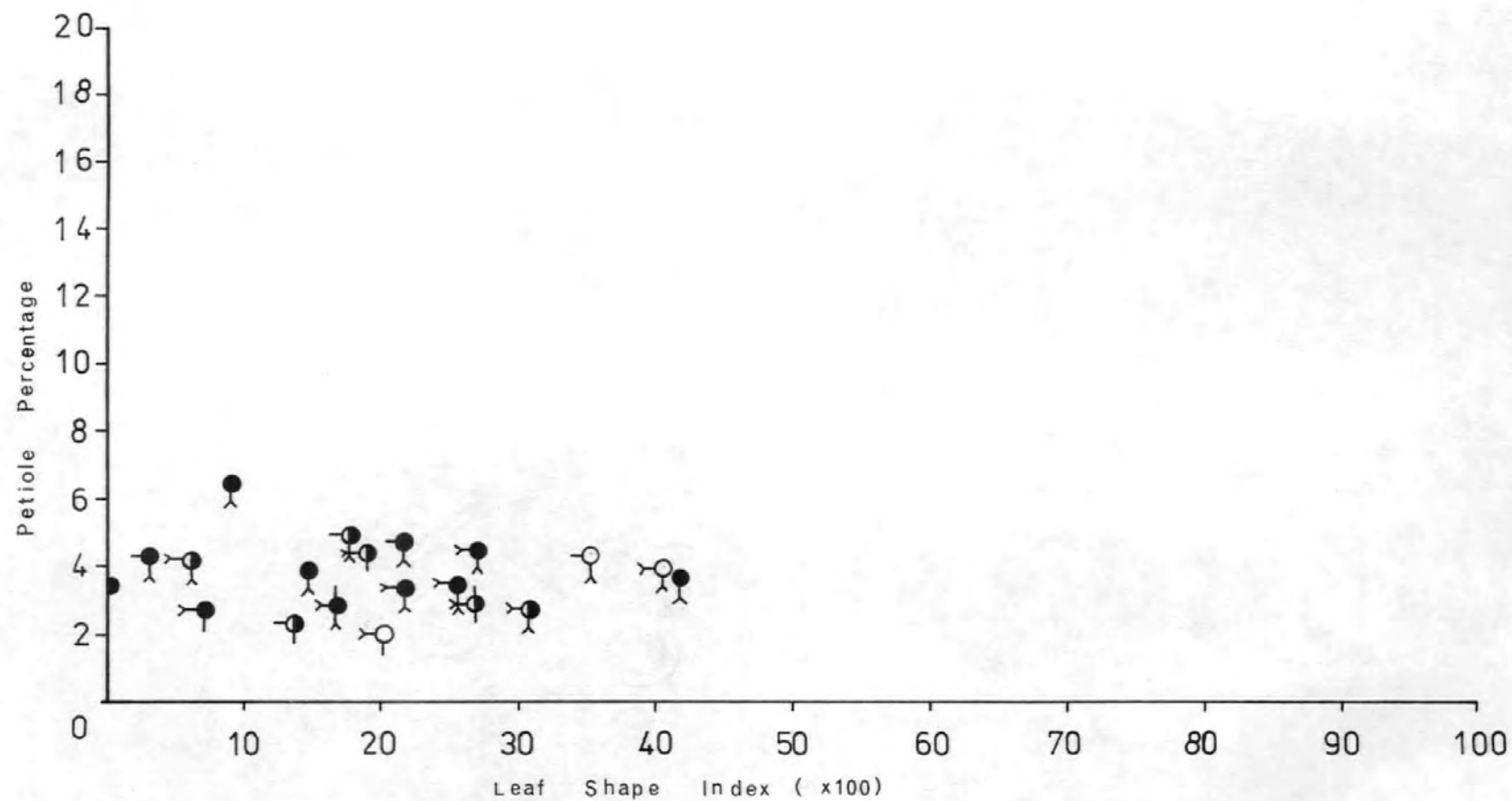
5. Grenofen weir (hybrid).



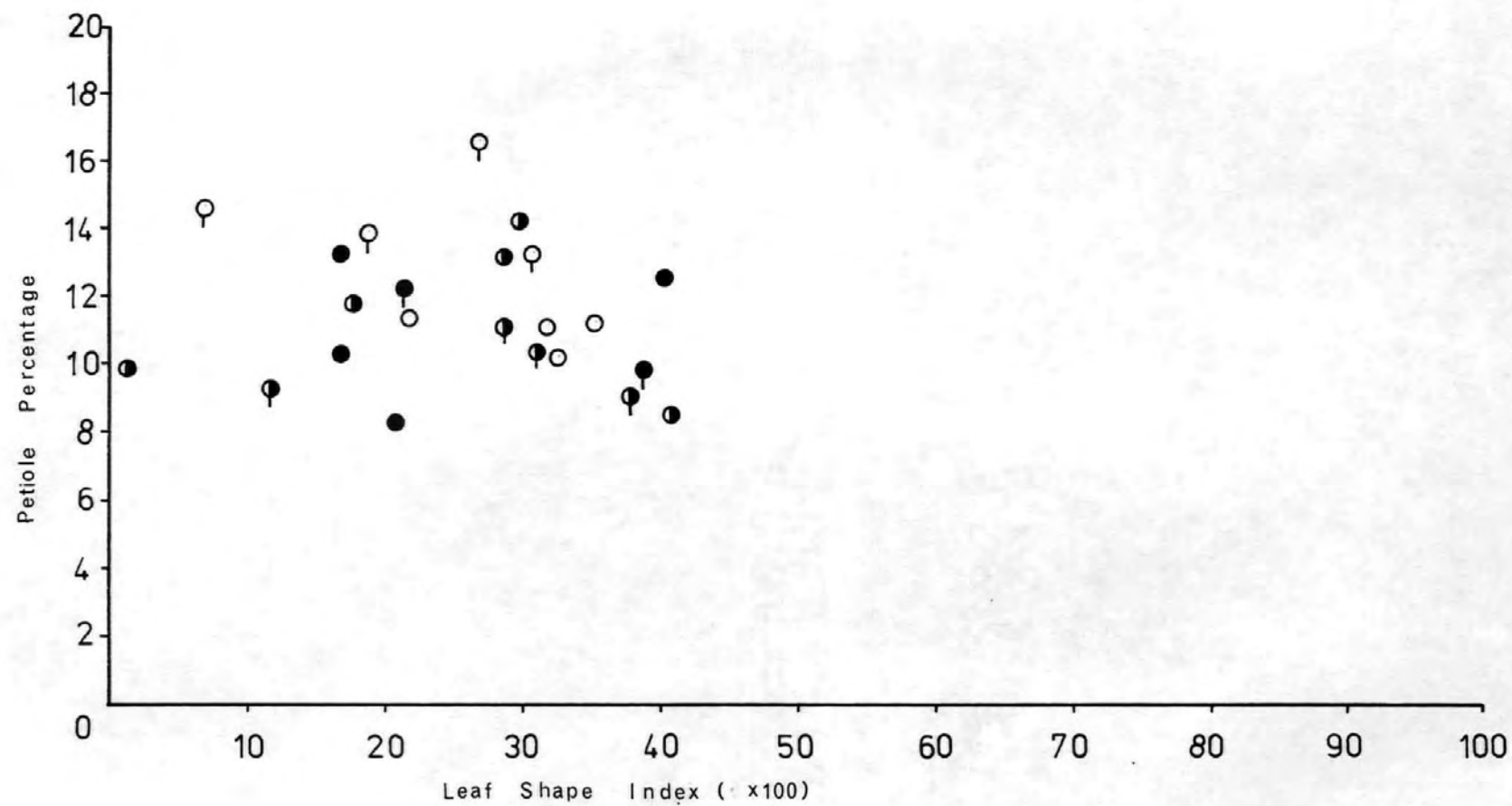


6. Double waters (hybrid).

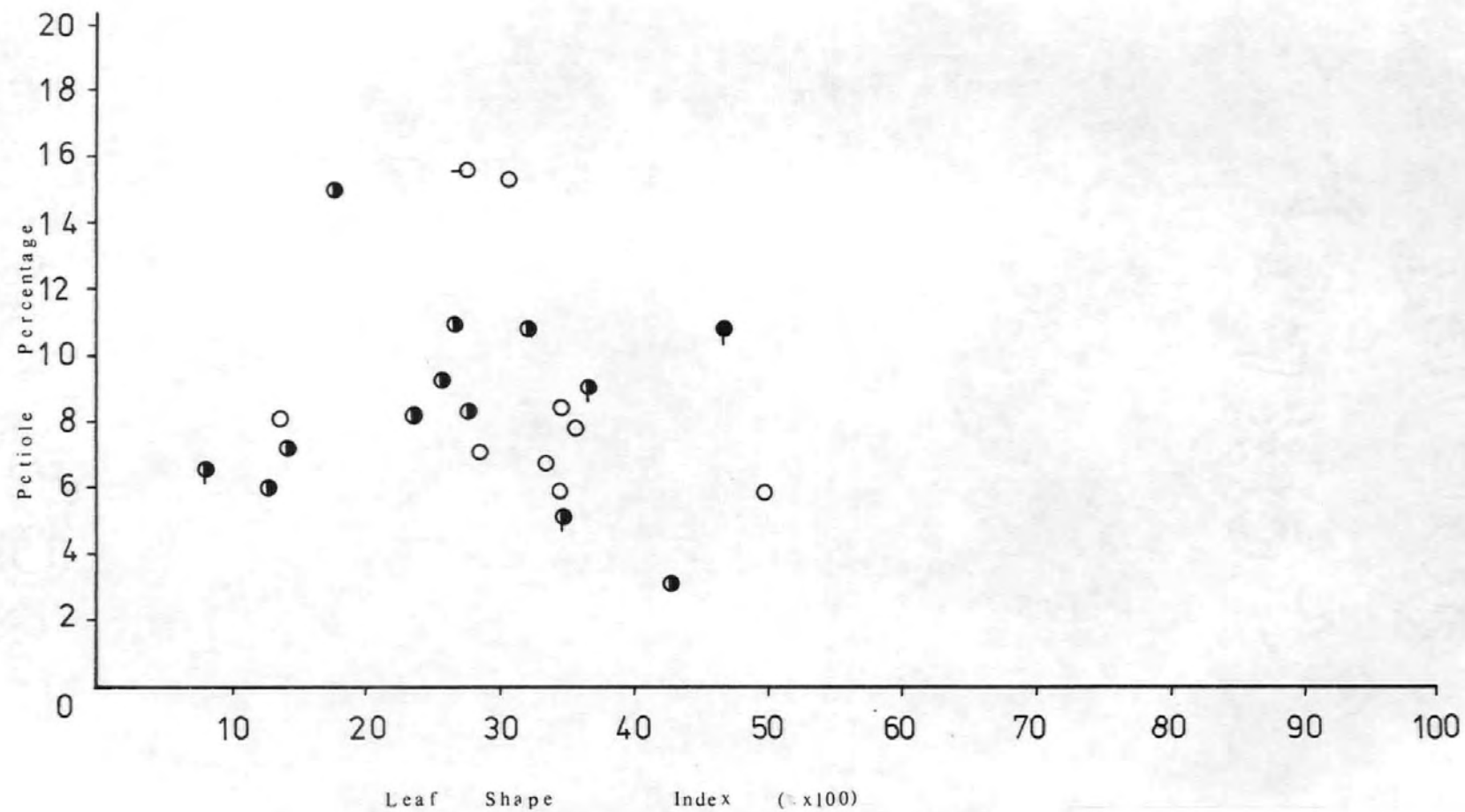




8.Lopwell dam (Q.petraea).



9. Blaxton wood (Q. petraea).



10. Warleigh wood (Q. petraea).

APPENDIX C.

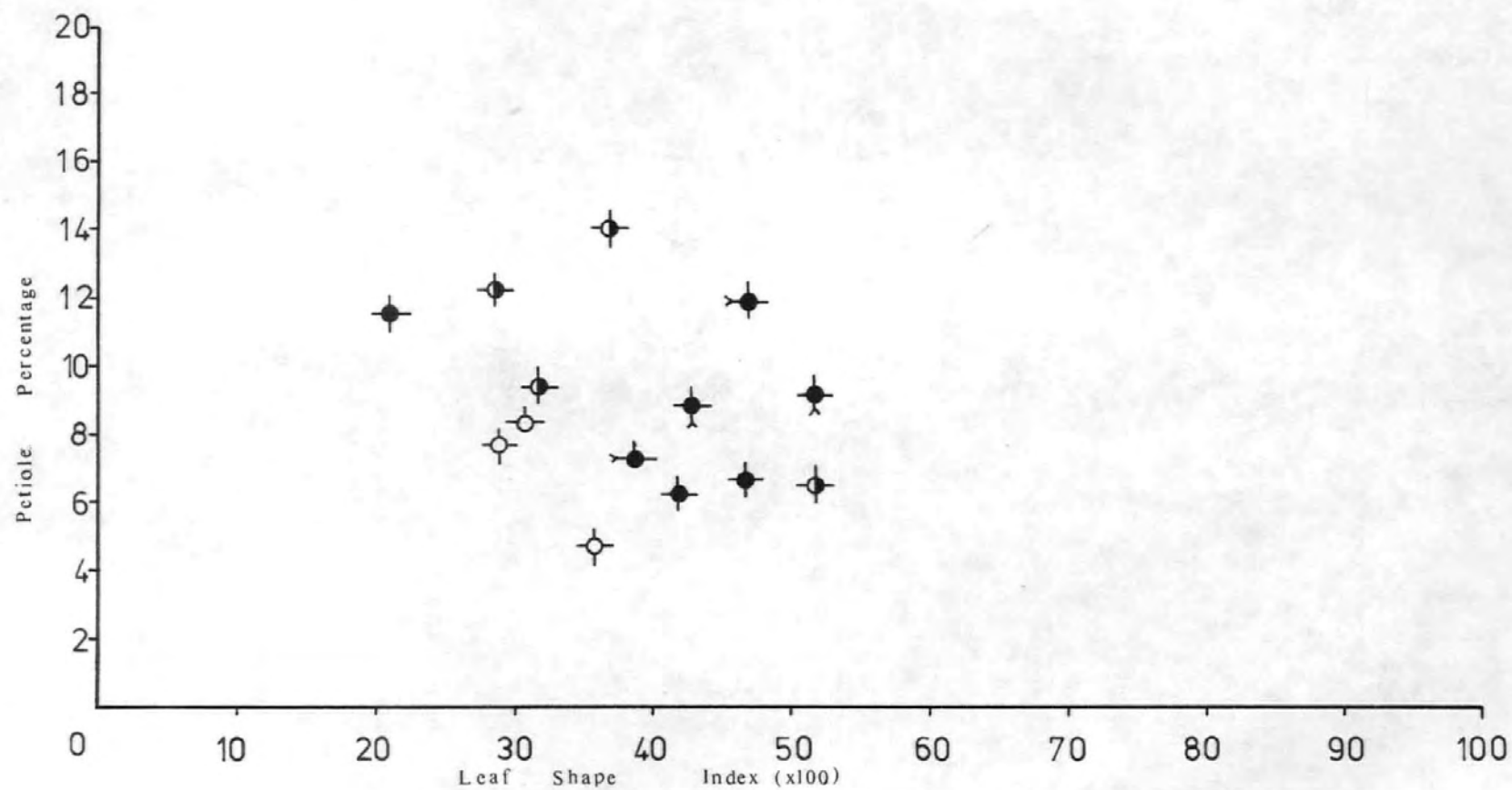
Pictorialised Scatter Diagrams for Yarner Wood  
transects.

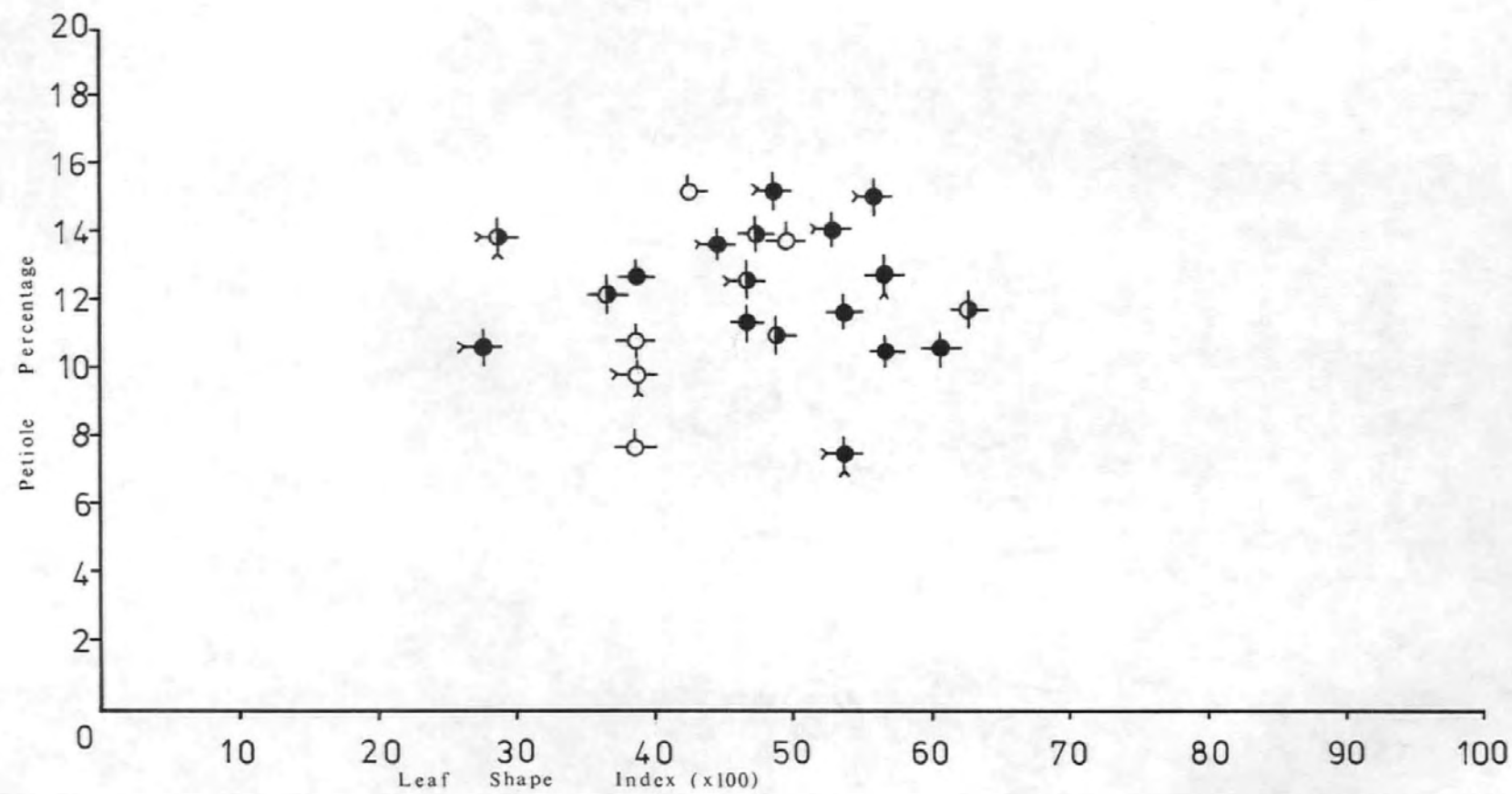
South - North Transect.

1.TG 27  
2.TG 26  
3.TG 21  
4.TG 18  
5.TG 15  
6.TG 11  
7.TG 8  
8.TG 5

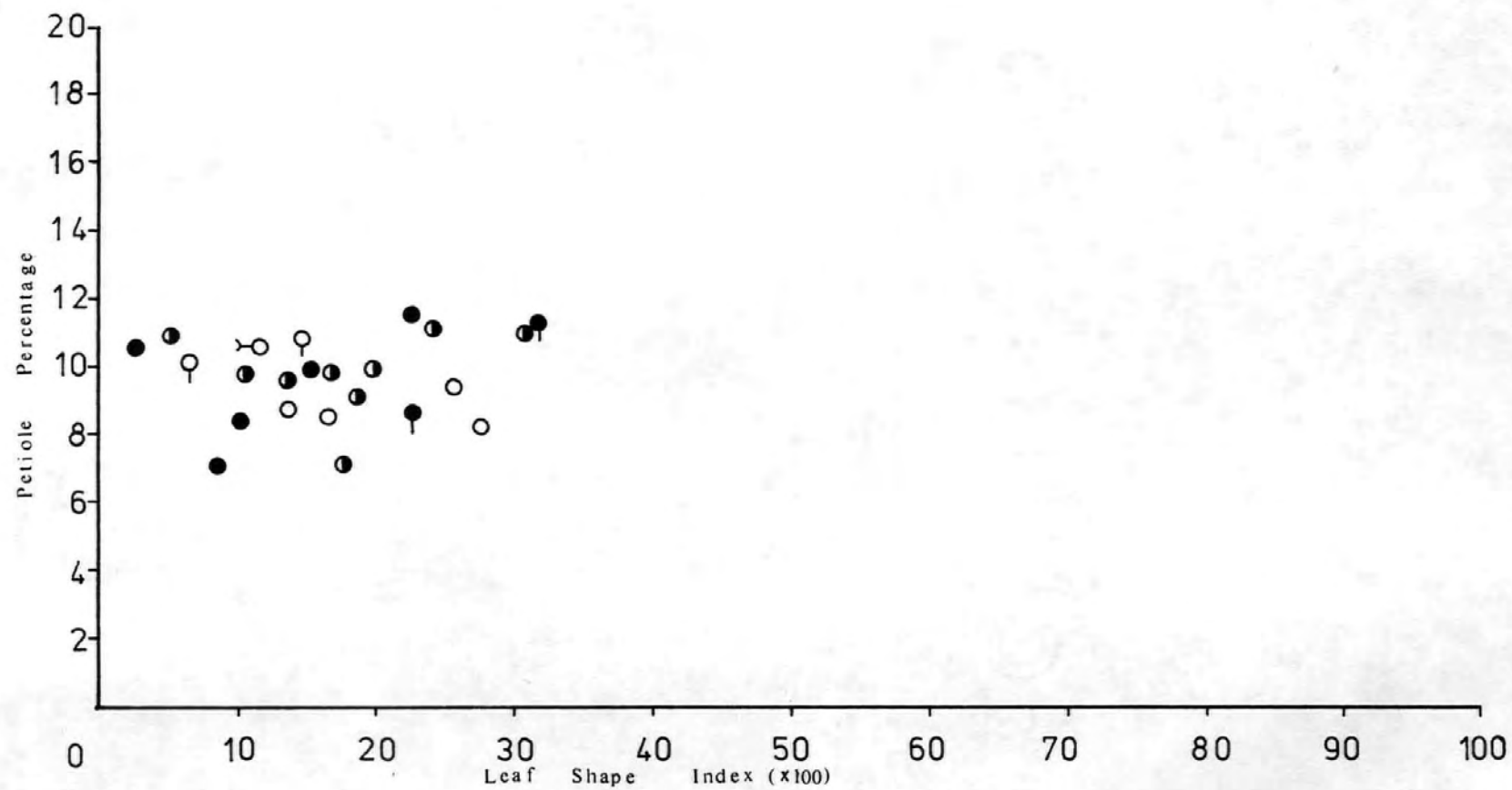
West - East Transect.

9.TL 4  
10.TL 6  
11.TF 2  
12.TC 4  
13.TB 6

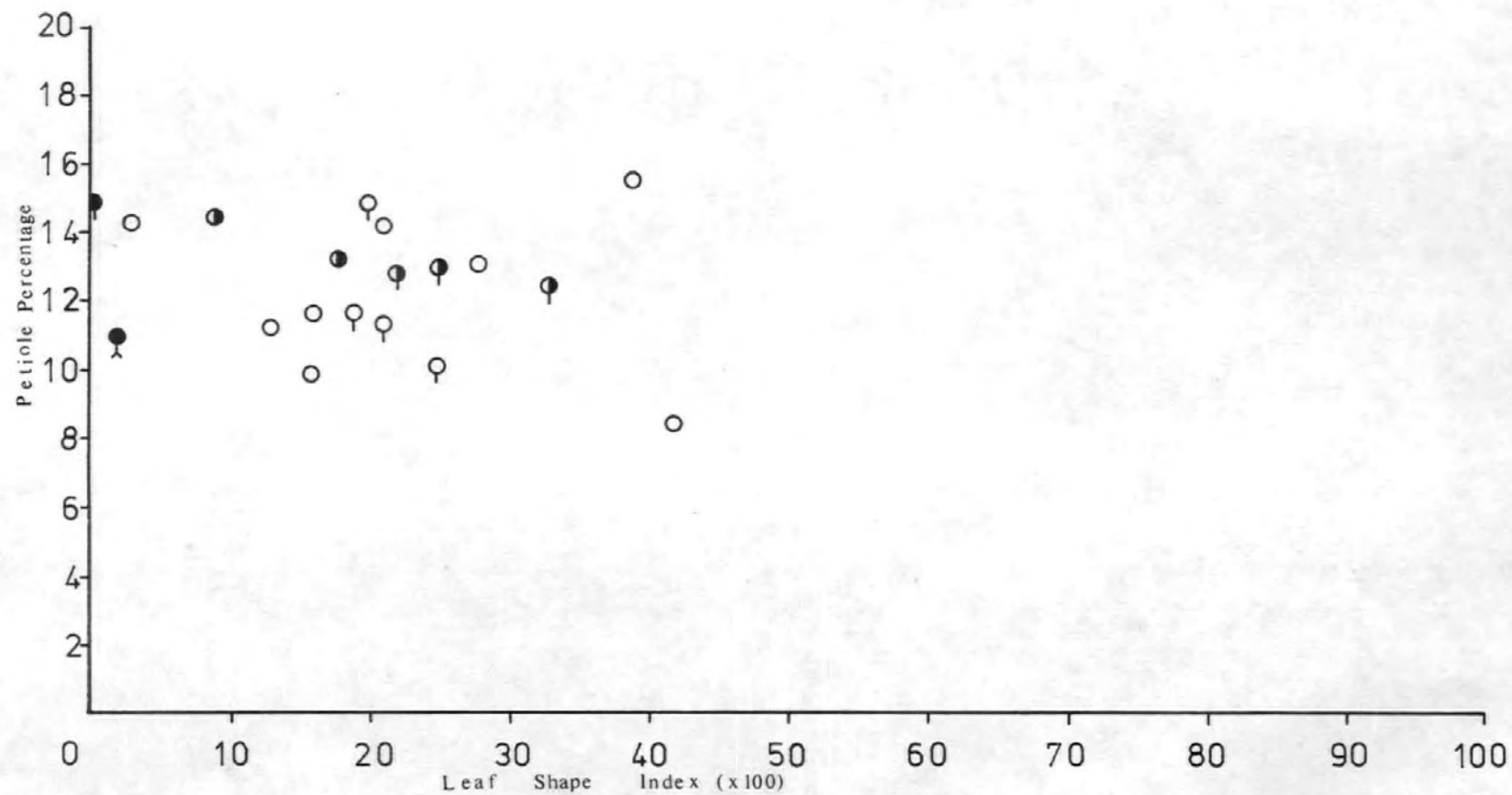


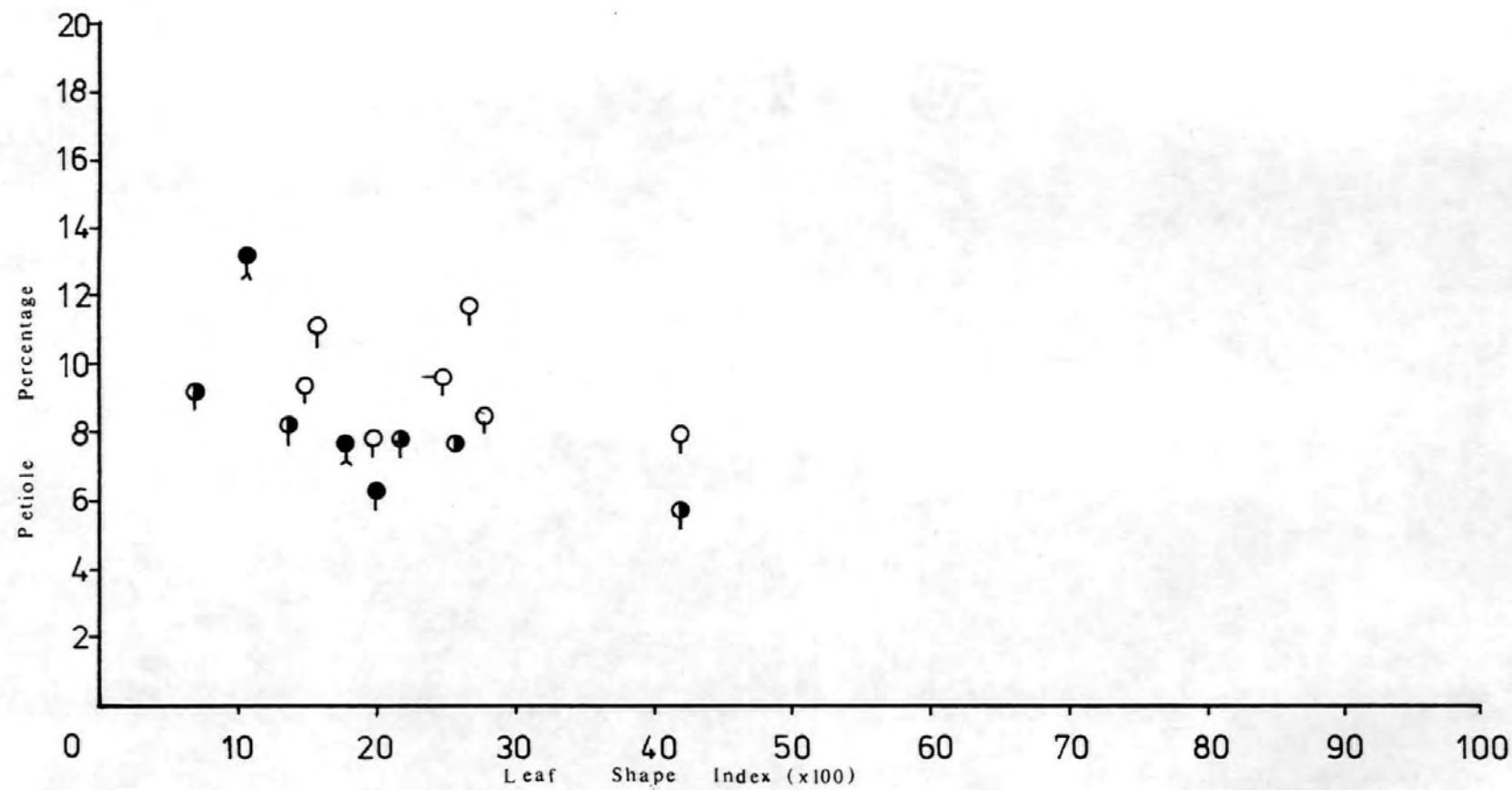




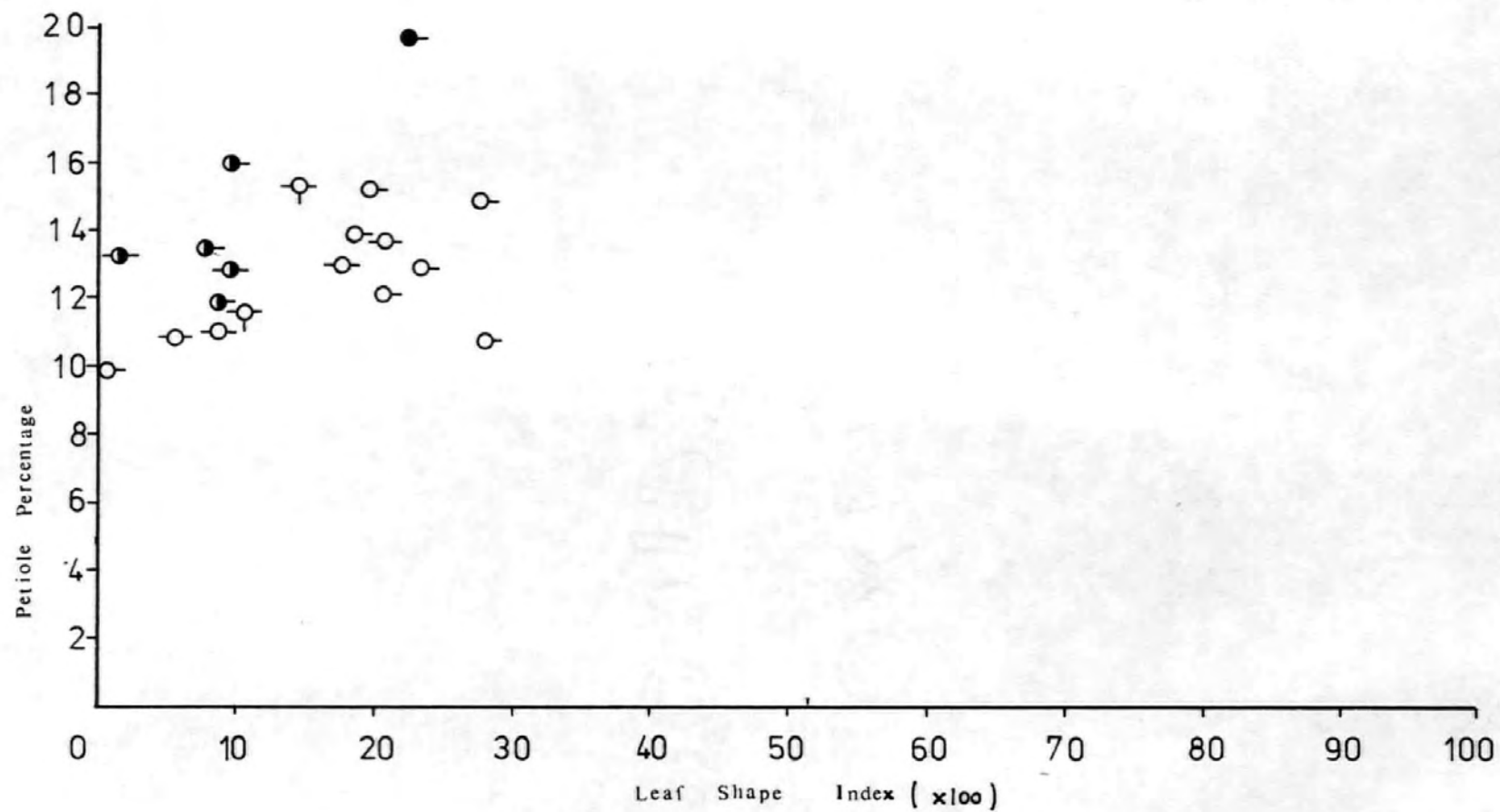


3.TG 21 (hybrid).

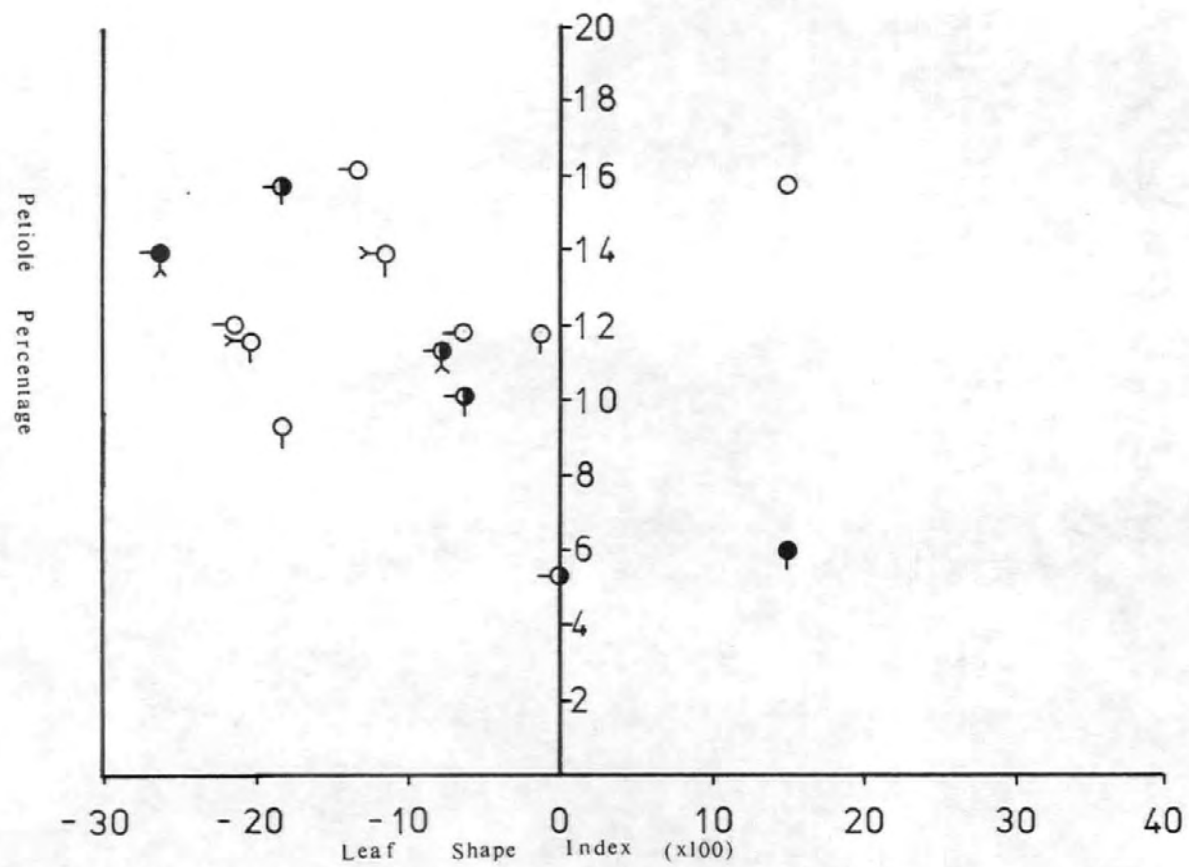




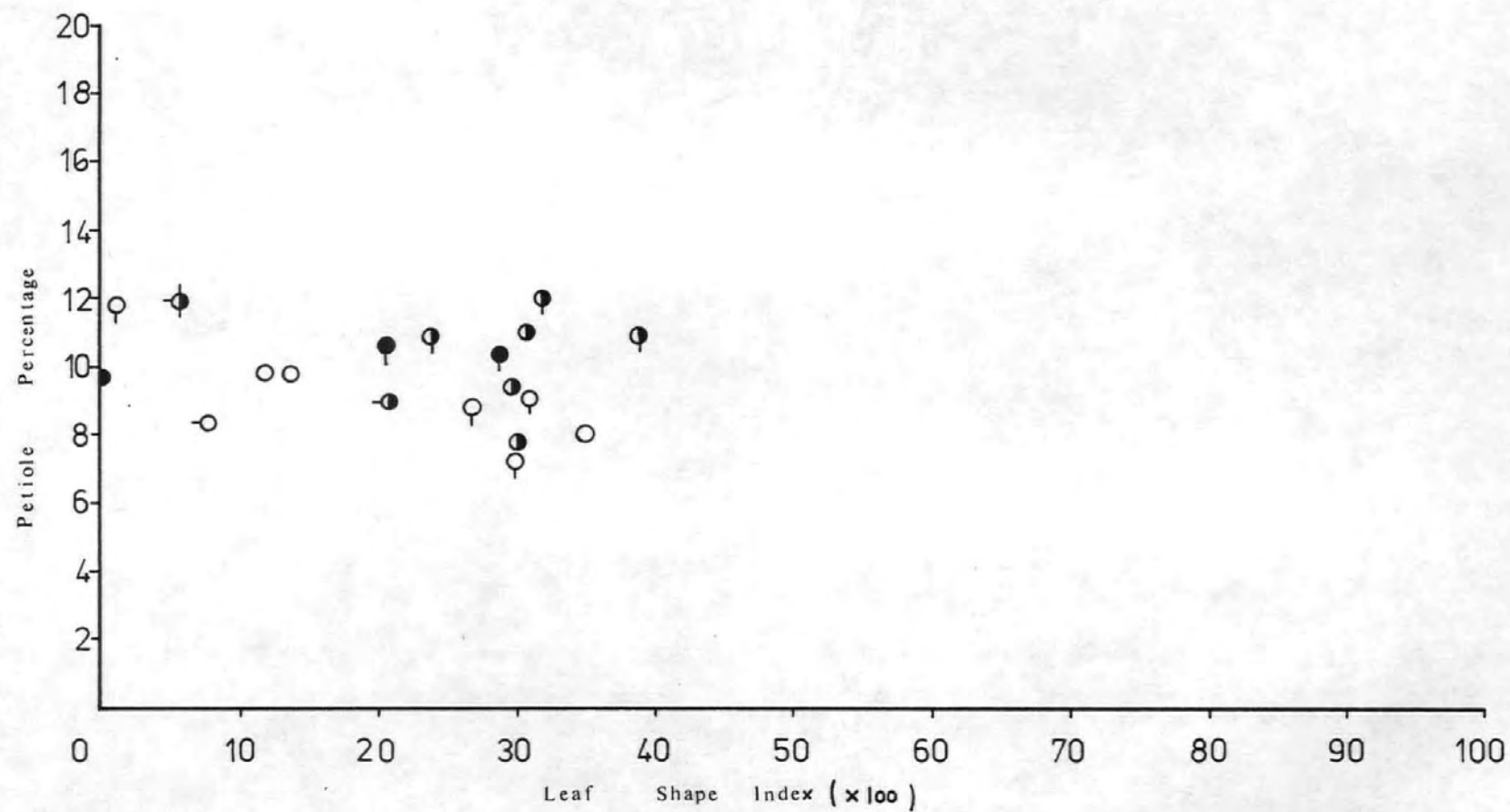
5.TG 15 (hybrid).



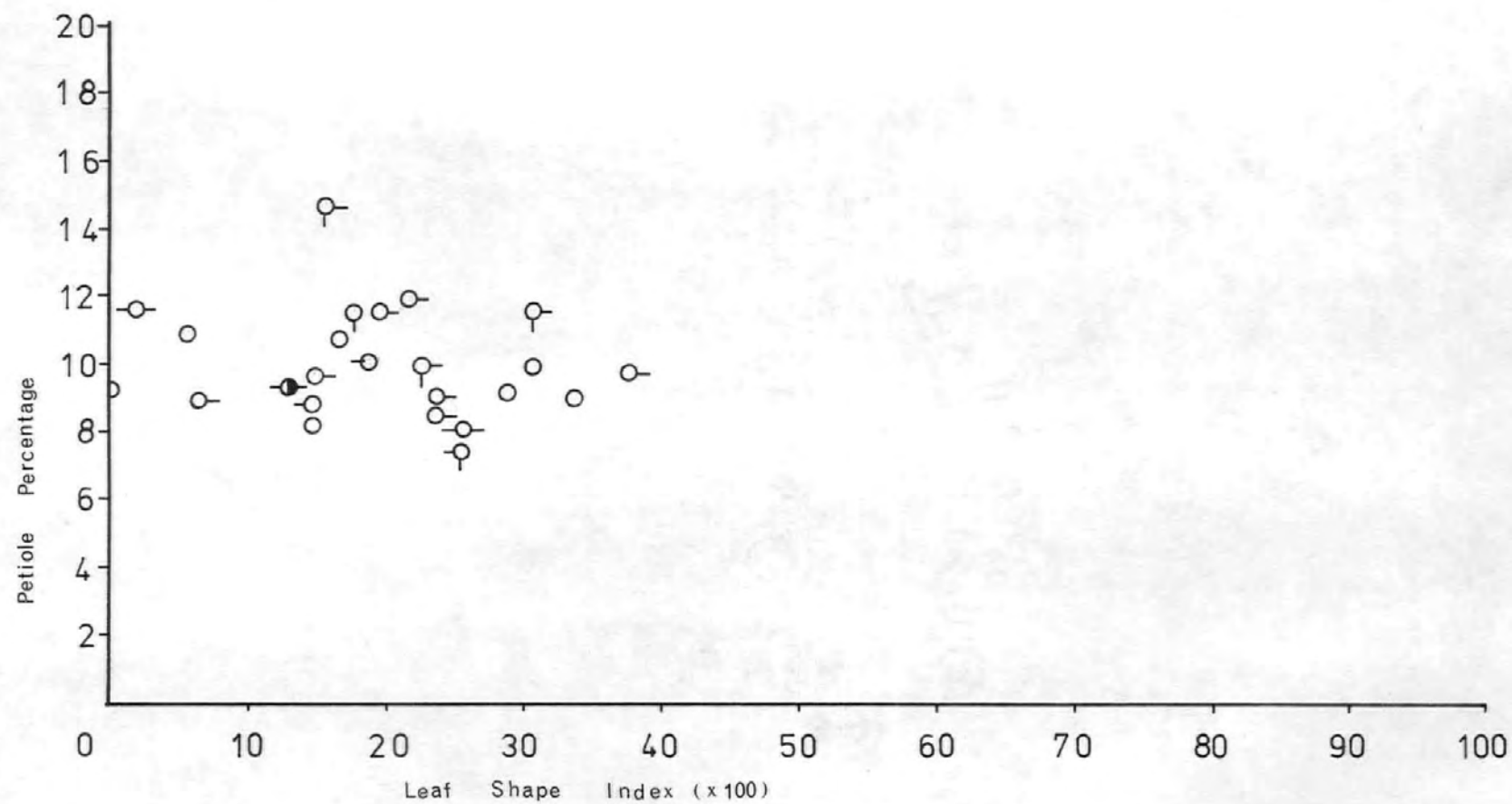
6.TG 11 (Q.petraea).

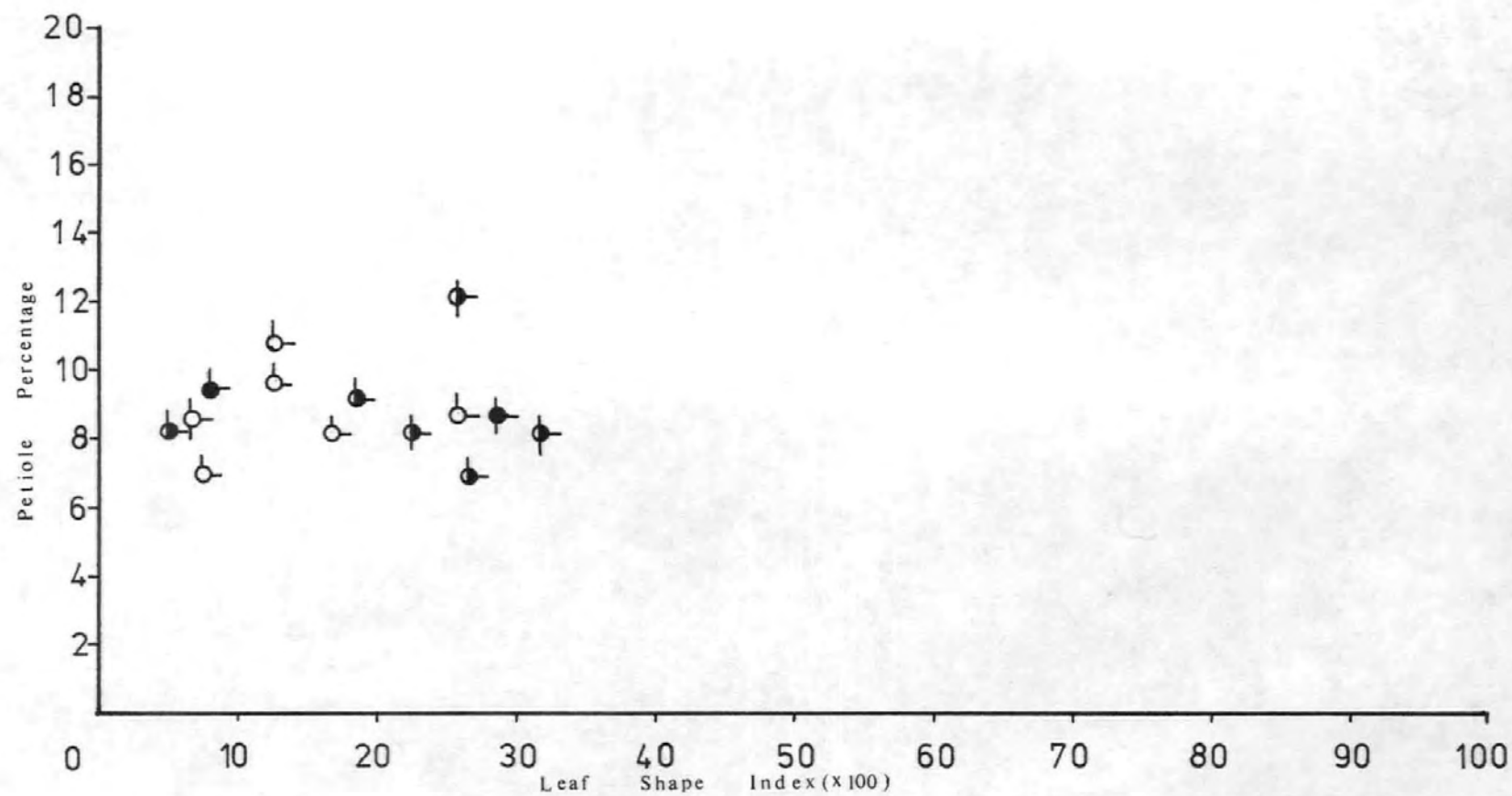


7.TG 8 (Q.petraea).



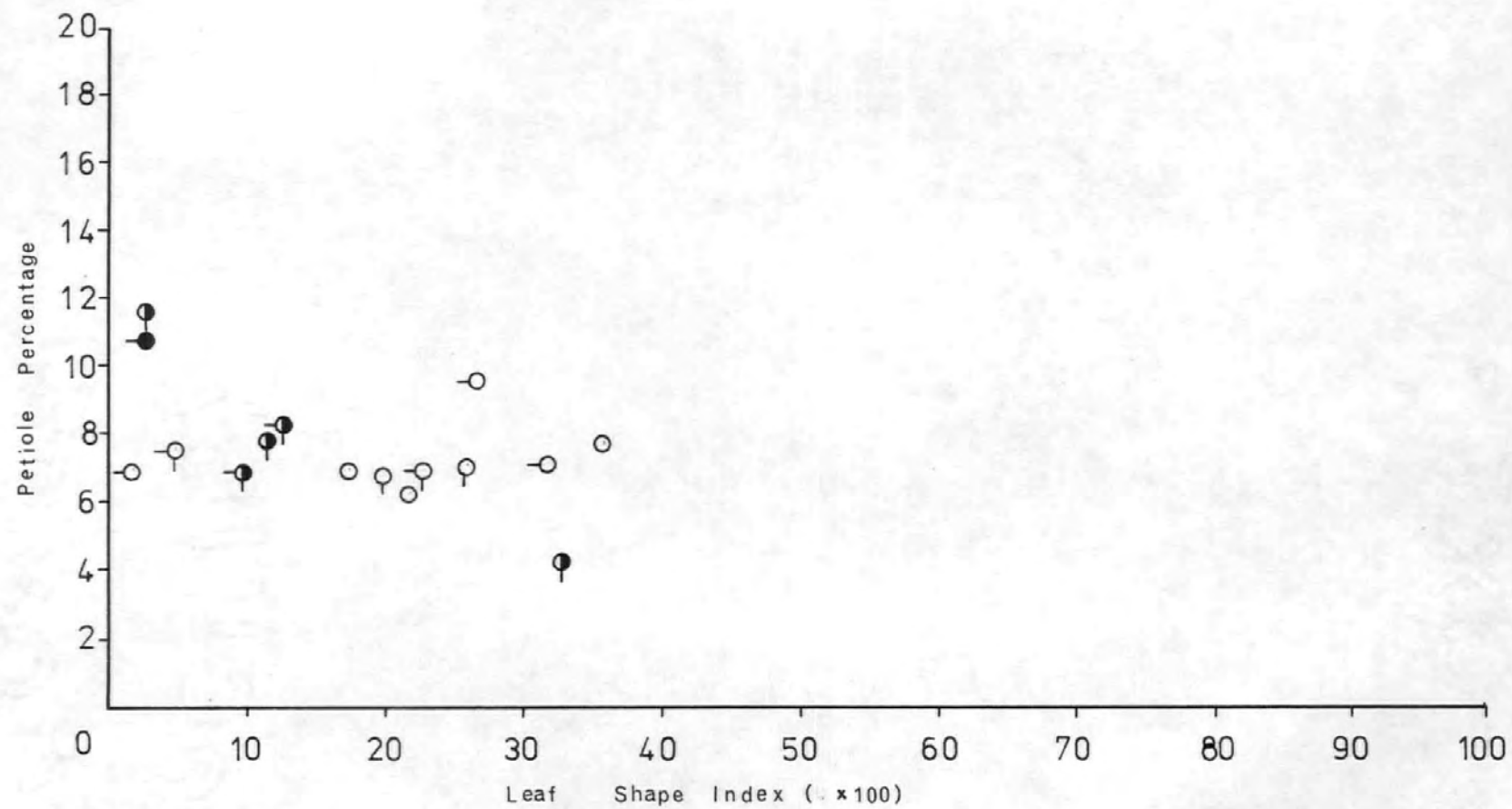
8.TG 5 (hybrid).



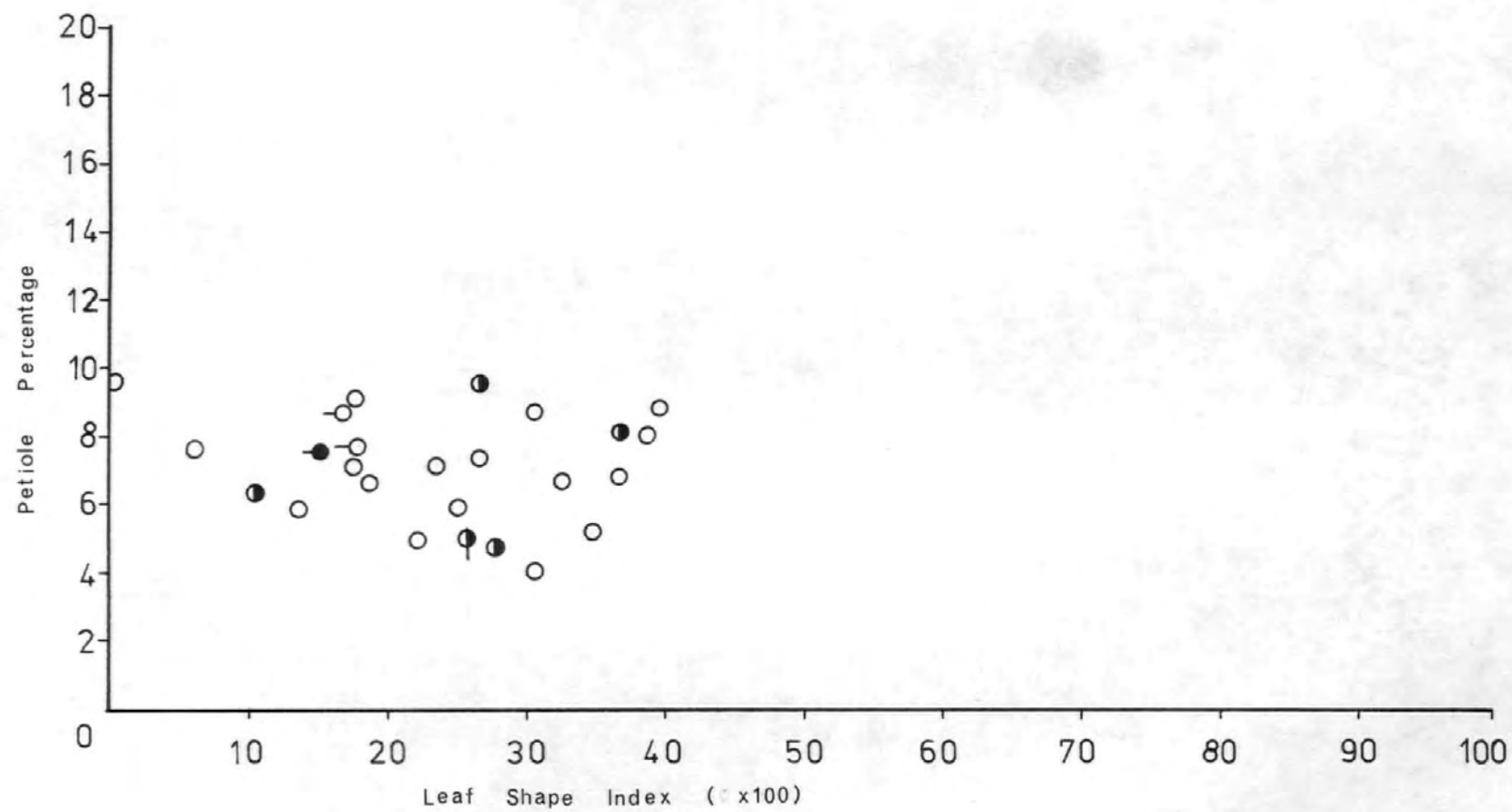


10.TL 6 (hybrid).

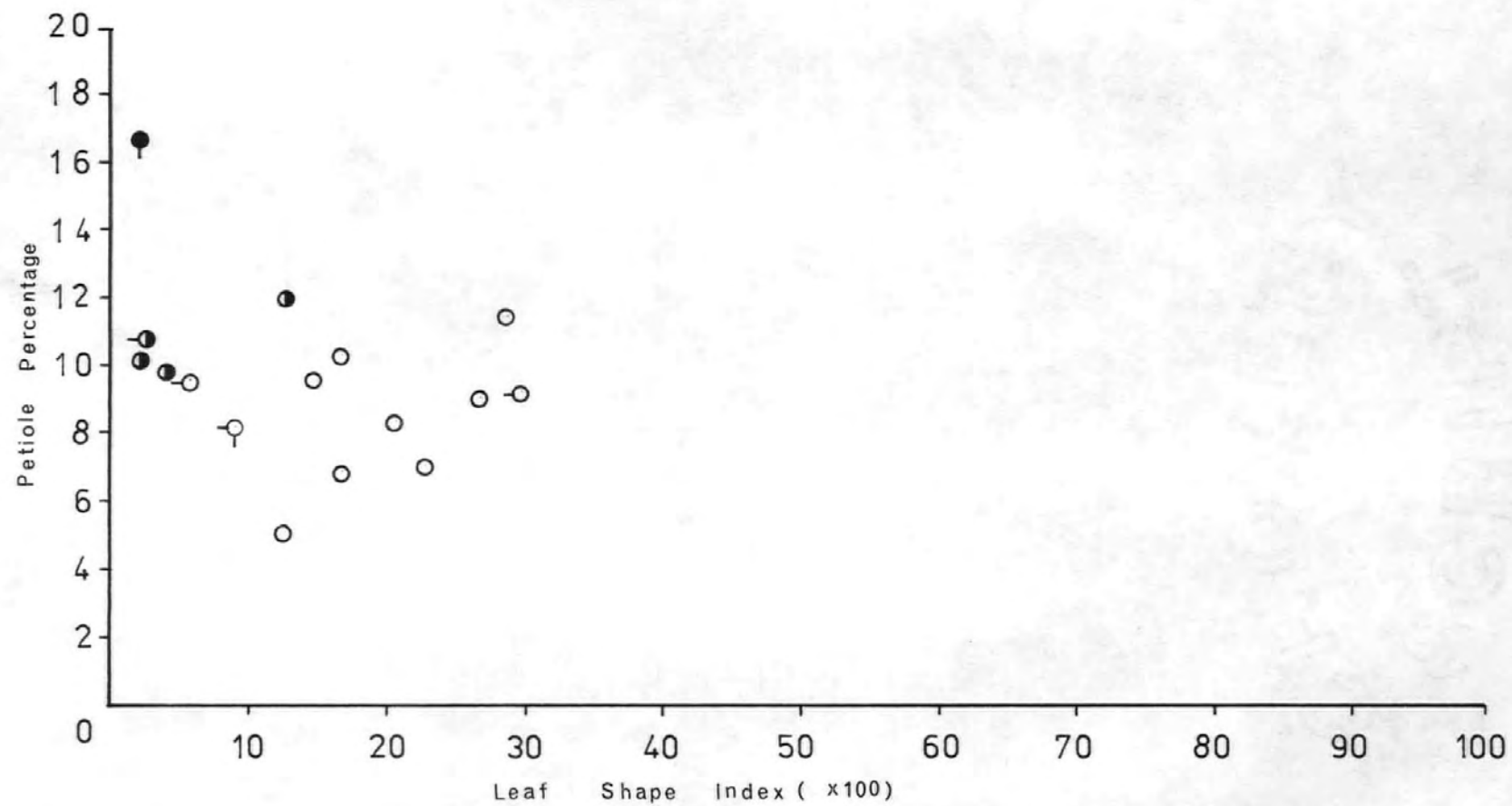




11.TF 2 (hybrid).

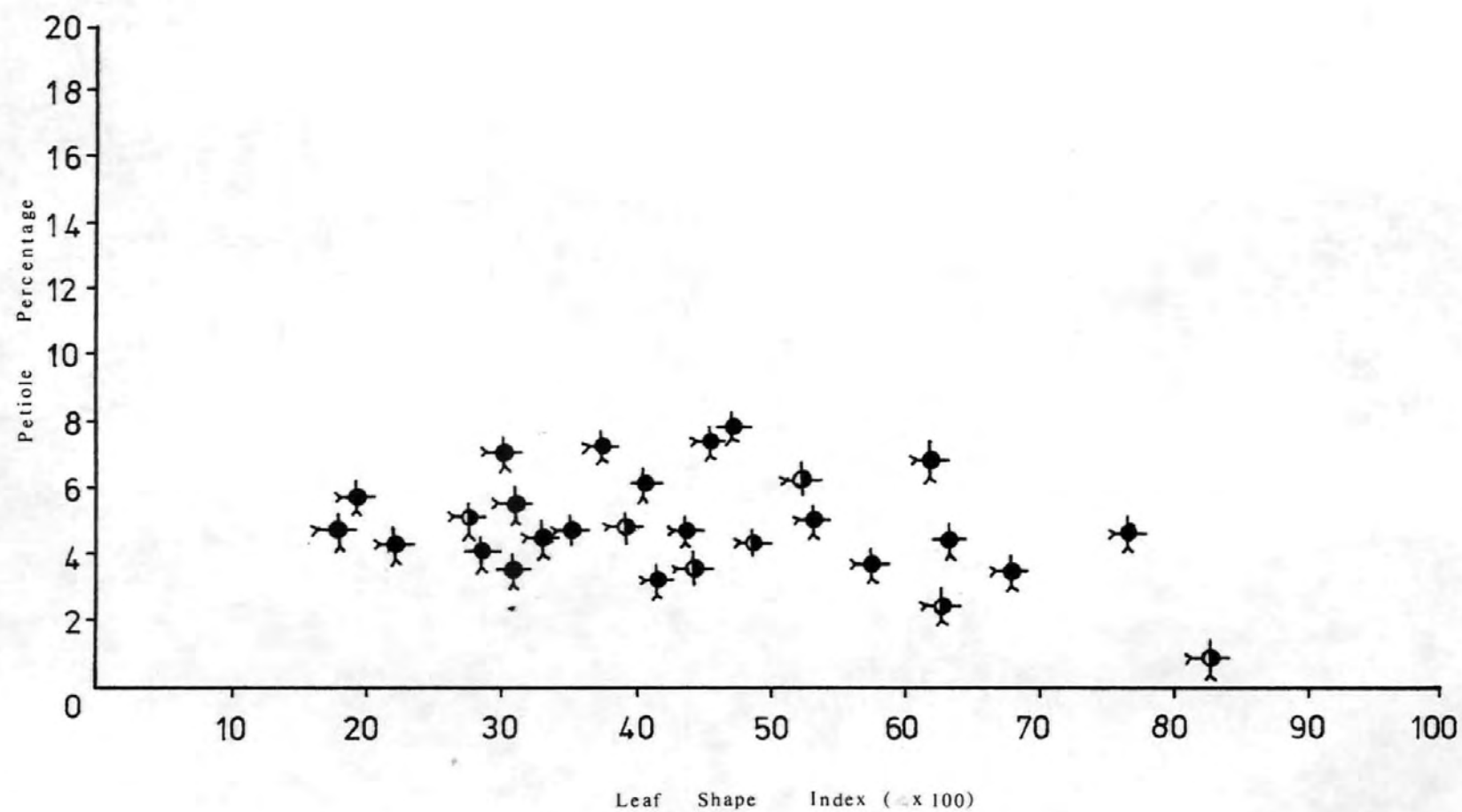


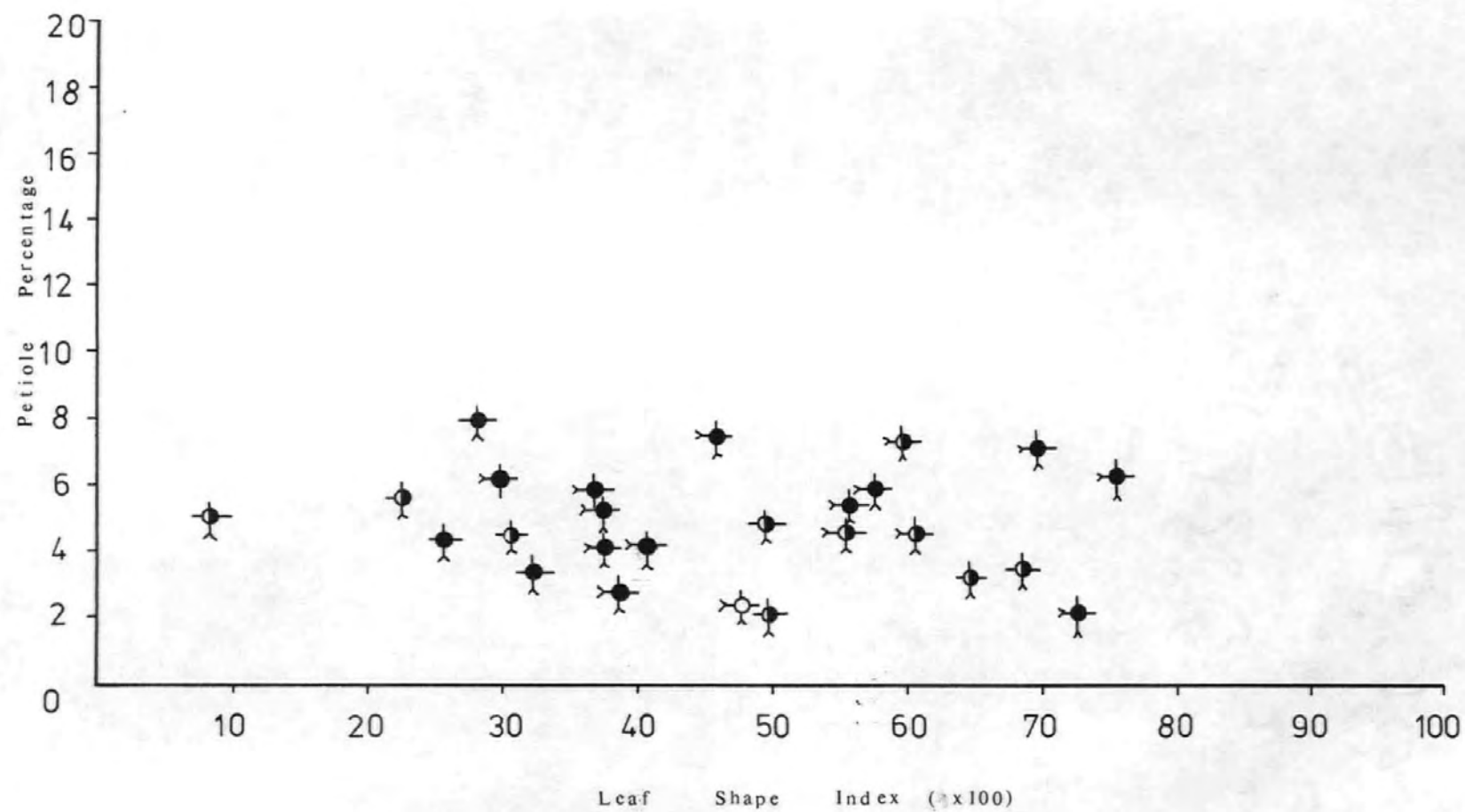
12.TC 4 (hybrid).

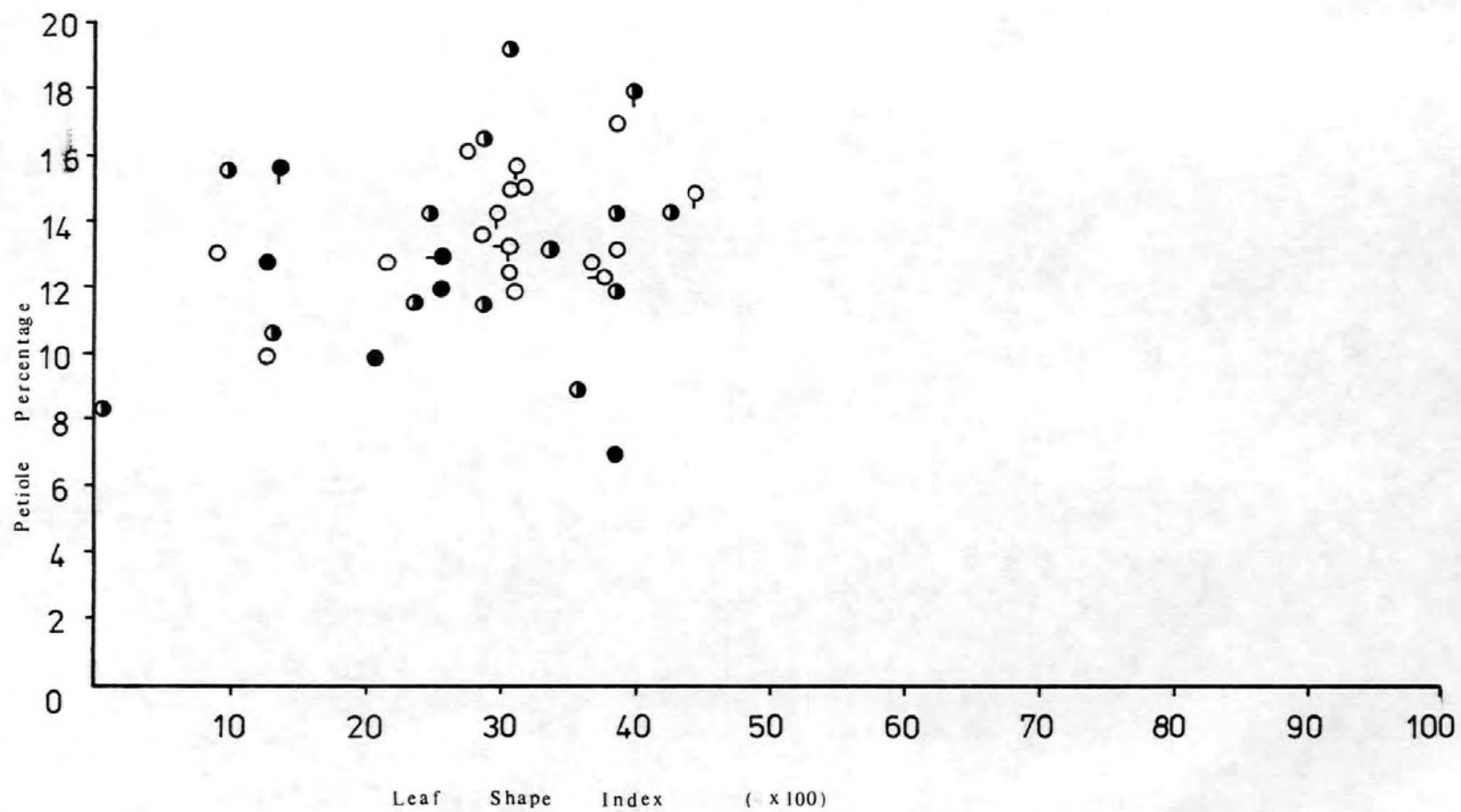


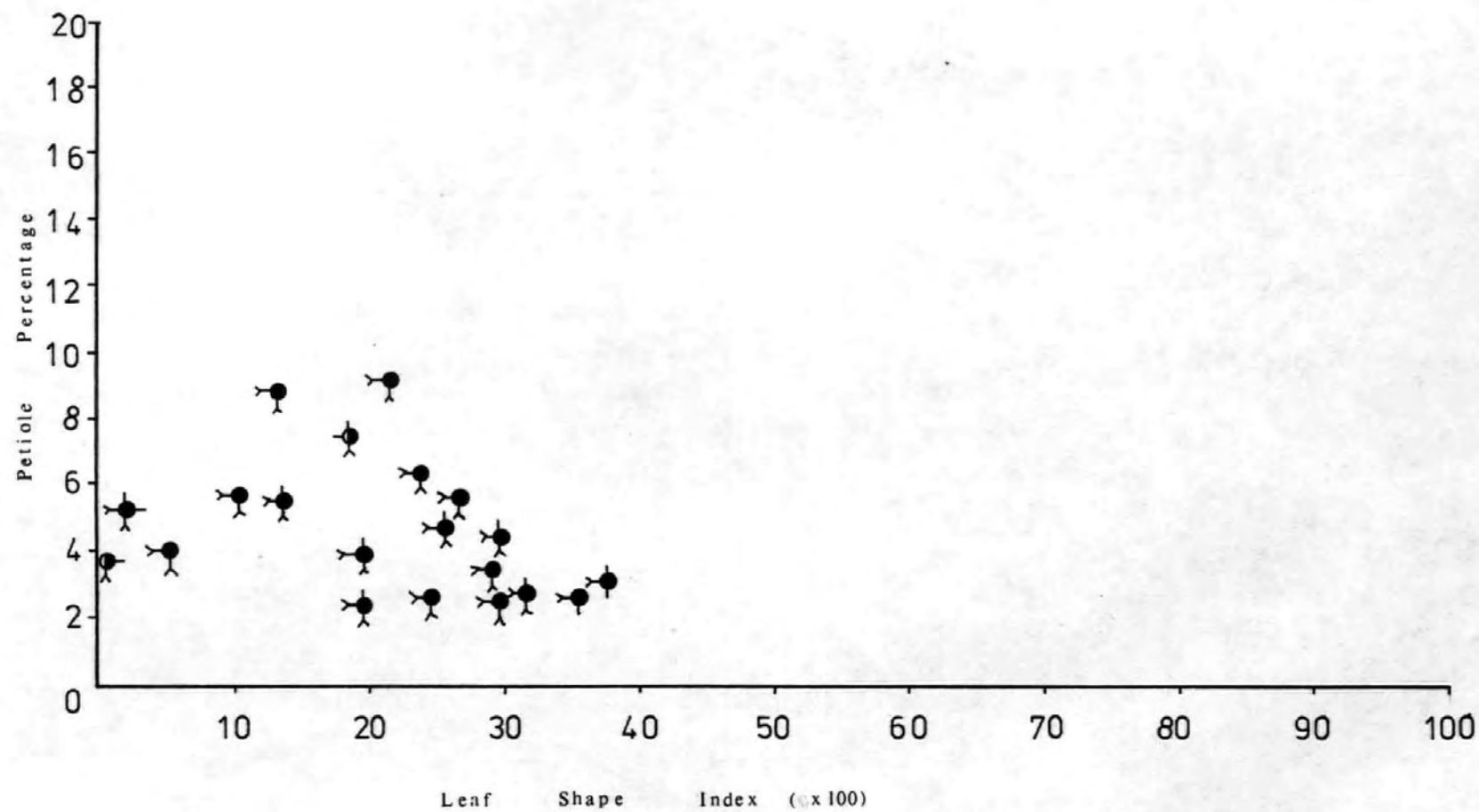
APPENDIX D.

- 1.PSD for Wistmans Wood.
- 2.PSD for Piles Copse.
- 3.PSD for Ausewell Rocks.
- 4.PSD for Harford.
- 5.PSD for Meavy.
- 6.PSD for Foborough.





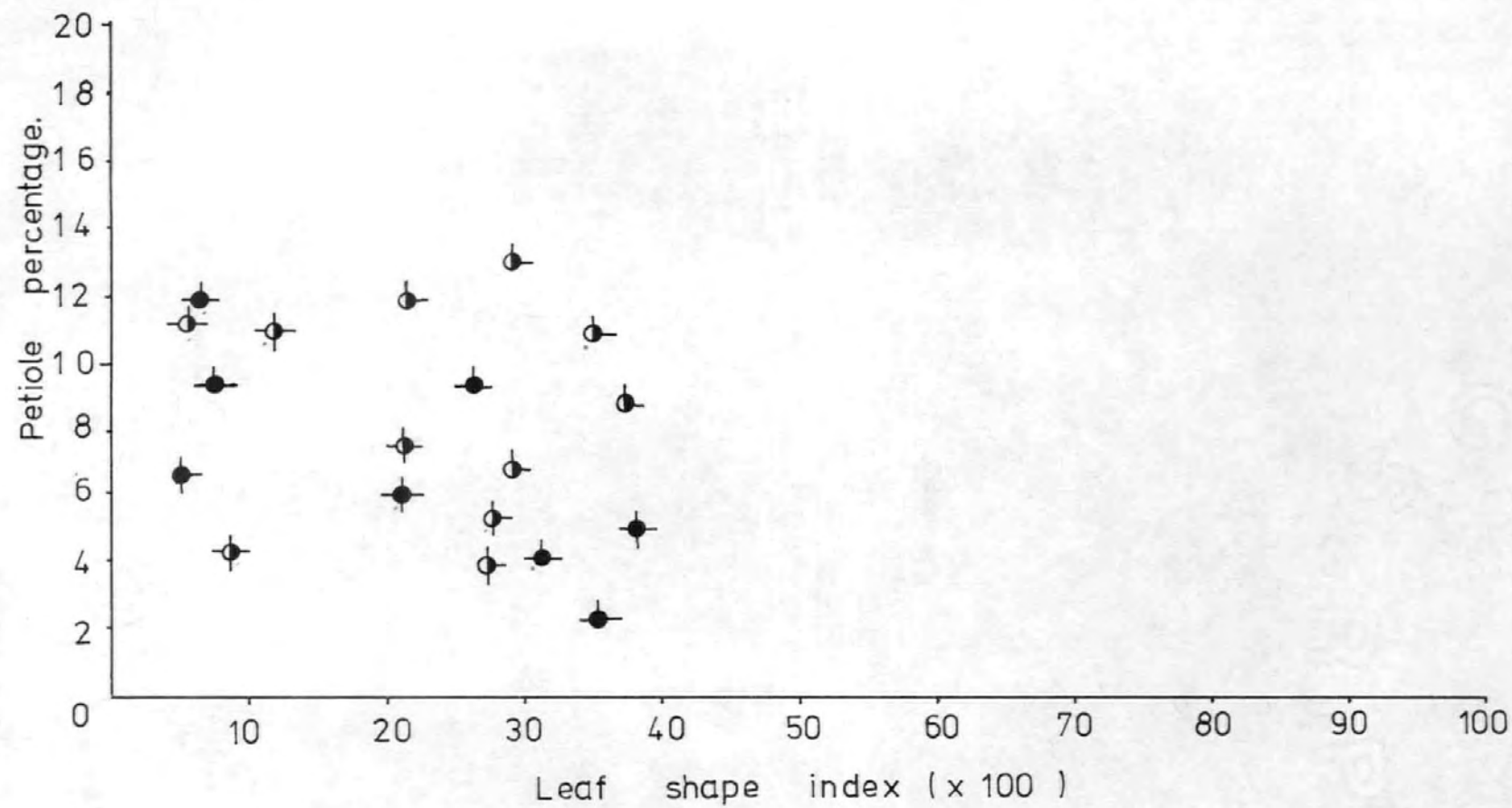




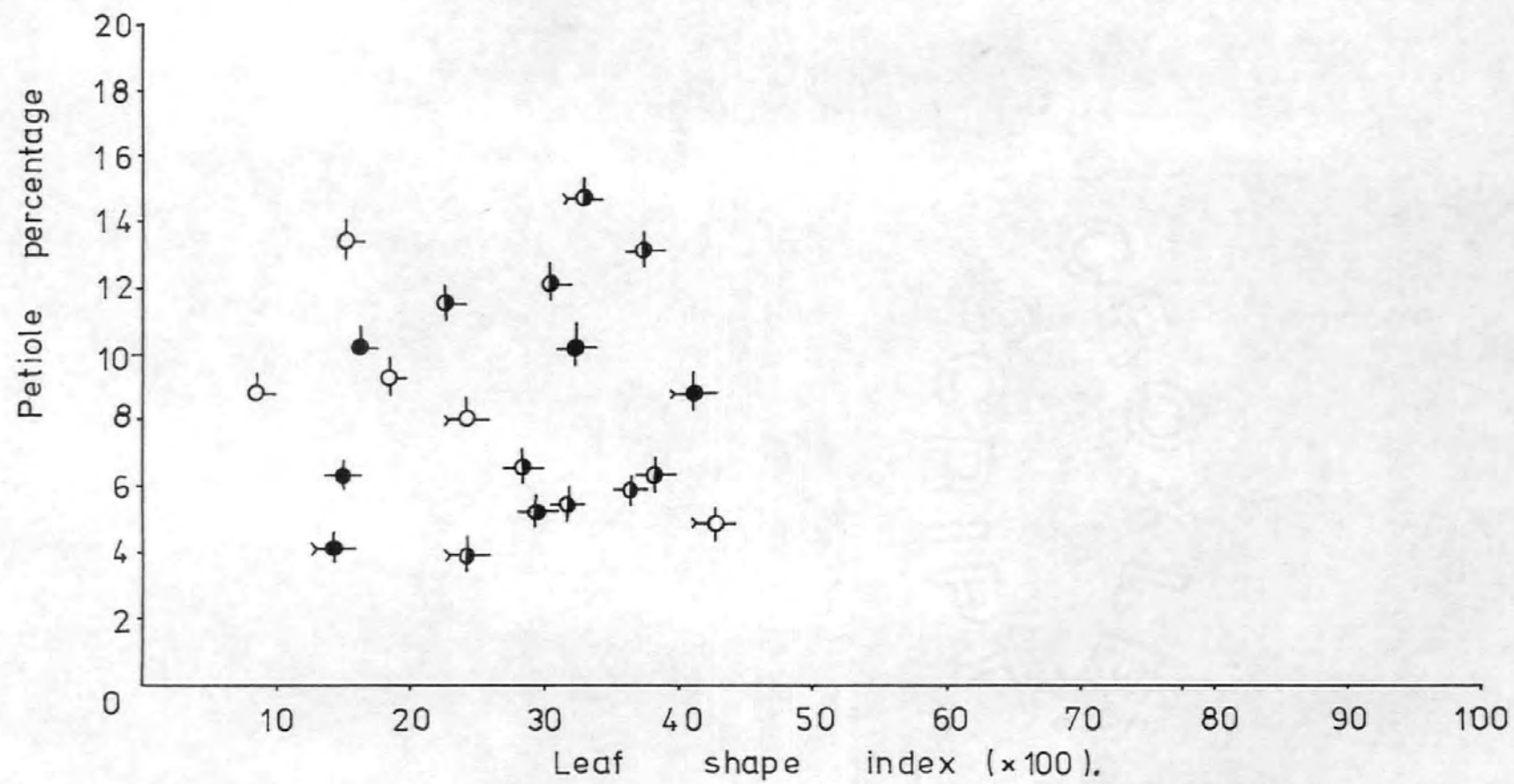
L. Herford (Q. robur).



5. Meavy (hybrid).



6. Roborough (hybrid).



Appendix E.

Plate I. Blister galls caused by the sexual  
generation of A.curvator, in the leaf  
lamina.



Appendix E.

Plate II. Agamic generation gall caused by A.fecundator,  
Artichoke gall.



Appendix E.

Plate III. Sexual generation gall caused by A.inflator.





Appendix E.

Plate IV. Marble galls caused by the agamic  
generation of A. kollari.



Appendix E.

Plate V. Sexual generation gall of A. quercusramuli,  
woolly catkin gall.

Sexual generation gall of N. quercusbaccarum,  
currant galls.



Appendix E.

Plate VI. Oak apple galls caused by the sexual  
generation of B. pallida.



Appendix E.

Plate VII. Pea galls caused by the agamic generation  
of C.divisa.







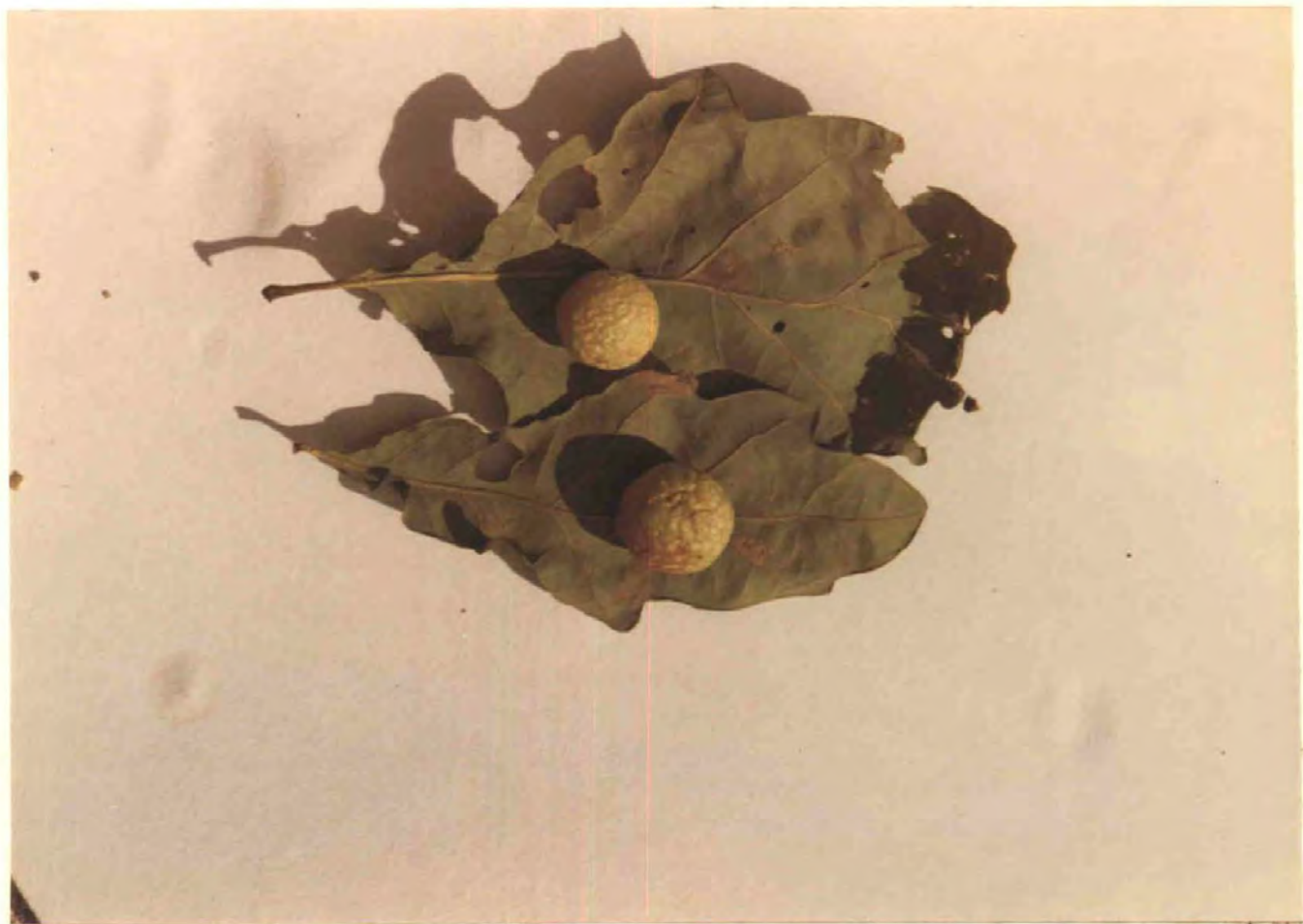
Appendix E.

Plate VIII. Agamic generation gall of C. longiventris.



Appendix E.

Plate IX. Agamic generation galls of C. quercusfolii.



Appendix E.

Plate X. Common spangle galls caused by the  
agamic generation of N. quercusbaccarum.





Appendix E.

Plate XI. Silk button spangle galls caused by the  
agamic generation of N.numismalis.

