ABSTRACT OF THESIS

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Title of Thesis Biological and population studies on the Larch Bark Beetle, Ips cembrae (Heer), (Coleoptera : Scolytidae).

A review of literature on bark beetles in general, and on Ips cembrae in particular indicates that while the origins and details of bark beetles outbreaks in any part of the world may differ, the general aspects of the situation examined on broad lines show great similarities. The economic status of bark beetles as pests of coniferous forests is examined in some detail, and measures to control their population are discussed.

Rearing techniques for the study of life-history and habits of Ips cembrae are devised in the laboratory, and these are supplemented by field observations. The results of the studies show that the bark beetle is univoltine but produces two broods in a year. The first broods result from egg-laying in May and June, producing adults in August and September and the second arise from eggs laid in September and October. These generally overwinter as larvae and pupae, and adults emerge in the following spring. The larvae pass through three instars before pupation. A characteristic feature of the bark beetle attack is the shoot tunnelling habit of the adult beetle, which can cause crown pruning and death of healthy trees.

The population studies on Ips cembrae are designed to reveal the nature of the bark beetle distribution at the Ord Wood in Nairnshire, the effects of heights of trees and bark thickness on this distribution, as well as the relationship between air and bark temperatures of trees infested by Ips cembrae. It is evident from the analysis of the sampling data that the bark beetle distribution is best described by the negative binomial.

Transformed data subjected to analysis of variance, indicate that heights of trees and bark thickness have significant effects on Ips cembrae /

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Ips cembrae population. The bark beetle density of attack decreases towards the tops of infested trees, which is due to very gradual decrease in the thickness of the bark.

Results from subcortical temperature investigations in relation to air temperature are presented graphically. Temperature under thin-barked trees tends to follow the trend of air temperature, but subcortical temperatures of thick-barked trees are much higher than air temperatures. The south side of a tree warms up rapidly during the day when the sun is shining on the bark, and subcortical temperatures rise higher than those on the north side of the same tree; the south side exhibiting higher bark temperature than the north side is more attractive to adults of *Ips cembrae*.

The practical application of these results to the control of *Ips cembrae* number in the Ord Wood is discussed, pointing out the importance of basing such control measures on forest management techniques.

Biological and population studies on the
Larch Bark Beetle, *Ips cembrae* (Heer),
(Coleoptera : Scolytidae).

BY

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M.Sc. Thesis.

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This thesis is an account of one year's studies on the biology and population density of the larch bark beetle Ips cembrae at the Ord Wood, Cawdor Estate, in Nairnshire, and is submitted for the Degree of M.Sc. at the University of Edinburgh, in accordance with the regulations.

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R. A. Balógun.

INTRODUCTION.

Various species of bark beetles are being introduced particularly from the continent of Europe into Britain, and the steadily increasing area of coniferous forests in this country, will doubtless provide greater facilities for these aliens to become established as resident breeding species. Munro (1926), in assessing the situation in Britain said that the British fauna was being increased by the introduction of various species of bark beetles such as Ips sexdentatus Boem., Ips erosus Woll., and Pityogenes chalcographus L. in the bark of pit timber, although some of these species failed to establish themselves.

The introduction of additional bark beetle species to the British fauna is still a recurrent feature, as in the recent case of the larch bark beetle, Ips cembrae Heer (Crooke and Bevan, 1957). The bark beetle was assumed to have entered the country on German timber in the same way that Ips typographus L., and Ips amitinus Eich. were imported in large numbers on German spruce and pine timber respectively at the end of the second World War (Laidlaw, 1947; Forestry Commission Leaflet, No. 26, 1948), although both species failed to establish themselves as permanent members of the British /

British fauna.

The larch bark beetle, Ips cembrae, is an interesting example of an insect which has within recent years appeared in Britain, mainly in the north-east of Scotland, and gradually establishing itself and extending its range as it adapts itself to its new environment and climatic conditions.

The studies undertaken were concerned with the biology and population density of Ips cembrae. The biological aspect of the work involved a detailed investigation into the life-history and habits of the beetle, with special reference to the developmental stages. Materials for the investigations were obtained from the Ord Wood, Cawdor Estate, in Nairnshire. The bark beetle was reared in the laboratory, studies were undertaken to define its life-history and habits, and these were supplemented by field observations.

The population studies were designed to reveal the nature of the bark beetle distribution at the Ord Wood, the effects of heights of trees and bark thickness on this distribution, as well as the relationship between air and bark temperatures of trees infested by Ips cembrae. These involved sampling of windblown larch in the wood, and statistical analysis of the data collected.

The /

The main practical objectives of the studies are to collect biological and ecological information about the bark beetle, so that preventive and remedial measures based on its life-history may be undertaken against this recently established and noxious forest insect in Britain.

Before presenting an account of the studies carried out, a review of literature on bark beetles in general, and on Ips cembrae in particular is given.

PART 1.

Review of literature.

Chapter 1.

A. Introduction.

Bark beetles are not only fascinating from the biological and ecological viewpoints, but have also been of great interest to foresters and forest entomologists because of the great economic damage they have inflicted on forests throughout the world. Extensive publications have resulted and the majority refer at least to some biological and ecological aspects. Kleine and Trédl (1911), published the first complete bibliography of bark beetles. This was followed by Kleine's (1939) new bibliography; since then Schedl (1946, 1947, 1949) has continued with bibliography on bark beetles.

After the second world war, and partly as a result of unavoidable neglect of forest management, severe outbreaks occurred in various countries and these prompted many intensive studies. Since Schedl's latest work in 1949, many publications could be listed including monographs on Ips typographus Linnaeus (Kuhn, 1949); on Ips curvidens Germar (Maksymov, 1950); on Polygraphus poligraphus L. (Lekander, 1959); and on Dendroctonus brevicomis LeConte (Miller and Keen, 1960).

In addition, monographic works containing complete bibliographies on bark beetles in various countries were published- Balachowsky (1949) in France, Schwerdtfeger (1957) in Germany; Schedl (1955) and Schwerdtfeger (1959, 1960) in Central America; Beal and Massey (1945), Blackman (1950), Keen (1952), Chamberlin (1958) and Anderson (1960) all in North America. All of these works contain a great deal of information on the biology and ecology of bark beetles.

The period since the second world war, and particularly the second half of the past decade are of special interest, because certain concepts and assumptions were then developed or clarified regarding the effects of parasites, predators, pathogens, and especially the physiological condition of the host trees on the population dynamics of bark beetles.

B. Historical review of studies on bark beetles with particular reference to the genus Ips.

In Britain.

British forestry, based as it is to such a large measure on the planting of exotic conifers, is open to some obvious risks of bark beetles attack. This has led to studies on these pests at various levels. Somerville (1891) carried out some observations on the life cycle of the pine beetle, Blastophagus piniperda L., and described it as one of the commonest and most destructive insects in pine areas in Britain. Macdougall (1902) studied the biology and forest importance of the same beetle and pointed out the damage it could cause to pine plantations in all stages of tree growth. Munro (1916, 1917) carried out a survey on the entomology of Scots pine, and discussed the importance of the genus Hylastes to British forestry.

Ritchie (1917) was the first British entomologist to undertake a comprehensive study on the structure, bionomics and forest importance of the smaller pine beetle, Blastophagus minor Hartig. The significance of his work was indicated in the results of his experiments and observations on the beetle. He ascertained that Blastophagus minor,

till /

till then scarcely known at all in Britain, and described as very rare, has been found in very large numbers over an area of fifteen square miles in Aberdeenshire, and could be as destructive to pine plantations as Blastophagus piniperda; firstly, by its attacking and boring into the tender shoots of pines; and secondly, by boring into pine stems for breeding purposes, the brood galleries in the bast and cambial regions ultimately causing the death of the trees. Munro (1926), pointed out in his work on British bark beetles that although no extensive outbreaks had occurred probably because of the limited extent of the forests, the possibility that considerable loss might occur, was proved as a result of the extensive felling of timber for war purposes, when considerable areas of pine in the New Forest and elsewhere were threatened by the pine beetles. Scots pine was severely attacked by the beetles which so pruned the leading shoots as to cause the death of the upper crown.

Hanson (1937, 1940) carried out extensive studies on the ecology and control of pine beetles in Britain, most particularly on the pine shoot beetle, Blastophagus piniperda. He performed

large /

large scale thinning experiments on 20 to 30 year-old plantations, to study the relationships between the beetles and their natural enemies. He thinned in strips, leaving the thin-barked material of small diameter on the ground to maintain a permanent population of the beetles natural enemies. Hanson has shown from the results of his studies that under normal forest conditions excessive increase of Blastophagus piniperda is to a great extent checked by the action of numerous ecological factors, including a large number of entomophagous parasites and predators. The useful work done by these parasites and predators can be facilitated by modifications in current forestry practice, and pine beetle control at a very low level of population density can be successfully accomplished under silvicultural conditions.

Some major European bark beetle pests have now been recorded in Britain, although it is fortunately true to say that these introduced beetles have not yet caused any catastrophic damage. The additional introduction of foreign species to the British list is relatively rare but it still occurs, as in the recent case of Ips cembrae Heer (Crooke and Bevan, 1957)- Review of literature dealing with this bark beetle is given in a later section. /

section.

Some species have certainly been introduced into Britain but have failed to establish themselves as permanent members of British fauna. For example, the spruce bark beetle, Ips typographus was imported into this country in large number on German timber at the end of the second world war (Laidlaw, 1947) but has failed to establish itself as a breeding species.

Crooke (1962) gave Britain's position in relation to the changed status of the giant spruce bark beetle, Dendroctonus micans Kug., in Europe. He reviewed the forest status of this bark beetle in Europe, pointing out most particularly the serious damage it has caused to plantations of Sitka spruce. He further indicated the danger involved in its possible importation to this country in view of the large scale afforestation already carried out with Sitka spruce. He outlined measures that have been taken to minimise the chances of its introduction, most of which are concerned with regulation of imported timber to the country.

In America and Canada.

The situation of bark beetles in North America can be reviewed in the following general terms, despite /

despite the vast areas and the multiplicity of coniferous species concerned. The primary species are mainly those of the genus Dendroctonus followed, and in a few instances preceded, by species of the genera Ips, Dryocoetes, etc.; Craighead (1942) summarised the enormous losses caused by some of the species of the above genera over the past 50 years. Evenden and Gibson (1940) recorded a destructive outbreak of the mountain pine beetle in lodgepole pine stands in Montana, when over 57 million trees from 3 inches diameter were killed. They pointed out the great fire hazard the destruction created, and they pleaded for an organised system of permanent forest surveys to collect data on the origin of outbreaks, thus enabling timely measures to be taken. Dendroctonus piceaperda, the Eastern Spruce bark beetle, was the subject of a controversial paper by Gobeil (1941) who discussed the question whether this species was to be regarded as detrimental or beneficial, dealing with losses caused by its attacks in Quebec. He emphasised the point that the beetle had concentrated on the overmature spruce stands, and concluded that the situation could only be remedied by better forest management. Balch (1942), commenting on Gobeil's paper, pointed out that studies in certain parts /

parts of the Gaspe peninsula in Quebec had shown that the attacks of the beetle coupled with those of the European Spruce sawfly, had actually caused the destruction of the greater part of a spruce stand of a most stable type. Under epidemic conditions, Balch observed that this bark beetle did not confine its attacks on overmature stands alone, but also destroyed a large part of merchantable volume of spruce forest, and caused undesirable changes in stand composition.

During the second world war and immediately after its close, several papers of great interest have appeared dealing with outbreaks of Dendroctonus species on Western coniferous forests. Evenden, Bedard, and Struble (1943), discussing the activities of the mountain pine beetle, <u>Dendroctonus monticolae</u>, recorded it as an important enemy of the valuable sugar pine, of which it destroyed many million cubic feet of timber in epidemic years. Various species of the genus Ips developed into primary pests in Central and North America and killed many healthy stands (Beal and Massey, 1945; Keen, 1952). Hoffmann and Anderson (1945) studied the southern pine beetle, <u>Dendroctonus frontalis</u> from a silvicultural viewpoint. Examining relationships between timber losses and natural restocking, they /

they concluded that pure stands of pine suffered more from insect attack than mixed ones.

Prebble (1944) discussed the place occupied by bark beetles in the forest economy of Canada, and estimated that over a 31-year period the annual depletion of stands by bark beetles attack amounted to 4%. He observed that the invasion of the bark beetle, Dryocoetes confusus on Balsam, and Dendroctonus engelmanni on spruce followed spruce budworm attacks on the species. Hopping and Geoffrey (1948) carried out studies to determine any possible correlation between tree diameter and incidence of attack by Dendroctonus monticolae. Attacked trees were statistically treated in relation to diameter and from the analysis of the data collected, it was apparent that the bark beetle infestation varied with the diameter of the trees. They concluded that the data might be useful in deciding tree and stand susceptibility to bark beetle attack in the management of Lodgepole pine forests in the Canadian Rocky Mountains.

In Europe.

Bark beetle outbreaks in Europe, especially during the last war and the period immediately following it, are recurrent features of forest insect /

insect literature. Butovitsch (1941) carried out detailed observations on the damage caused by Ips typographus and Blastophagus piniperda to Spruce and Pine, following three great storms which caused severe windblow to large areas of the two species in Central and Southern Sweden. From his observations, some interesting features emerged, first of which was the 'Strip-survey' method devised by the investigator to study the densities of bark beetle population in different areas; secondly, the question of prompt removal of windblown trees in such areas where it could be effected, damage thus being considerably reduced; and thirdly, the best methods of setting trap logs and of stacking timber in the forest in places where prompt removal was impossible. Butovitsch (l.c.) showed that continuation of attack was directly affected by rate of removal of fallen trees, the principal species, Ips typographus, showing a static phase in which attack was confined to fallen trees, followed by a dynamic phase when migration occurred and centres of infestation shifted. Earlier,Trägårdh (1939) has investigated the damage caused by a severe storm in the North region of Sweden, when 760,000 trees were windblown. He found Ips acuminatus, Ips sexdentatus and Monochamus sutor present in numbers sufficient /

cient to justify prompt removal of bark from all trees where frass was observed.

Thomsen (1939) described attacks by Pityogenes chalcographus on young spruce and Douglas fir in Denmark. The bark beetle, normally considered of secondary importance caused severe damage to the young stands resulting in the death of many trees. The primary cause of attack was attributed to abnormal spring weather, causing premature growth, followed by late frost which caused frost rings to develop in the active cambium, thus rendering the majority of the trees, while in a weakened state, susceptible to bark beetle attack. Galoux (1947), studying the biology of the same bark beetle referred to it as a species of growing importance especially in polestage stands, and he attributed its increase on the continent to the spread of spruce plantation. He recognised the customary secondary status of the beetle, but observed that under continental conditions it may become epidemic in plantations which have been weakened by physiological factors.

Ips typographus is one of the most destructive bark beetles in Europe and, since the last war has been studied most extensively. Schimitschek (1948) carried out a comprehensive survey in the spruce forests /

forests of Upper and Lower Austria during a serious epidemic of _Ips typographus_. He observed that the origin of the invasion was the unusually dry and warm weather of the regions in 1945-1946, and the extensive monoculture of spruce on unsuitable sites. Merker (1949) also showed from his biological studies on _Ips typographus_ that a hot summer encouraged the outbreak of the pest in Germany. Schneider-Orelli (1947), reporting on his observations of _Ips typographus_ outbreaks on the Swiss plateau, ascribed the attacks primarily to exceptionally favourable weather conditions in the summer and spring of 1945-1946, together with lack of normal forest tending owing to war conditions, which resulted in large numbers of stems being left unbarked. An attack of _Ips typographus_ and _Ips curvidens_ in Silver fir and Spruce forests in Selestat-Ville region of the Vosges was investigated by Aubert (1947). He observed that unsuitable site conditions originated this attack, the region being one of the driest in the Vosges, and he recommended the substitution of Scots pine for Silver fir.

Groups of bark beetles according to breeding material.

Of /

Of major concern to forest entomologists has been the question whether bark beetles are secondary pests or whether they can become primarily destructive to the forests. Although certain bark beetles show definite preferences in their environmental requirements, it is known that both the physiological condition of the host tree and the population level of the beetles must be considered in ascertaining the degree of damage. (Kangas, 1950, 1952; Saalas, 1951; Merker, 1956; Miller and Keen, 1960). In some cases, it may be difficult to decide whether the primary attack of bark beetles is due to increase in their population or whether it is caused by a temporary weakening in the physiological condition of the forest stand. Gauss (1960) has pointed out that such grouping is often difficult and that no valid comparison among the various beetle species from published literature is possible unless conditions under which the invasions occurred are closely identified.

According to Keen (1958), who defined primary insects as those which prefer completely healthy trees in full vigour, most of the bark beetles must be considered secondary pests. Under endemic population levels, they breed in trees of abnormal physiological conditions, such as windthrown, fire-killed, /

killed, or freshly cut trees, or trees temporarily or permanently weakened by drought, defoliators, fungus or other agents. Under epidemic conditions, many of these secondary bark beetles become primary pests and invade trees of normal health. Zwölfer (1957) explained that the term "to become primary" as commonly used in forest entomology, implies the temporary ability of the beetle to kill healthy trees and not its constant preference to breed in such trees. The term "secondary pest" then does not refer to economic losses, but to brood physiological requirements. Other bark beetles are known to develop into mass populations on their preferred material but never to invade and kill healthy trees even under population pressure. These species of bark beetles can be classified as secondary beetles in the strict sense.

Apart from differences in destructiveness, most bark beetles attacking living trees show preference for certain age, size, bark thickness etc. Thus, Dendroctonus frontalis and Dendroctonus monticolae have been observed to perfer standing young trees (Beal and Massey, 1945); Dendroctonus brevicomis prefers older decadent trees; Dendroctonus pseudotsugae and Dendroctonus engelmanni prefer fresh windthrown or cut trees, and Ips confusus, younger /

younger trees or tops of older ones (Anderson, 1960). Regional differences have been observed within a species, for instance, Lekander (1959) has reported that Polygraphus poligraphus mostly invaded standing suppressed trees in Sweden but logs in Central America. Dendroctonus valens Leconte can become primary in Central America, whereas it is a secondary pest in North America (Schwerdtfeger, 1959, 1960). That differences exist between various broods of Ips typographus in in Central Europe is indicated by Martinek (1955), who suggested that the differences may arise from variation in the type of breeding material present or to different population densities of the beetles. Such change in preference can be forced by an increased beetle population and complete lack of fresh windthrown trees, with the result that weakened standing trees are invaded.

Changes in destructiveness.

Drastic change in beetle behaviour after a secondary pest has become primary is one of the most interesting phenomena in bark beetle research, and also most important in the epidemiology of beetle outbreaks. Several investigators studied the conditions and progress of such changes in various /

various bark beetles but most intensively in _Ips typographus_ (Kangas, 1950, Lekander, 1959, Merker, 1956, Miller and Keen, 1960). With normal _Ips typographus_ population, invasion of healthy trees has been observed to be a rare occurrence. The small number of susceptible trees, prevents any increase of population because of the great density of invasion. As soon as there is more susceptible material the latent population goes into extensive phase and increases greatly. The increased beetle population thus fulfils the first condition for a mass outbreak, which may materialise when large areas of trees are weakened or when the increased beetle population invades and kills healthy trees as a result of lack of susceptible material. Zwölfer (1957) reporting on his studies on outbreaks of seven Scolytids, showed that the direct cause of the epidemics was the great number of susceptible trees and the presence of increased population at the beginning of the invasion.

Host selection and beetle concentration.

How bark beetles find their hosts and then select the most suitable one has often been considered, and determination of the factors that influence their selection has become an important problem. /

problem. Two general theories were formed- one is called the theory of host attraction and the other of mass attraction caused through the initial attack. Each seems to apply to different hosts and bark beetle species. Person (1931), working on Dendroctonus brevicomis attacking ponderosa pines tested the attractivity of the trees to adult beetles by inoculating the phloem with yeast. He observed that yeast-inoculated phloem was the most attractive material to the beetles. He conjectured that the odours resulting from fermentation in the inner bark of susceptible ponderosa pines may attract a few Dendroctonus brevicomis to begin an attack. After a few invasions have occurred, a stronger, secondary attraction, begun by the fermentation product of the introduced yeast followed. Callaham and Shifrine (1960) have pointed out that although yeasts introduced into the cambium by various bark beetles have been thought to be the source of subsequent attraction, the information is still fragmentary. On the basis of his studies of the relationship between the osmotic pressure of conifers and bark beetle attack, Chararas (1959) generalises that since most bark beetles are specific to certain tree families or species, the insect attraction to these botanical groups can be explained from /

from the point of view of chemical compounds peculiar to a tree group. He states that the attraction of bark beetles to susceptible conifers is governed by chemotactic responses of the beetles to such turpentine components as pinene and limonene.

Anderson (1948), studying the host selection behaviour of Ips pini on Pinus banksiana Lambert, advanced a theory which suggests that suitable breeding material by itself does not produce sufficient attraction to draw the beetles from a distance. He observed that the yeasts he cultured from Ips pini did not produce an attrahent for that bark beetle. Instead, host selection by the beetles depends more on the activity of the first attacking beetles (so-called pioneer beetles) than on the attractiveness of the host itself. After the first beetles have become established, more beetles are attracted until there is no space for additional invasion. Wood and Vité (1961) made the same observation on Ips confusus attacking ponderosa pine; it was experimentally shown that both sexes of flying Ips confusus were strongly attracted to males boring in fresh phloem, and excess beetles invaded adjacent trees. Callaham (in Miller and Keen, 1960) investigating Dendroctonus brevicomis, has suggested that the first attack on trees is made at random. On resistant /

resistant trees the attempted invasion fails because a great quantity of resin is exuded, whereas on susceptible trees the beetles succeed.

Neither of these theories had been corroborated until recently, when Vité and Wood (1961), studying the resistance of ponderosa pines to Dendroctonus brevicomis and Dendroctonus monticolae under outbreak and latent population conditions in California, were able to show that both species invaded the host tree at random without preference for resistant or weakened trees. Mass concentration and invasion occurred only after the initial attack by a few beetles had succeeded. In ponderosa pine, Vité and Wood (l.c.) observed that success of initial beetle invasion was frequent on trees of abnormal physiological condition under both outbreak and latent population levels.

Just as individual bark beetles become concentrated on a single tree, so an entire population may be distributed within certain areas of the forest. Bedard (1950), Massey and Wygant (1954), studying outbreaks of Douglas fir beetle and Engelmann spruce beetle respectively have observed such concentration in places with many windblown trees.

Host resistance to bark beetles.

The question why certain trees are more susceptible to bark beetle invasion than others of the same species has been asked often, and it is clear that the answer to this question is particularly important to the solution of problems in forest protection.

Although the dependence of bark beetle outbreaks on susceptible host material was recognised rather early, causal-analytical investigations into the nature of host susceptibility were undertaken mainly during the past decade - Krämer (1953), Merker (1956), Zwölfer (1957), Hall (1958), and Vité (1961). It was concluded that only such trees become susceptible to bark beetles whose natural resistance has been lowered by disturbances in the water balance. Because of the importance of the water balance in the condition of a tree, it is essential first to find measurable and dependable indicators. Mere quantitative determination of phloem moisture measured in percentage of dry weight, does not constitute a valid expression of the physiological condition of a tree or its water balance, although Inouye (1954) concluded from field observations that the moisture content of the phloem and sapwood may be somewhat related to the invasion /

invasion of windblown trees by Ips typographus, while Zwölfer (1957) states that the state of water is important, not its quantity.

Determination of host condition.

Several workers have used measurements of osmotic pressure as basis to determine tree susceptibility to bark beetle attack, notably Krämer (l.c.), Merker (l.c.), Zwölfer (l.c.) and Chararas (1959). Applying the kryoscopic method for determination of osmotic pressures in the sap pressed from phloem tissue, Merker and Zwölfer in particular succeeded in proving convincingly the dependence of outbreaks of subcortical-feeding insects, especially of Ips typographus on disturbances in the water relation of the host trees. Chararas (l.c.) tried as Krämer (l.c.) has done earlier, to establish critical values of osmotic pressure which are related to the ability of various bark beetles to invade the host tree. He considered Ips typographus a primary pest because of its ability to invade spruce exhibiting optimal osmotic pressure of about 9 atmospheres at 2 metres above ground, whereas such beetles as Hylurgops palliatus Gyllenhall and Hylurgops glabratus Zetterstedt are unable to establish themselves above the pressure of /

of 4 to 5 atmospheres. There is reasonable doubt that such data have a species-specific significance since the population levels during the invasion of these species and the availability of suitable material were not considered. Zwölfer (1957) has shown that the wide variation of osmotic pressure obtainable from a single tree, from different trees in a group, as well as from trees on different soils and throughout a season, does not allow the establishment of critical values for practical application in risk rating. Other indicators for determining the susceptibility of trees to bark beetle attack have been proposed, such as the measurements of Ph value of phloem sap (Schimitschek, 1931), the oleoresin production (Miller and Keen, 1960), and the oleoresin exudation pressure with Bourdon-type manometers inserted into the sapwood (Rudinsky, 1961; Vité, 1961).

The ability of resin-producing conifers to ward off beetle invasion by copious oleoresin flow has been observed repeatedly, but systematic investigations of this phenomenon were made recently. Vité and Wood (1961), investigating the resistance of ponderosa pines to Dendroctonus species concluded that host resistance depends on resin potential. A weakened tree with decreased resin flow can be overcome /

overcome by small number of beetles, but only rapid invasion can break the resistance of a healthy tree with great resin potential. Thus the threshold of beetle invasion is observed to be directly proportional to the oleoresin potential.

Population dynamics.

One of the most intriguing problems in bark beetle research is perhaps population dynamics. Since the last war there has been a clear tendency in forest entomological investigations to elucidate the inter-relationships of those forces within the forest biocoenose whose disturbances lead to mass increases of destructive insects in general and of bark beetles in particular. This tendency, according to Zwölfer (1957), will dominate forest entomological studies for a long time.

The population trend of subcortical-feeding insects seems to be less predictable than that of any other ecological groups of insects, and it has been emphasised lately that since bark beetles are influenced indirectly by all forces that affect the physiology of their food plant, from the view point of population dynamics both the beetles and their host trees must be intensively investigated (Kangas, 1950; Rudinsky, 1961).

Factors favouring population rise.

Abundance of suitable breeding material has been identified as one of the conditions favouring outbreaks of bark beetles. Zwölfer (1957), while studying gradations of seven bark beetle species in Bavaria (Ips typographus, Ips curvidens, Ips acuminatus, Pityogenes bidentatus, Pityogenes chalcographus, Polygraphus poligraphus, and Blastophagus minor) found that from ecological viewpoint, all outbreaks studied had two factors in common- abundance of breeding material and somewhat increased beetle population.

Abundance of susceptible material may occur in several ways. Extensive area of windblown trees has been the beginning of enormous outbreaks of various Dendroctonus species in mature and overmature stands in North America (Beal and Massey, 1945; Bedard, 1950; Massey and Wygant, 1954). Defoliation by caterpillars, if it does not kill the tree, reduces its resistance so that bark beetle can invade and outbreaks develop. Simpson (1929), investigating the seasonal history of Dendroctonus Simplex Lec. in Eastern Canada observed that the beetle attack was usually severe in larch stands weakened by the larch sawfly. Defoliation of a mixed stand of Balsam and Spruce by the Spruce budworm /

worm has been observed to be followed by invasion of bark beetles especially of the genus Dendroctonus (Prebble, 1944; Morris et al, 1958).

Prolonged drought has been observed to decrease the resistance of trees over large areas to the points of susceptibility to bark beetle attack. One of the first observations of this factor was made by Felt (1914) who noted that the hickory bark beetle Scolytus quadrispinosus Say. was favoured by drought- an observation which has been confirmed by other workers (Blackman, 1924; Craighead, 1925a; and St. George, 1929, 1930). Similarly, some outbreaks of Ips typographus in Europe have been caused by drought (Balachowsky, 1949; Schimitschek, 1948). Zwölfer (1957) has shown that humus rich soils have great water-holding capacity and that the post war outbreaks of bark beetles are more frequent in areas of poor soil conditions.

Various tree-infesting fungi reduce the resistance of trees to such a degree that they become susceptible to bark beetle attack. Spread of sap-staining fungi in association with bark beetle attack is a universal phenomenon. Several of the fungi concerned are pathogenic, killing the cambium of living trees as they invade the tissues. Wright (1938) found fungi of the genera Trichosporium and Spicaria /

Spicaria associated with Scolytus species attacking White fir in North America, and there was evidence that the fungi had probably been introduced by the beetles, their association being helpful in the establishment of the broods. Craighead and St. George (1940) described an outbreak of the Southern pine beetle in Virginia, in which the attacked trees died rapidly owing to penetration by blue stain accompanied by rapid desiccation which caused complete breakdown of the phloem region. Shepherd and Watson (1959) have also described a complex invasion by a number of fungi accompanying Dendroctonus attack. Their interruption with water conduction hastened the death of the trees.

High temperatures may affect the rate of development so much that bark beetles which do not go through obligatory diapause may develop several additional generations during the growing season. In such favourable temperatures the emergence of the beetles is sufficiently concentrated and the boring activities sufficiently increased to cause rapid invasion that breaks down even less susceptible trees. High temperatures are usually accompanied by drought and affect, at the same time the vigour of the host trees. Thus increased insect populations together with an abundance of weakened material /

material have been the cause of many bark beetle outbreaks (Beal and Massey, 1945; Schwerdtfeger, 1959, 1960).

Factors of population decline.

Apart from man's controlling activities, lack of susceptible material is usually the most decisive factor in the sudden collapse of bark beetle outbreaks (Keen, 1958; Vité, 1961). Utilisation of susceptible hosts by bark beetles may leave only resistant trees in an area and cause the population to decline. The survival of offspring in such resistant tree is always substantially smaller than in susceptible trees (Vité and Wood, 1961).

Competition, both interspecific and intraspecific has been found to contribute significantly to the decline of bark beetle populations. This is more evident among species with very similar food requirements. Intraspecific competition for food and space, especially in *Dendroctonus pseudotsugae* and *Dendroctonus monticolae* has been observed to reduce the population substantially (Rudinsky, 1961). At times very dense beetle invasion effected almost total mortality of the later instars. Such saturated invasions were observed particularly where the supply of suitable host material was not quite /

quite adequate to absorb the existing population, yet was too small to cause a primary invasion in healthy trees. The effect of overcrowding as a factor in the limitation of the rate of reproduction, and as the cause, directly or indirectly, of heavy mortality among the bark beetle broods is a subject of considerable importance.

Although biotic factors are not generally considered decisive in the collapse of a beetle outbreak (Zwölfer 1957), nevertheless, they are important and in a few instances effective in controlling bark beetle epidemic. Galoux (1947) has discussed in some detail the animal complex which as parasite or direct predator, groups itself round the bark beetles. The idea of manipulating thinnings, and other methods of encouraging and conserving natural enemies formed the basis of Hanson's work (1937, 1940) on the ecology and control of Myelophilus (Blastophagus) piniperda, the pine shoot beetle. He described a number of important parasites and predators of this species, and regarded the nitidulid beetles of the genus Rhizophagus as by far the most important, much more so, than the clerid, Thanasimus formicarius, which he considered a menace to the parasites also doing good work in destroying the bark beetle broods. He found /

found parasites and predators at their greatest concentration in young, unthinned polestage stands at which stage he considered the bark beetles were biologically controlled. Person (1940) studying the clerid, Thanasimus lecontei, a predator on the Western pine beetle, found that when the clerid larvae averaged 18 per square foot of bark, beetle mortality was three times as great as when clerids were absent. Rudinsky (1961) observed Coeloides brunneri Viereck, a braconid parasite on Douglas fir beetle causing nearly 100 per cent mortality in localised areas.

The effect of nematodes on the populations of various bark beetles has been the subject of several studies with varying results. Fuchs (1914) states that the effects of parasitic nematodes on bark beetle is to lower the general activity and in particular, its egg-laying capacity, parasitised beetles laying about half the number of eggs laid by healthy individuals. Oldham (1930) studied a nematode parasite of the elm bark beetles, Scolytus destructor Ol., and Scolytus multistriatus, Marsh., and observed that about 60 per cent of the beetles examined contained nematodes within the body cavity, the effects being to reduce the reproductive organs of the host. Similar observations were made by

Massey /

Massey (1956) on Dendroctonus engelmanni and by Reid (1958) on Dendroctonus monticolae, who found that the fecundity of female beetles infested by nematode species was substantially reduced. Hetrick (1940), discussing the natural enemies of the Southern pine beetle in Virginia, referred to the activities of nematodes, and concluded that they could not be reckoned upon as a major factor except in conjuction with other biotic agents.

The economic status of birds in relation to forest insects in general and bark beetles in particular has received considerable attention from time to time and conflicting evidence has been produced. Hanson (1937) observed little evidence of their usefulness in the destruction of pine shoot beetle broods. But Knight (1958), studying the effects of woodpeckers on populations of the Engelmann spruce beetle observed that the birds appeared to effect reduction up to 98 per cent, especially under the conditions of dense beetle infestation.

Among abiotic factors, extremely high temperatures during the summer and very low winter temperatures have sometimes resulted in substantial reduction of beetle population. Graham (1924) observed high mortality in broods of Ips pini when temperature /

temperature reached 44.5° C. Somewhat similar high temperatures were found to be fatal to broods of Dendroctonus monticolae (Patterson, 1930); Dendroctonus brevicomis (Miller, 1931) and Dendroctonus frontalis (Beal, 1933). Anderson (1960) has shown that the percentage of mortality effected by low temperatures depends on the duration, the time of occurrence, the cold hardiness of the insects, and the developmental stage entering hibernation.

C. Review of literature on *Ips cembrae*.

Introduction and systematics.

The fact that most of the past work on the larch bark beetle, *Ips cembrae*, was undertaken by European workers is not surprising. The beetle is native to Europe, and it has at one time or the other inflicted great damage on forests in this continent, most especially in Austria and Germany. This has prompted studies on the bark beetle.

The difficulty in distinguishing *Ips cembrae* from *Ips typographus* and *Ips amitinus*, the species with which it shares close morphological similarity, has aroused much confusion in the past, resulting in contradictory statements by different workers in regard to its systematic position.

Keller (1903) identified *Ips cembrae* on the basis of the structure of its antennal club and showed that it was the most reliable feature to distinguish it from *Ips typographus* and *Ips amitinus*. His further remark that the beetle was an exclusive pest of larch was criticised by other workers who had observed the insect on other coniferous trees as a secondary pest. Fuchs (1913) later description of *Ips cembrae* as *Ips montanus* caused further confusion because the beetle is not exactly an Alpine species. Further studies on the systematic /

systematic position of the beetle were made by Schimitschek (1926) who compared it with Ips amitinus, and reliable characteristics for its identification are now recognised (Schimitschek, 1931; Schwerdtfeger, 1950; Sorauer, 1954; Crooke and Bevan, 1957).

Prevalence and distribution.

The occurrence of Ips cembrae has been recorded in a number of countries although opinion differs as to the limit of its geographical distribution. Blandford (1894) was the first to report the occurrence of the beetle in the Fuji districts of Japan. He remarked that the specimens he found showed no essential difference from the European species. Ceislar (1904) stated that the beetle was found more frequently in the artificial stands of larch in Poland than in the natural forests. He attributed this to the warmer and drier climate of the former which is favourable to the beetle development. Komarek (1925), and Prell (1926) observed that the distribution of Ips cembrae in Czekoslovakia was widespread in districts having warm climate and low rainfall. Schimitschek (1931) referred to the occurrence of the bark beetle in Russia as local in view of the small area /

area of larch there, and indicated that its distribution in Austria and Germany did not only follow that of natural larch forests but the beetle also colonised plantations of European larch outside the normal range of that tree species.

Crooke and Bevan (1957) gave the report of its first occurrence in Britain when it was found in Monaughty Forest, Morayshire in 1955. Following the discovery a survey showed that the bark beetle was fairly well distributed in 29 localities in north-east of Scotland with its centre in Morayshire but also extending to Nairnshire, Banffshire, Invernessshire and Ross-shire. Subsequent surveys undertaken by Crooke and Kirkland (1960); Crooke, Bevan and Davies (1961) revealed that it had extended its distribution to the east coast as far north as there are any appreciable larch stands, and has also extended its range some ten miles from the previous most southerly recorded locality near Ballindaloch. Crooke and Bevan (1957) assumed that its source of introduction might be the large quantity of German timber shipped into this country in 1946-1948, especially to ports in north-east Scotland, from where the logs were distributed to sawmills throughout the region.

Two /

Two closely related species, *Ips typographus* and *Ips amitinus* were reported to have entered the country in large numbers on German Spruce and pine in the immediate post-war years (Laidlaw, 1947; Forestry Commission Leaflet No. 26, 1948). But neither of them appears to have become a breeding species here, although Duffy (1953) includes *Ips typographus* in his British key. Since its introduction, *Ips cembrae* must have persisted in small numbers in larch stands or could have existed solely in logs in the sawmill until the damage to woodlands caused by the gale of 1953 (Crooke 1955), provided favourable conditions for its increase in population.

Host tree.

Much confusion has existed in the past about the host tree of *Ips cembrae*, partly because of the close morphological similarity that it shares with *Ips typographus* and *Ips amitinus*, and partly because of some overlap in their ranges of host tree preference. The bark beetle has been recorded breeding on a number of conifers. Blandford (1894) has observed *Ips cembrae* breeding occasionally on Japanese larch. Keller (1903) reported it as a pest of European larch in Germany and Nechleba /

Nechleba (1923) has also indicated from his studies on the beetle in Czeckoslovakia that its preferred host tree was the European larch, and was only found breeding on pine during overpopulation and lack of suitable larch. Escherich (1923), and Komarek (1925) have recorded the beetle breeding occasionally on Picea species, while Prell (1926) has observed it breeding on Douglas fir and Hybrid larch. Since the report of its occurrence in Britain (Crooke and Bevan, 1957), its main host tree has been European larch, although it is occasionally found breeding on Japanese larch and Scots pine. The fairly recent continental workers on this bark beetle (Schimitschek, 1931; Schwerdtfeger, 1950; and Sorauer, 1954) are agreed that its normal host in Europe is the European larch, *Larix decidua Mill*.

Economic importance of *Ips cembrae*.

The bark beetle is regarded as a primary pest of European larch on the continent of Europe, especially in those countries where large areas of larch plantations exist and are not well managed.

Prell,(1926) studying the feeding habits of the bark beetle in North Czekoslovakia observed that the newly emerged beetles bored into the shoots /

shoots of both young and old larch and at points below the boring, the shoots broke off and fell to the ground. The shoot boring activities were more severe in young stands than in the old ones, and Prell (l.c.) indicated that the damage caused by the beetle to larch in the region followed a severe nun moth attack which had weakened the stand. As the beetle population increased and suitable larch material for breeding purposes decreased, Japanese larch, Douglas fir, and Norway Spruce in the surrounding areas were also attacked due to the breeding congestion in the larch stands.

Schimitschek (1931) has indicated the economic importance of Ips cembrae in larch forests in Austria, following his comprehensive studies on the biology and ecology of the beetle. He referred to the insect as secondary pest of larch in areas where the tree species occurred naturally, but observed that the bark beetle epidemics usually occurred in artificial stands of larch with poor rainfall and favourable climatic conditions for the beetle increase. Schimitschek (l.c.) has observed that the secondary attack of the beetle in Austria consists of larval feeding and regeneration feeding of the old beetles inside the tunnel, as well as the maturation feeding of the young beetles /

beetles as an extension of the mother tunnel. The trees usually attacked are windblows, fire-killed or freshly cut trees or trees temporarily or permanently weakened by drought, defoliators and fungi. Schimitschek (l.c.) stated that when the regeneration feeding of the old beetles took place outside the tunnel, the bark beetle attacks were usually severe, and great damage was done to both young and old larch stands. He referred to an instance in the Schlagl districts, in Austria where Ips cembrae attacked a 15 year old larch stand, causing the death of many trees as a result of the regeneration feeding of the beetle. The attack was characterised by shoot boring activities of the beetle especially towards the top of the trees, and branches of about 4 inches diameter were also invaded. The maturation feeding of young beetles outside their brood galleries had been observed to cause considerable damage to larch stands in the Slavietitz districts in Austria. Shoot boring activities of the beetles were also responsible for the damage, and branches of young healthy larch were hollowed to a length of 2 inches, following overpopulation of the bark beetle.

Schindler (1948) stated that the death of

European /

European larch in the experimental forest of Bramwald in Germany was caused by Ips cembrae, usually regarded as a secondary pest of this species in the area. The infestation was confined to almost flat or sloping southerly sites where larch was growing in mixture with spruce and pine. Schindler (l.c.) indicated that the previous attack of larch canker on the stand, together with the drought of 1947 in the area contributed to the susceptibility of the larch trees to the beetle infestation. Schremmer (1955) described the characteristic shoot tunnelling of Ips cembrae in larch forests of the Wienerwald districts in Germany. Maturing beetles were observed hollowing out shoots, causing them to break off. For one site it was estimated that in one month every larch tree had lost 200 twigs, 50-70 centimetres (20-28 inches) long, and the damage was most particularly severe in 6-8 year old larch stands.

Since the report of its occurrence in Britain (Crooke and Bevan, 1957) felled logs, windblown stems and standing trees have been observed as media providing sites for breeding. Shoot tunnelling activities of the beetle have also been observed as an obvious feature of attack, somewhat similar to the activities of Blastophagus on pine. This /

This was particularly noticeable during the survey of the area of infestation in 1955 (Crooke and Bevan, 1957). Twig boring had been observed on European larch, Japanese larch, and Hybrid larch, but European larch was the worst affected, since wind damage is a most frequent occurrence amongst stands of this species. The shoot tunnelling of the beetle can produce serious crown damage in standing trees. In one locality, Crooke and Bevan (l.c.) observed that Ips cembrae succeeded in breeding and killing standing trees, which were the remnants of a windblown middle-aged European larch stand. The results of the survey indicate that the bark beetle can become a primary pest of larch in Britain, particularly in drought years and on poor dry sites.

D. Discussion.

The primary role played by Scolytid bark beetles as pests of coniferous forests is a recurrent feature of forest insect literature. It is well known that the factors favouring multiplication of these insects to epidemic proportions originate from such primary causes as susceptibility of the stand due to overmaturity, disturbance of the environmental balance by adverse weather conditions such as drought, catastrophic destruction by storms, heavy damage by defoliators, and damage caused by the stress and neglect of war (Chrystal, 1949).

In epidemiological studies of bark beetles, susceptibility of host material has been known to be one of the principal conditions favouring outbreak (Keen, 1958). Many bark beetles prefer trees of older age, while some favour young trees. In general, trees of slow growth and poor vigour are more susceptible to beetle attack than the more vigorous ones. As the epidemics increase in intensity, large areas of the forest rather than the individual tree become the unit of susceptibility.

While the origins and details of bark beetle attacks in any part of the world may differ, the general aspects of the situation examined on broad lines /

lines show great similarities. One can also see that the modern views on the question of prevention and control of such attacks have many points in common in many parts of the world, running as they do increasingly along management techniques. General recommendations for preventing bark beetle outbreak through forest management techniques should be based on the concepts of maintaining stand vigour, controlling the abundance of component species and distribution of age classes, preventing the accumulation of overmature and senile stands, avoiding the planting of species unsuited to soil and climate, and adhering to stand mixtures found in the healthy forests characteristic of the site and the region. Such management practices will not only improve growth and yield, but will also tend to reduce the danger of bark beetle outbreaks.

PART 2

Biological studies.

Chapter 2.

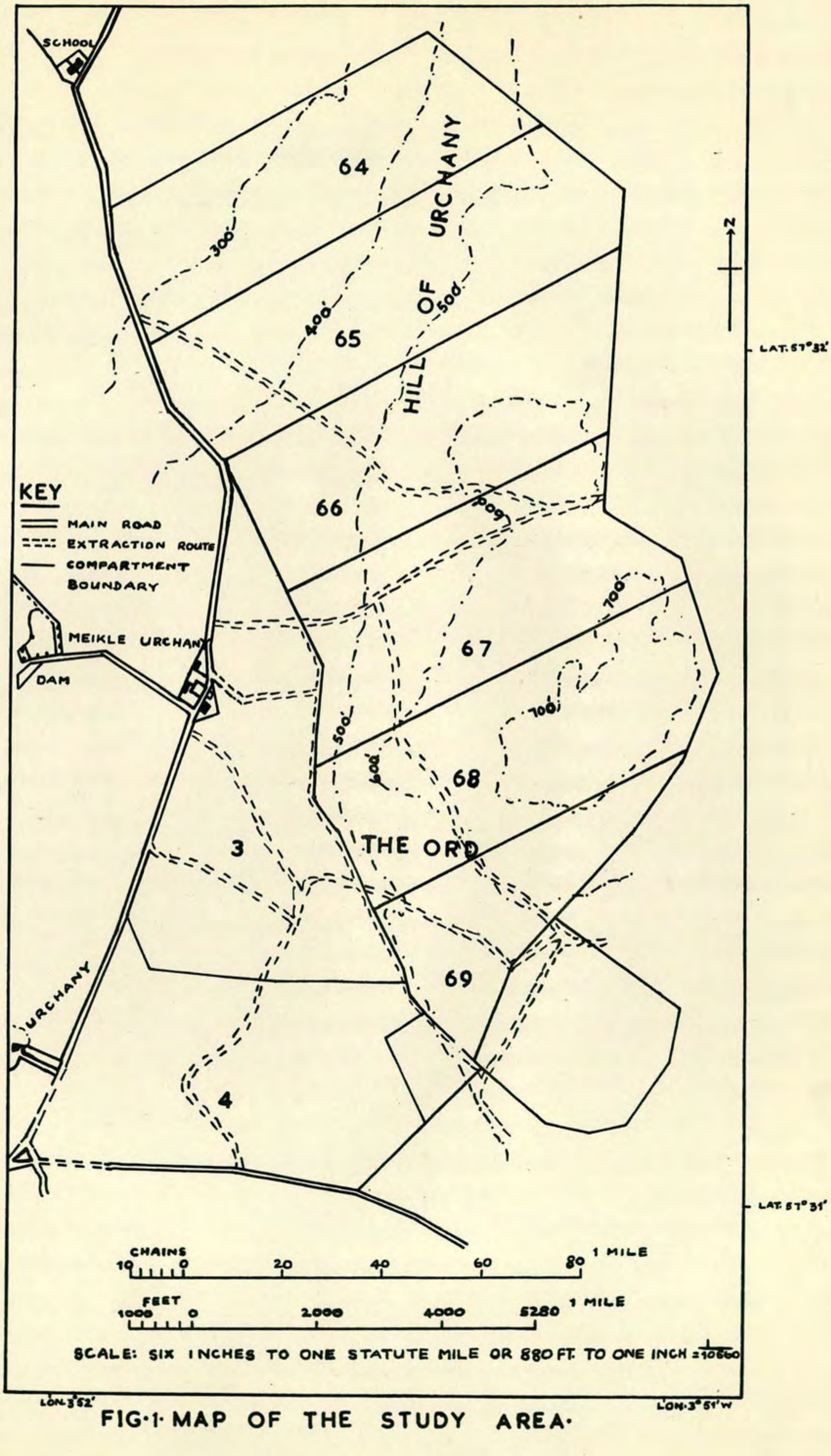
Description of the study area.

Location.

The studies were carried out at the Ord Wood, Cawdor Estate, in the County of Nairn, north-east of Scotland. The area is situated within 57° 32' latitude and 3° 52' longitude and it is about 5 miles south-west of Nairn, the nearest town. Map of the study area is presented in Fig. 1

The Ord Wood.

The wood has not been properly managed in the past, and this has contributed to its present poor state. The whole wood is 585 acres in area, but the working site (compartments 64 to 68) is 359 acres in extent. Compartments 64 and 65 are predominantly European larch stands of about 70 to 80 years old, with some Scots pine, Norway spruce and Douglas fir. Compartments 66 to 68 consist mainly of a mixture of European larch and Scots pine ranging from 90 to 100 years of age, the European larch being the dominant species. The stands have suffered great damage in the last few years as a result of successive windblows. Most of the windblown /



FIG·1· MAP OF THE STUDY AREA·

windblown trees are larch with heart rot, and they provide suitable breeding material for <u>Ips cembrae</u>.

Altitude and topography.

The working area lies within an elevation of 300 feet in the north-east to 700 feet in the south-east. Aspect is north to north-east, the slope being moderately steep with a number of undulating ridges and hollows following the south-west to north-east ice flow direction of the last glaciation.

Geology.

Ord Wood lies on basal breccia and conglomerate of the Middle Old Red Sandstone series, and the whole area exhibits evidence of glaciation, which is well marked on the topography and soil of the area.

Climate.

The climate of the working area is not extensively investigated, and meteorological data from which to draw more than the most general conclusions are not available; but Anderson and Fairbairn (1955) placed the area in their Climatic Sub-Region Bla, which is characterised from the forester's /

forester's points of view as the second warmest and the second driest area in Scotland. The rainfall during growing season of 170 to 213 days is between 25 inches to 30 inches, with an average of over 50 days of frost annually.

Soil and ground vegetation.

The soils in the working area vary from well drained degraded brown earths to peats which are moderately podsolised, and the ground vegetation is mainly a mixture of fine and soft grasses, with feather mosses in places where light passes the canopy in sufficient quantity. Patches of Calluna and Vaccinium myrtillus L. occur under the Scots pine in mixture with the European larch.

Chapter 3.

Rearing methods.

Introduction.

It is known that long-term studies of the biology of bark and cambium-feeding insects under natural conditions are difficult to conduct without sacrificing essential data on the number of moults or on developmental periods of various stadia. Methods used for the rearing of bark and wood-boring insects are varied. The simplest methods consist of the collection of infested woody material, the caging of such and the capture of adults on emergence. Of necessity the observation of growth, metamorphosis and behaviour of the larvae and pupae cannot be accomplished without a disruption of the habitat.

Bedard (1933), Kaston and Riggs (1937), Warren (1958), Hopping (1961) and others recognised this difficulty, and they devised rearing techniques for the species of bark and cambium-feeding insects they studied. Bedard's (l.c.) novel and practical rearing method for Dendroctonus pseudotsugae consisted of a cut section of bark containing a colony of the bark beetles, placed between two plates of glass, which were held together by elastic bands. Moistened absorbent cotton was packed around the bark /

bark to keep it from drying quickly. Kaston and Riggs (l.c.) used essentially the same method for rearing larvae of the Elm bark beetle, Hylurgopinus rufipes Eich, but substituted a wooden press for the elastic bands. They considered that Bedard's method was inadequate because elastic bands were not strong enough to hold the glass plates tightly against the bark. However, they experienced difficulty with their own technique which caused excessive breakage of glass within the press.

Warren (1958), working on Hylobius warreni Wood used three types of rearing media. One was simply moistened absorbent cotton used for rearing eggs. The other two media which he described as "Bark Homogenate" and "Whole Bark" were used in rearing pupae and larvae respectively. "Bark homogenate" was prepared from bark stripped from the roots of living host trees, minced with a household blender and granulated agar and heated to 80° C. before cooling it to room temperature to form a homogeneous mash. He observed that the homogenate was not a satisfactory rearing medium for the larvae, because of their high mortality as a result of profuse development of moulds on the medium. The preparation of "Whole Bark" was similar /

similar to that described by Bedard (l.c.) and Kaston and Riggs (l.c.) for rearing bark beetles.

A simplification of the glass-bark sandwich method of Bedard was devised by Paim and Beckel (1960) for rearing Cerambycid larvae. Instead of placing a piece of infested white pine bark between two plates of glass, the larvae were implanted in the bark and the inner surface of it was coated with solution "Vinylite" resin in acetone, which could bend with the bark but would not deeply impregnate it or prove toxic to the broods. The larvae mined the inner bark layers next to the plastic film only, and were never becoming obscured from view. The device was suspended in a large battery-jar above aqueous solution of sodium propionate in order to prevent a profuse development of moulds on the frass expelled from the chambers. Hopping (1961) used a method similar to Bedard's for rearing Ips species but he substituted two sheets of lucite plastic for glass plates, and he sealed up the edges of the plastic with adhesive tape. Thomas (1961) used essentially the same method as Hopping (l.c.) to rear Ips pini.

Materials and techniques used for rearing Ips cembrae in the laboratory.

It was realised very early on that observations under natural conditions in the plantation on an internally feeding insect such as Ips cembrae, would not give all the precise information on its life history, therefore breeding techniques were devised in the laboratory, in order to supplement field observations with laboratory investigations.

The first method employed was satisfactory for the rearing of reasonably large number of broods for continuing generations. Sections 14 inches long were sawn from freshly cut larch logs 4 to 8 inches in diameter. The ends of each section were dipped in melted paraffin to prevent rapid loss of moisture. At convenient points between the ends of each log section, "starter" holes were drilled through the bark. These were not essential but they usually speed up the entry of the beetles into the bark. The beetles were placed in the "starter" holes which were then sealed with adehsive tape. The log sections were then placed in rearing cages (Fig. 2), after the beetles had disappeared beneath the bark. This prevented the beetles from escaping when they bored out through the bark, although this rarely happened. Each rearing /

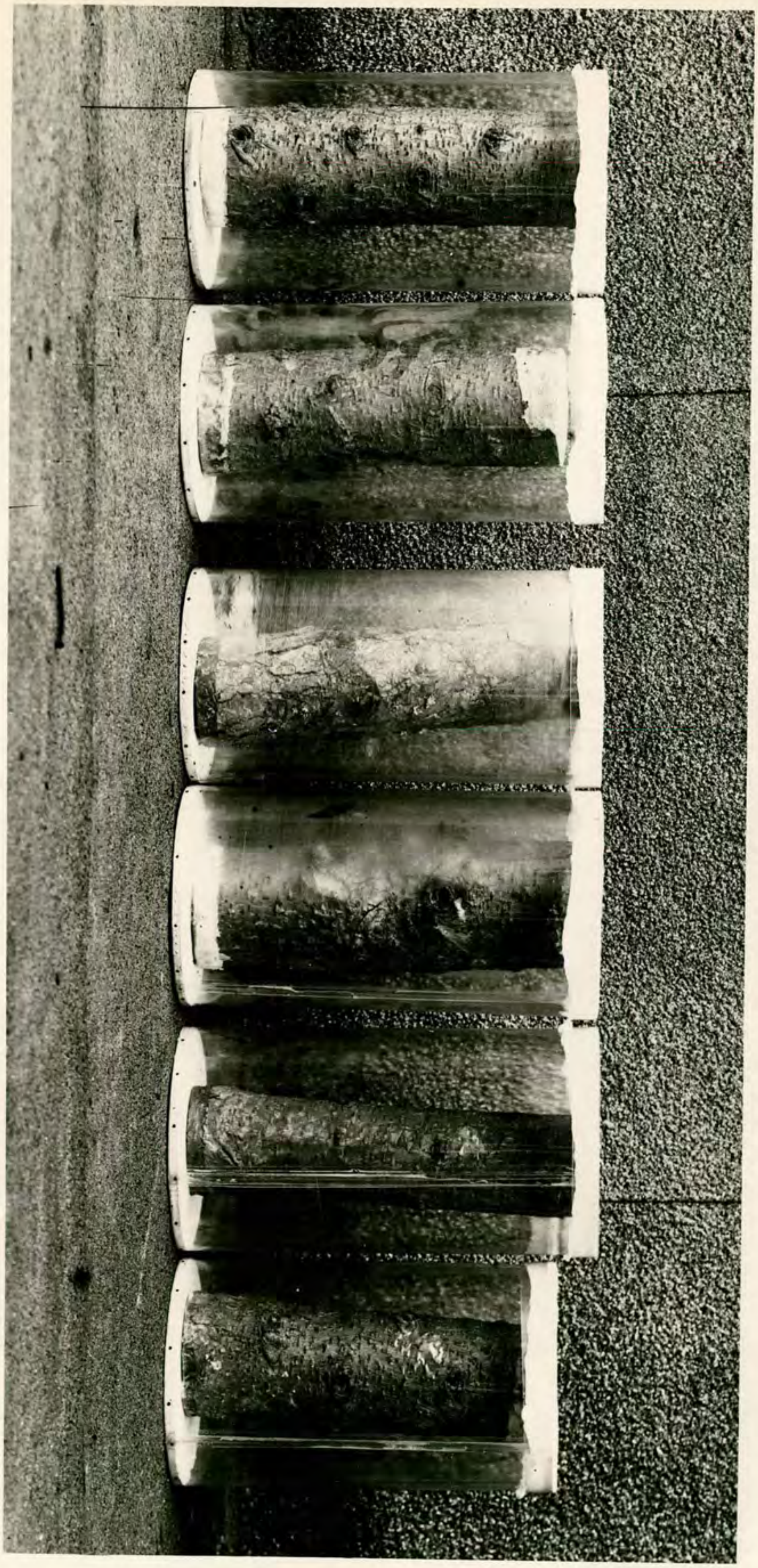


Fig. 2. Vinyl rearing cages for Ips cembrae.

rearing cage consists of a circular base 9 inches in diameter cut from ¾ inch plywood, on to which a sheet of vinyl is stapled to form a cylinder 16 inches high, the lid of the cage being made by sewing a double thickness of butter cloth, held in position by a circular strip of vinyl sheeting. Fig. 3 illustrates one rearing cage. The beetles activities were followed by removing small sections of bark every few days, and fresh materials were placed in the cages as necessary.

The second rearing technique was devised with a view to making direct daily observations on the bark beetle. The device is as illustrated in Fig. 4. For the best results, a piece of bark which contained a large number of eggs and adult beetles in a gallery at least several inches removed from other galleries was selected. The bark was selected from a rectangular area of about 5 inches by 7 inches, after which its external surface was smoothed off as much as possible. This is essential in order to provide bark of fairly uniform thickness throughout. The bark was then removed from the infested tree or log and immediately placed between two plates of perspex, 8 inches by 9½ inches. It required considerable pressure to keep the plates close to the bark and thus prevent warping /

Fig. 3. One vinyl rearing cage for *Ips cembrae*.

Fig. 4. Device for rearing Ips cembrae so as to keep it under daily observation.

warping with the subsequent falling of the active larvae out of the tunnels. The success of this rearing method depended in large measure upon keeping the inner surface of the bark in intimate contact with the perspex. Therefore, four strips of wood, each about $8\frac{1}{2}$ inches long by $1\frac{1}{2}$ inches wide by $\frac{1}{4}$ inch thick were used as two pairs of clamps. Screws were placed about one inch from each end. In this way, on tightening the knots of the screws, pressure was applied directly over the bark. It was observed that the larvae were developing normally when the bark was kept damp, so cotton was packed around the bark and moistened daily. This maintained a humid atmosphere around the bark. The cotton was renewed regularly to prevent development of moulds on the bark. Rearing was effected at uncontrolled room temperature, and only at the initial setting up of the device were the beetles handled. When no observations were carried out, the apparatus was wrapped in black cloth to exclude light, thus making conditions more natural for the insects.

This rearing technique provides excellent opportunity to observe the activities of the beetles, during gallery construction, mating, egg laying, and the development of the brood. It has also /

also been possible to determine the number of larval instars and to estimate the approximate duration of each stadium by direct observation.

Chapter 4.

Life history and habits of Ips cembrae.

Systematic position.

The genus Ips is one of four closely related genera in the tribe Ipini, sub-tribe Ipina (Balachowsky, 1949; Hopping 1963).

Description of stages.

Egg.

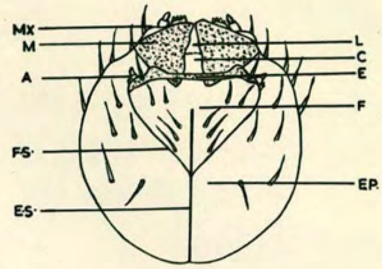
The egg (Fig. 5) of Ips cembrae is ellipsoidal in shape, averaging 1.23mm. in length and 0.70 mm. in greatest width. It is white, translucent, shiny and soft, but as incubation progresses the colour gradually changes to creamy-white, with brown tinges marking the mandibles of the embryo. Dimensions of the egg and other stages of the beetle are given in Table 1.

Table 1.

Dimensions of the different stages of Ips cembrae.

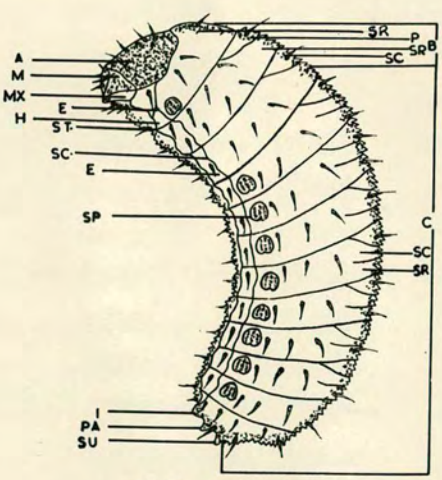
Stage	Number measured	Mean (mm.)		Range (mm.)
Egg.	100	Length :	1.23	1.10 - 1.40
		Width :	0.70	0.65 - 0.74
Larva.				
1st instar	40	Length :	2.50	1.70 - 2.80
		Width :	1.10	1.00 - 1.20
2nd instar	40	Length :	3.70	3.10 - 4.00
		Width :	1.55	1.50 - 1.75
3rd instar	40	Length :	5.00	4.20 - 6.20
		Width :	1.70	1.80 - 2.00
Pupa.	100	Length :	4.80	4.20 - 6.00
		Width :	2.17	1.80 - 2.90
Adult.	100	Length :	4.95	4.20 - 5.50
		Width :	2.00	1.80 - 2.10

FIG·5· EGG· (X10)

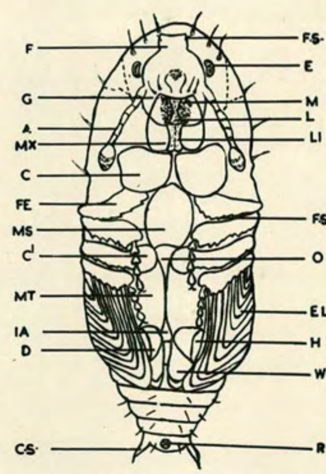


FIG·7· HEAD OF LARVA FROM ABOVE· (X20)

A, ANTENNA; C, CLYPEUS; E, EPISTOME; EP, EPICRANIUM; E·S·, EPICRANIAL SUTURE; F, FRONS, F·S·, FRONTAL SUTURE; L, LABRUM; M, MANDIBLE; MX, MAXILLA.



FIG· 6· LARVA· (X12)
A, HEAD; B, THORAX; C, ABDOMEN; E, EPIPLEURAL FOLD; H, HYPOPLEURAL FOLD; I, INFRA-ANAL LOBE; M, MANDIBLE; MX, MAXILLA; P, PRESCUTAL FOLD; PA, PARA-ANAL LOBE; SC, SCUTAL FOLD; SP, SPIRACLE; SR, SCUTELLAR FOLD; ST. STERNELLAR FOLD; SU, SUPRA-ANAL LOBE.



FIG· 8· PUPA· (X12)
A, ANTENNA; C, COXA OF FRONT LEG, C'. COXA OF MIDDLE LEG; C·S·, CAUDAL SPINE; D, COXA OF HIND LEG; E, EYE; EL, ELYTRA; F, FRONS; FE, FEMUR; F.S, FRONTAL SPINES, F.SP., FEMORAL SPINES; G, GENA; H, FEMUR OF HIND LEG; I.A, INTERCOXAL AREA; L, LABRUM; LI, LABIUM; M, MANDIBLE; MS, MESOSTERNUM; MT, METASTERNUM; MX, MAXILLA; O, MEDIAL GROOVE; R. TENTH ABDOMINAL SEGMENT; W, FLYING WING.

Larva.

The larva fig. 6 is a soft cylindrical grub, apodous, with curved body and an average length of 5.00 mm. (Table 1.) when fully grown. The colour is creamy-white, except the hard chitinous head and mouth parts, which are yellowish-brown and dark-brown respectively. The body is deeply wrinkled, with numerous hairs over it. The larva is made up of the chitinous head-piece and thirteen segments, the first three segments forming the thorax (B, Fig. 6), and the remaining ten the abdomen (C, Fig. 6). The thoracic segments are slightly larger than the abdominal ones. The 8th and 9th abdominal segments are smaller than the first seven, while the 10th is made up of three lobes around the anus. The first thoracic segment and the first eight abdominal segments bear each a pair of spiracles (SP).

The head of the larva (Fig. 7), viewed from above with the aid of a microscope, shows the following:- In the centre of the chitinous head-piece is seen a triangular region called the frons (F); at the anterior corners of the frons lie the antennae (A), each single jointed and sunk in a pit; along the anterior base of the frons is a narrow area, the epistome (E), composed of a thick band /

band of chitin extending from one antennal pit to the other and supporting anteriorly the clypeus (C); anterior and jointed on to the clypeus is the labrum (L). On either side of the frons lies posteriorly the epicranium (EP), divided into two by the distinct frontal suture (F.S.) anteriorly, and by the epicranial suture posteriorly (E.S.). Examined from above, the maxillae (MX) can be seen in part projecting beyond the mandibles (M), which are dark brown and highly chitinised.

Pupa.

The pupa of Ips cembrae has general features of the adult beetle. Its mean length is 4.80 mm. with a mean width of 2.17 mm. (Table 1). Its colour is at first uniformly white but later becomes pale-brown. The darkening of colour first reveals itself in the eyes, which show as two black spots, and in the mandibles, which show as two dark-brown patches.

In a ventral view of the pupa (Fig. 8), the chief divisions of the body and their appendages are visible. On each side of the head region there is present the antenna (A), at the anterior base of which is situated the eye (E).

The three pairs of legs are folded along the surface /

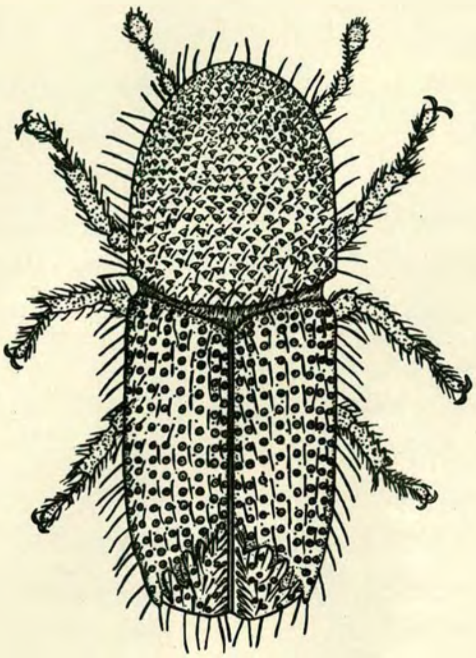
surface of the body, the hind pair is more or less overlapped by the elytra (EL.) and wings (W.).

Of the thorax, the mesosternum (MS.) and metasternum (MT) are visible; a deep groove (O) runs up the centre of metasternum.

The sternal parts of the last seven segments of the abdomen are visible, the 9th segment bears two prominent fleshy spines (C.S.), the presence of which is characteristic of Scolytid pupae; the 10th segment (R) appears only as an oval patch intersected by grooves.

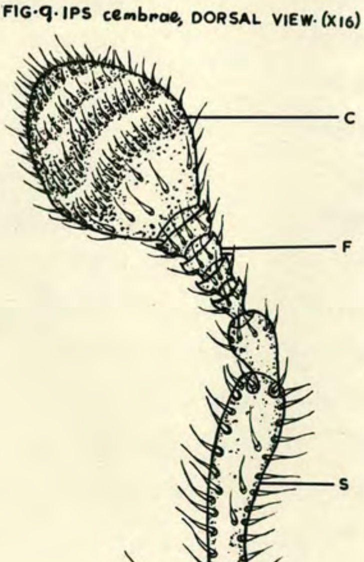
Adult.

The adult beetle (Fig. 9) has a mean length of 4.95 mm.; and 2 mm. for mean width of prothorax (Table 1.). Young specimens are light brown in colour, but old adults are dark brown to blackish. The head is concealed from above by the domed prothorax, the front half and sides of the pronotum are roughened by minute teeth and wrinkles. The beetle is conical towards the back. The apices of the elytra are excavated and the sides of this excavation are armed with teeth. Ips cembrae has four teeth on each side of the declivity, the third tooth from the top being the largest (Fig. 10). The surface of the declivity is shinning, densely and /



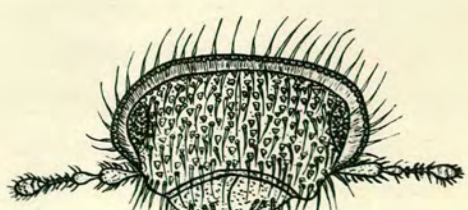
FIG·9· IPS *cembrae*, DORSAL VIEW· (X16)

FIG·10·ELYTRON SHOWING TEETH· (X24)



FIG·11· ANTENNA· (X80)

C, CLUB; F, FUNICULUS; S, SCAPE·



FIG·12· FRONT OF HEAD· (X20)

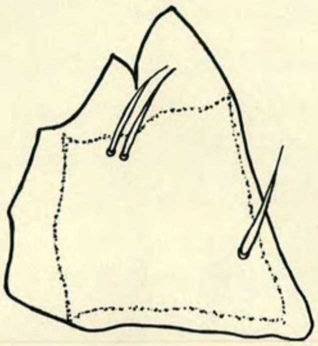
and coarsely punctate. Small piliferous granules ornamented with long yellow setae, regularly or irregularly spaced are present along suture of declivity and extending to its top. The elytra have rows of punctured striae which are deep and more or less angular. The whole beetle is shining and distinctly hairy.

Ips cembrae has a geniculate antenna (Fig. 11) The scape (S) is longer than the funiculus (F.) which is 5-jointed. The antennal club (C) is solid and oval in shape, and its sutures are undulating. The form of the sutures of antennal club of the beetle, is an important diagnostic feature for distinguishing it from closely related species, especially Ips typographus and Ips amitinus, which have antennal clubs with straight sutures.

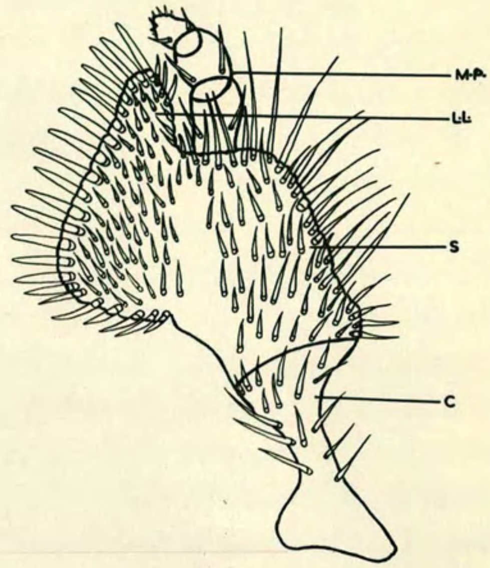
The head (Fig. 12) is clothed with thick yellow hairs, which are also present along the edge of the neck-shield. Both sexes are without tubercle on frons, which is entirely and coarsely granular.

Mouth parts.

The mandibles are strong, subtriangular, and with broad base. They are dark brown in colour, and highly chitinised. Each mandible (Fig. 13) is provided /

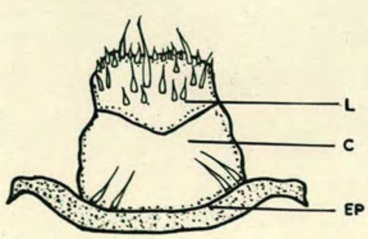


FIG·13· MANDIBLE· (X80)



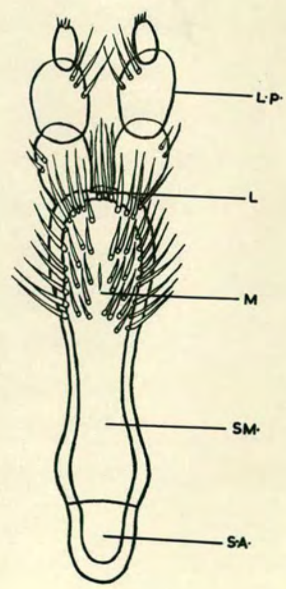
FIG·14· MAXILLA· (X100)

C, CARDO; L·L·, LACINIAL LOBE; MP, MAXILLARY PALP; S, STIPES.



FIG·15· REGION OF EPISTOME· (X100)

C, CLYPEUS; EP, EPISTOME; L, LABRUM.



FIG·16· LABIUM· (X100)

L, LIGULAE; L·P· LABIAL PALP;

M, MENTUM; S·A·, SUBMENTAL AREA; SM·, SUBMENTUM.

provided with an apical and a subapical tooth, and with two other smaller teeth along the slightly curved inner margin. There are three setae on the external face. From the dorsal view, the main divisions of maxillae are visible. Each maxilla (Fig. 14) is composed of three main parts : posteriorly is the cardo (C) with few bristles, anterior to this is the Stipe (S), which bears the three-jointed maxillary palp (M.P.) as well as short and long bristles; thirdly is the lacinial lobe (L.L.) which bears short bristles on its surface and stout ones along the edge. Labium (L, Fig. 15) is transverse, length about half of width of clypeus (C) to which it is joined; it bears short and comparatively long setae. Labium (Fig. 16) comprises the mentum (M) with numerous bristles over it, and anteriorly bearing two labial palps (L.P.), each of which is three-jointed.

Development and habits.

Hibernation.

Studies on the life history of _Ips cembrae_ at the Ord Wood, Cawdor Estate showed that this beetle hibernates under the bark of larch as larvae, pupae and adults. Observations of some adult beetles in the forest litter during the winter suggest that they also use this habitat as overwintering quarters. Some of the adults which hibernate under the bark were found in short tunnels cut away from their characteristic egg tunnels. Most of the beetles in these short tunnels were young adults, lighter brown in colour than the old ones which are almost black after completion of their egg laying activities. Specimens of the young adults which were collected from their winter tunnels later constructed egg galleries in logs in the laboratory, and gave rise to a generation of beetles in summer.

Emergence and dispersal flight.

The phenomenon of emergence and flight by _Ips cembrae_ was first noticed in the field on 25th of May. Such emergence occurred when the threshold temperature necessary for flight existed previously in the hibernating quarters. The mean subcortical temperature /

temperature of the logs from which the beetles were observed emerging was 22° C., while the air temperature was 18° C. Observations in the Ord Wood show that Ips cembrae has two main flight periods in a year. The spring flight commencing generally from late May till late June, and the summer flight beginning from late August till mid-September. Flight period of the beetles has been observed to vary in different parts of the stands. It was longer at the exposed edges of the stands than in a sheltered environment, and flights were more frequent on a bright sunny day than on a dull day. The goal of the beetle flight was to locate host trees of preferred quality for feeding, breeding or hibernation.

Gallery construction and pattern.

The method of gallery establishment follows fairly closely that described by Reid (1955) for Ips perroti Sw., and by Thomas (1961) for Ips pini. Both in the field and laboratory, males of Ips cembrae were observed boring into logs through the bark, and then proceeded to construct the nuptial chambers (Fig. 17) varying from triangular to oval in shape. When these have been completed, the male was joined by several females, each of which constructed /

Fig. 17. Gallery system of Ips cembrae showing nuptial chamber, egg gallery, and egg niches.

constructed individual egg tunnel. The number of egg galleries radiating from each nuptial chamber varied from two to five, the most frequent being three. The stellate gallery pattern (Figs. 18, 19) gave rise to larval tunnels, terminating in the pupal chambers. The average daily rate of gallery construction calculated from the date of initial attack was 8 mm.

Mating and oviposition.

Direct observation of the beetles in the rearing apparatus (Fig. 4) already described, showed that mating usually took place at the junction of the egg gallery and nuptial chamber, the male assuming a direction opposite to that of the female. Both beetles then turned on their sides so that the ventral surfaces of the posterior segments were in contact. Copulation lasted 30 to 40 seconds and was repeated at intervals during the egg-laying period. Repeated copulation appeared not to be essential for, in some cases, the females continued to lay fertile eggs after being isolated from the male by packed boring dust.

As the females elongated their egg galleries, they excavated minute egg niches, laid an egg in each niche, and then covered it with boring dust. The /

Fig. 18. Gallery system of <u>Ips cembrae</u> with larvae and pupae in the larval mines and pupal chambers respectively.

Fig. 19. Gallery system of Ips cembrae with adult beetles.

The eggs were at intervals of about 5.5 mm., usually along both sides of the main galleries (Fig. 17). The number of egg niches plotted over gallery length fitted a linear relationship (Fig. 20). The equation for the regression of number of egg niches on gallery length is shown in Fig. 20. The calculated mean number of egg niches per centimetre of gallery for the brood was 2.78. The average number of eggs laid in 50 completed galleries examined was 28.6 with a minimum of 20 and a maximum of 55.

Data obtained from measurements of different parts of the gallery system of Ips cembrae are given in Table 2 below.

Table 2.

Measurements of different parts of Ips cembrae gallery system (cm.).

Feature	Mean	Range
Length of egg gallery	14.23	6.25 - 33.50
Length of larval mine	4.64	2.25 - 6.25
Distance between two egg niches	0.55	0.25 - 1.15

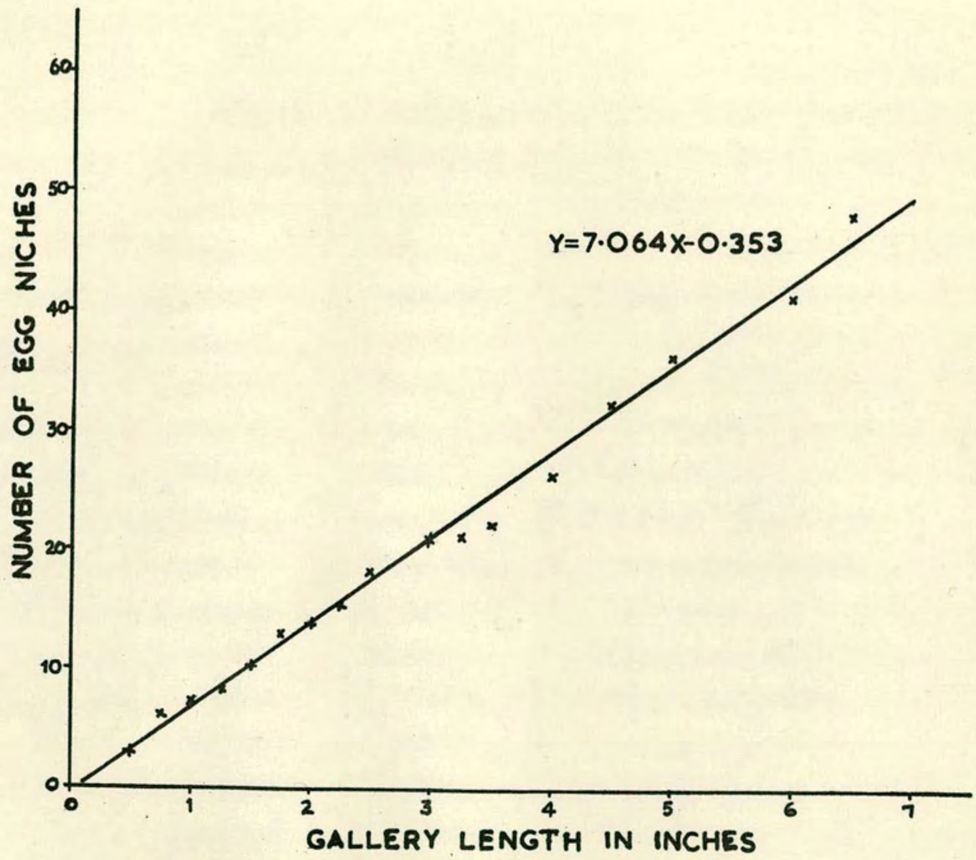


FIG. 20. REGRESSION OF NUMBER OF EGG NICHES OVER GALLERY LENGTH OF IPS *cembrae* IN LARCH AT THE ORD, CAWDOR ESTATE. EACH CROSS INDICATES THE AVERAGE NUMBER OF EGG NICHES (Y) AND AVERAGE GALLERY LENGTH (X).

Developmental stages.

Egg.

Observations in the laboratory showed the average incubation period to be 12 days. The minimum number of days recorded for the eggs to hatch was 10, with an average temperature of 18° C., while the maximum was 14 days with a mean temperature of 14.5° C.

Changes during incubation were observed on eggs. Within a few days, the milky-white colour changed to creamy-white, soon to be followed by a faint but noticeable darkening towards one end, marking the position of the developing mandibles. Prior to hatching, the outline of the pale-brown head capsule was seen. The shape of the egg became slightly altered. Late in the incubation period the larval body was flexed ventrally, and alterations in the position of the grub in the egg could be effected by a backward movement. This was sometimes necessary in order to attain the correct orientation for emergence. The small emergence hole made by the sharp mandibles corresponds in size with the head capsule and is always located on the outermost surface towards one end of the egg. Once the head capsule- the widest part of the young grub's body was free, the remainder of the body was /

was slowly withdrawn from the egg.

Larva.

In the subsequent determination of the number of larval stages and duration of instars, it is necessary to state that the observations were carried out on the larvae of the summer broods, which provided adequate number of larvae for measurement. The duration of the instars, therefore, does not refer to the larvae of the winter broods, where feeding and, consequently, growth is much slower and where the length of similar instars varies to a greater extent than in larvae of the summer broods.

Determination of the number of larval instars.

Introduction.

Measurement of the rate of growth in insect larvae is a subject which has attracted increasing attention in recent years. The pioneer in this field of investigation was Dyar (1890), who as a result of his studies on 28 species of lepideptерous larvae, came to the conclusion that the rate of growth in successive instars as measured by the increasing size of the head capsules, was in regular geometrical progression. Consequently, with a knowledge /

knowledge of the measurements of the head capsule widths of the first and the last larval instars of the species concerned, the total number of instars could be determined. This method has been widely applied not only in lepidepterous life-history studies, but also in the study of other insect larvae. Taylor (1931) tested Dyar's Law on the sawfly, Phyllotoma nemorata (Fallen), and on other 46 species of sawfly larvae, and got satisfactory results. Miles (1931), working on four species of Tenthredinidae found that the widths of the head capsule or of the frons, in successive instars followed a regular geometrical progression in the initial stages of growth, but that in the later instars growth became irregular owing to sex differentiation, and the occurrence of prepupal stadium. Metcalfe (1932) used Dyar's method in an attempt to determine from random collections of the Anobiid beetle, Sitodrepa panicea L., the number of early stages of the species, but no satisfactory conclusions were drawn as to the number of instars, due to an inadequate number of measurements, and to complication introduced in the form of sex differences in size among the larvae.

Determination of the number of larval instars, and the approximate period of the larval stadia by measurement /

measurement of the head capsule widths of several larvae, has been successfully used by many investigators, working independently on bark beetles- Bedard (1933) on Dendroctonus pseudotsugae; Prebble (1933) on Ips pini, Pityokteines sparsus Lec., and Dendroctonus simplex Lec.; Kaston and Riggs (1937), and Becker (1939) on Hylurgopinus rufipes Eich.; McMullen and Atkins (1959, 1962) on Scolytus tsugae Swaine, and Scolytus unispinosus Lec. respectively, and by Thomas (1961) on Ips pini.

Method.

In order to determine the number of larval instars of Ips cembrae, larvae were collected from experimental logs in the field in June and July, and they were preserved in 70 per cent alcohol. The date of each collection was recorded. Head-capsule widths of 1,034 larvae were later measured in the laboratory to the nearest division of a calibrated ocular micrometer, at a magnification of 125x.

Analysis of data and results.

The data were smoothed and analysed according to the method described by Prebble (1933). A histogram of the frequency distribution of the head-capsule /

head-capsule widths is presented in Fig. 21, and the analysis of the data is as shown in Table 3 below.

Table 3.

Head-capsule widths of the larvae of <u>Ips cembrae</u> (mm)

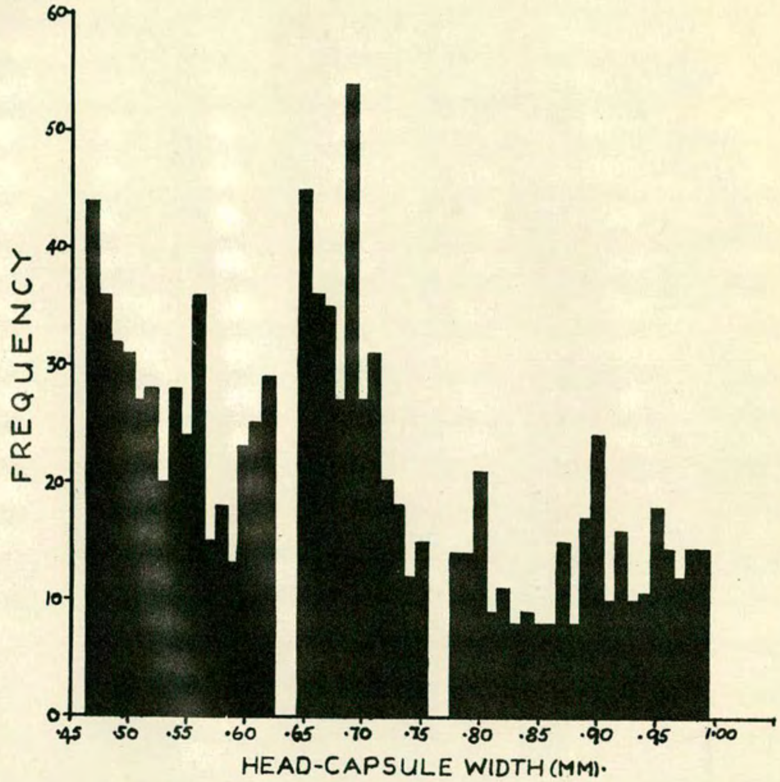
	1st instar	2nd instar	3rd instar
No. of larvae measured	429	320	285
Range in width	0.47 - 0.62	0.65 - 0.75	0.78 - 0.99
Mean head width	0.54	0.71	0.89
Calculated mean[a] (R = 1.284)	0.54	0.69	0.89
Standard deviation[b]	0.0482	0.0354	0.0648
Standard error of mean[c]	± 0.00232	± 0.00198	± 0.00384

a. The average ratio of increase has been used. The calculated means of later instars were obtained by multiplying the average head-capsule width of the 1st instar by successive powers of the average ratio.

b. The following formula has been used:-

$$\text{Standard deviation} = \sqrt{\frac{e_1^2 + e_2^2 + e_3^2 \ldots e_n^2}{n}}$$

e_1 /



FIG·21· HISTOGRAM OF FREQUENCY DISTRIBUTION OF 1,034 LARVAL HEAD-CAPSULE WIDTHS OF IPS *cembrae*, ORD WOOD, CAWDOR ESTATE, 1963

e_1, e_2, etc., being the deviations of the various head-capsule widths from the mean, and n the number of measurements.

c. The following formula has been used:-

Standard error of mean $= \frac{s}{\sqrt{n}}$, where s is the standard deviation, and n the number of measurements for each instar.

In order to estimate approximate duration for each instar, the population was analysed for each date of collection. From these analyses the approximate duration of each instar was estimated, each stadium being considered equivalent to the interval between the date when the instar formed the majority, 50 per cent or more, of the population, and the date when the succeeding instar formed similar proportion of the population.

Table 4. gives a summary of the estimate.

Table 4.

Duration in days of larval instars of _Ips cembrae_.

June - July, 1963.

Stadium	Duration	
	Mean	Range
1st instar	11	10 - 12
2nd instar	10	8 - 11
3rd instar	12	11 - 14
Total	33	29 - 37

The frequency distribution and the analysis of head-capsule widths measurements indicate three instars. This agreed satisfactorily with the result from direct observation in the rearing apparatus in the laboratory. The mean developmental period for the larval stages under laboratory conditions was 26 days, with an average temperature of 18.5° C.

Larval food and habits.

Newly hatched larvae were observed in the rearing apparatus burrowing along the inner bark layers. They mined for a short distance at right angles to the egg galleries, feeding on the inner surface of the phloem, which constitutes a satisfactory diet. With increase in larval growth, the tunnel contained a greater proportion of phloem, consequently tissue destruction by the more mature larvae was comparatively rapid. Periodically the larvae reversed their positions and, using their heads, compressed the non-ingested material into the older part of the tunnel, giving it a characteristic backwardly curved appearance. In the field, as in the laboratory, a noticeable larval characteristic was the tunnelling in the phloem.

The final larval instars accounted for the remainder of the mines, and constructed the pupal cells at their ends. By this time feeding has ceased, and a period of inactivity followed the final smoothing of the pupal chamber. The larvae first extended themselves lengthwise, then very gradually shrank, and equally slowly the head and thorax became ventrally inclined. A slight enlargement appeared dorsally on the prothorax, where the larval skin soon ruptured, revealing the anterior portion of the pupa. The exuvium was then gradually worked back along the body and was shed at the posterior end. The time elapsing between the cessation of tunnelling and pupation, based on direct observation, averaged 5 days.

Pupa.

Like that of most other insects, the pupa of Ips cembrae is quiescent, though it revolves atimes in the pupal chamber. The following changes were observed in particular individuals bred in the laboratory. A few days following transformation from larva, minute dark spots were discernible on the white background towards the posterior region of the eye surface. These spots were the embryonic facets of the eye. The spotted area extended to one-third /

one-third of the distance across the eye, and the first spots to appear have become larger. Later, the dark spots spread to two-thirds of the distance across the eye, and the facets became discernible over the whole eye surface. The colour of the eye gradually deepened from pale-brown to dark-brown and then to blue-black. In the meantime, the dots of colour have individually coalesced, and the dark colour covered the whole eye. Then a faint colour was apparent in the region of the mandibles and this later became dark-brown. The creamy ground colour of the elytra and prothorax turned darker, and the general body colour changed to pale-brown. A representative series of individuals bred through the pupal stage showed a minimum pupal period of 11 days and a maximum of 15 days, with a mean of 12 days. Table 5 gives a summary of the total developmental period from egg to young beetle.

Table 5.

Duration of stages of Ips cembrae (in days).

Stage	Duration	
	Mean	Range
Egg	12	10 - 14
1st instar larva	11	10 - 12
2nd instar larva	10	8 - 11
3rd instar larva	12	11 - 14
Pupa	12	11 - 15
Adult emergence	15	12 - 18
Total	72	62 - 84

The adult.

The adult beetle is fragile at first and then remains quiescent within the pupal chamber. The period elapsing between transformation to the adult and emergence from the pupal chamber showed variation, ranging from 12 to 18 days. Emergence of adult beetles was first observed in the rearing cages in the laboratory on August 24th, but not until early September in the field.

Habits.

Observations in the field show that the young adults usually feed for some time in the logs in which they developed, by extending the galleries in the bark, after which they emerged to continue with their maturation feeding by invading new material. Regeneration feeding of the parent beetles has also been observed to take place as an extension of the galleries in the bark, followed by emergence and attack of new host tree for feeding and breeding purposes. After a short period of flight, the parent beetles were observed laying eggs for the second brood in late September.

Experiment was carried out in the laboratory to study the feeding habits of adult beetles. Larch twigs were placed in glass cylinder into which /

which beetles were put, and the top of the cylinder was covered with a lid of wire mesh (Fig. 22) to prevent the beetles from escaping. A few hours after the introduction of the beetles into the glass cylinder, they started boring into the twigs. They were observed cutting short tunnels towards the tops of the twigs. These tunnels varied from 4 to 10 millimetres in length.

Symptoms of attacks and economic importance of *Ips cembrae*.

Indications of *Ips cembrae* attacks on larch are noticeable by the occurrence of orange frass thrown out at the entrance-holes of the mother galleries. The frass can be traced in streaks down the bark, and sometimes occurs in little heaps either on the forest floor or on the bark scales.

In the present study at the Ord Wood, attacks on larch by *Ips cembrae* have been observed mostly on felled logs and windblown trees. Although some standing trees were also infested, in many cases the trees attacked have very small crowns and have been invaded by Fomes.

The greatest damage done to the host tree by the beetle is through its shoot tunnelling feeding activities in the shoots of healthy trees. This feeding,characteristic of the beetle was not

commonly /

Fig. 22. Device for studying the feeding habits of adult beetles on twigs.

commonly observed in the present study, probably because of availability of suitable breeding materials in the form of logs and windblown trees.

In a primary attack by the beetle, the result of the tunnelling in the shoots of healthy trees can lead to a great loss of foliage as the tunnelled shoots are broken off by the wind. The damage by this sort of attack, if it does not result in the immediate death of a tree, reduces its resistance to attack by other insects. The result is not only a direct loss to the stand, but an indirect loss to the forest owing to soil deterioration by opening the way for light.

Then there is the damage done by the larvae which after emergence from the eggs enter the cambial region of the bark. Feeding takes place largely on the inner bark tissue, but may include the thin cambium and the newly-formed tissue on the surface of the wood. Thus, if a piece of infested bark is removed from the stem, the mother and larval galleries are very well marked on it. The mother and larval tunnels sometimes encircle young stems, and as a result, the passage of sap is interfered with.

Although the foregoing observations on _Ips cembrae_ were confined to the Ord Wood, where larch logs /

logs and windblown trees were the materials generally attacked, it is important to know that the bark beetle can become a primary pest of larch when conditions favour its increase to epidemic level.

Discussion.

Rearing techniques.

The Vinyl sheeting cages (Fig. 2) used in rearing Ips cembrae gave satisfactory results, from the point of view of producing reasonably large number of broods for continuing generations. Apart from the fact that the technique provides a simple means for bulk rearing of the beetles, it has the additional advantage that the cages are not heavy, and cost of materials is reasonable.

The perspex-bark sandwich method (Fig. 4) used to rear Ips cembrae broods so as to keep them under daily observation is a novel and practical rearing method for this bark beetle. The technique so closely simulated the normal habitat that the behaviour of the broods was similar to that in undisturbed trees in the field. As evidence of normality of the habitat in the device, was the fact that larval mines were always in the inner bark; also, the broods did not attempt to escape from the rearing medium even when they became adults, because of the even thickness of bark used, and the intimate contact between the bark and perspex plates. The use of perspex plates in the rearing device, eliminated breakage within the press as Bedard (1933), and Kaston and Riggs (1937) experienced /

experienced with their own glass-bark sandwich technique.

In addition to the excellent opportunity to observe the activities of the broods throughout the entire cycle of development, the technique provides a simple means for rearing Ips cembrae at a reasonable cost of materials. The regular renewal of absorbent cotton packed round the bark within the two plates of perspex, affords virtually complete freedom from mortality which might be caused by introduction of pathogens.

With this technique, it has been possible to follow the life cycle of 42 eggs to adult beetles.

Life history and habits.

Observations on the life history and habits of Ips cembrae at the Ord Wood show that the beetle overwinters in the larval, pupal and adult stages under the bark of larch, and some adults also hibernate in the forest litter. Prell (1926), Schimitschek (1931), Crooke and Bevan (1957) have made similar observations on the overwintering habits of the beetle.

Adult beetles were observed emerging from their hibernating quarters in the field in late May when temperature was about 18° C; but emergence took place /

place earlier in May from the caged logs in the laboratory when average temperature of 22° C was recorded. Flight was observed twice in the field. The first was in late May to late June and the second occurred in late August to mid-September, before the establishment of the overwintering broods. Schimitschek (1931) has shown that Ips cembrae has two main flight periods in Austria- the spring flight, starting in late April and continuing till the end of May, and the summer flight beginning generally towards the middle of August to early September, depending on the weather conditions.

The indication of a habit of feeding on small twigs prior to making its attack is not surprising. Such feeding habit of the beetle has also been observed by Prell (l.c.); Schimitschek (l.c.); Schindler (1948) and Shremmer (1955), and might cause death of the twigs especially during outbreak.

Egg-laying followed the period of flight, and observations in the laboratory showed the minimum incubation period to be 10 days at an average temperature of 18° C, while some eggs hatched after 14 days at a mean temperature of 14.5° C. Such a difference indicates that temperature has a /

a decided effect on the development of the broods. As exemplifying the effects which temperature and exposure have in hastening or retarding development under field conditions, it was observed from logs chosen for experiments in the field that adults were emerging from the sides of the stems exposed to full sunlight in early September while corresponding broods in the shaded parts of the logs were in the pupal stage.

The distribution of larvae by head-capsule widths measurements indicates three instars, and the calculation of three larval instars in this study was substantiated by locating head capsules in the frass in the larval mines. Of the 40 larval mines examined under the microscope, 3 head capsules were found in 39 larval mines and 2 in 1 mine. In the latter case, the positions of the head capsules in the mine indicated that the other head capsule had in all probability been missed. The result (Table 3) conforms fairly satisfactorily to Dyar's law (1890), as shown by the close similarity between actual and calculated head-widths, the low standard deviation, and the low standard error of the mean for each instar.

Schimitschek (1931) stated that under the most favourable conditions at low altitudes in Austria,

<u>Ips</u> /

Ips cembrae has two generations a year, but at high elevations there is apparently one generation per year. Observations both in the field and laboratory on the life-history of _Ips cembrae_ in 1962 to 1963, indicate that there is a single generation a year in the Ord Wood, although two broods are normally produced. The first brood arises from egg-laying by the parent beetles in May and June, producing adults in late August and early September. The parent beetles emerge from the first breeding logs and feed for varying length of time, for the purpose of regenerating their sexual organs. Eggs for the second broods are laid in late September and early October, and these overwinter as larvae and pupae, and the adults emerge in April and May.

Conclusions.

The results of the biological studies on the Larch bark beetle, Ips cembrae, conducted from 1962 to 1963 at the Ord Wood, Cawdor Estate, and in the laboratory at Edinburgh indicate that the bark beetle is univoltine, but produces two broods a year. The first broods result from egg-laying in the months of May and June, producing young adults in August and September, and the second broods arise from eggs laid in late September and early October. These generally overwinter in the larval and pupal stages, and the adults emerge the following spring.

Felled logs, windblown, and weakened standing trees are attacked by Ips cembrae for breeding purposes. Breeding takes place both in thick and thin barked material, and larch stems of down to 2 inches diameter are occasionally used as breeding media. Eggs are laid singly in niches under the bark of infested larch. The maximum number of eggs laid by a female under laboratory conditions was 55. Temperature influences the rate of development, the minimum incubation period in the laboratory being 10 days at an average temperature of 18° C, and maximum was 14 days at 14.5° C.

The newly emerged larvae feed on inner bark layers /

layers of the host tree. There are three larval instars, and a mean larval period of 26 days is recorded under laboratory conditions.

The pupa is quiescent except for the abdomen which wriggles if the pupa is disturbed. The mean pupal period in the laboratory is 12 days.

Observations both in the field and laboratory have shown that maturation feeding of the young beetles and regeneration feeding of the old beetles take place either in the bark where broods have developed, or in the shoots of host trees. This habit of shoot boring by the adult beetles can cause crown pruning and death of healthy trees.

Suggested control measures against Ips cembrae outbreak in larch stands.

In view of the information which has been gathered about the life-history of Ips cembrae in the Ord Wood, Cawdor Estate, it is suggested that control measures should be directed towards the maintenance of forest hygiene, and where infestation is severe, trapping.

Special attention should be paid to windblows and felled trees lying in the wood during breeding periods. The critical period is while the bark is in a fresh condition for breeding purposes. It is recommended /

recommended that such windblown and felled trees should have their bark peeled off and burnt during flight periods to eliminate infestation, if extraction and conversion are not practicable.

The timing of thinning, felling, and extraction operations is of great importance in the reduction of Ips cembrae numbers. It is advisable to carry out these operations during winter when the beetle is in hibernation, and the extraction of the logs should be completed before the beetle's emergence in April, so that little or no suitable breeding material is available.

The danger of storing infested logs in the saw-mills without peeling and bark burning is a real one. Such practice leads to the distribution of the bark beetle to neighbouring forests, particularly in fencing materials, thus increasing its area of infestation. Infested material should therefore be debarked before transportation to saw-mills.

Care should be taken to avoid planting larch on marginal sites, particularly where there is a history of Fomes damage, since beetles make what amounts to primary attack on larch in early stage Fomes infestation. Particular importance should be attached to regulation of thinning in possible infestation areas, to ensure early removal of suppressed /

suppressed trees.

Where infestation is severe the use of trap-logs and stems to control Ips cembrae populations is recommended. As the bark beetle has two flight periods in a year- spring and summer, it is suggested that trap-logs should be laid from March to October, to provide suitable breeding material during the egg-laying period. Standing trees used as trap-stems should be selected at intervals throughout the wood. Trees with badly shaped crowns, unhealthy, damaged, or those suppressed by taller surrounding trees should be selected, if possible on the southern exposure of the plantation, and a ring of bark removed just above the surface of the ground. Trap-logs should be located in exposed areas of the wood which receive sunlight because the beetle is more attracted to logs in sunlight than those in the shade. Trap-stems and logs should be examined at regular intervals throughout the breeding season in spring and summer, and those utilised should be debarked to destroy the broods. Maximum period for any trap laid should be three months.

PART 3.

Population studies.

Chapter 5.

Methods.

Introduction.

A population is a concept, which can be defined for specific purpose and in different ways. It can either refer to many species of animals occupying an area determined by some special factor, such as time or space limitation. On the other hand, one species may make up a population, which may share specific habitats with many other single species, but with some specialisations, to allow it. In population studies, it is the student's prerogative to determine his concept of population in his own investigation, and in doing so the aims of the investigation will be supreme.

Populations can be thought of both in the absolute and relative sense. The former is the expression of numbers in terms of a unit that does not vary, particularly an area unit of the earth's surface, and the latter refers to the number of organisms per unit of space they occupy. This is commonly called "population density", and the spatial unit may be any suitable measure, depending on the type of animal studied and the judgement of the /

the investigator.

It is apparent that, since the population problem revolves around the question of enumeration, the techniques employed in this count are of vital importance, and should therefore be designed to fulfil the aims of the investigation.

In the study of bark beetles populations, various methods have been devised by investigators in order to get the information required. Thus Miller and Patterson (1927), investigating the part played by forest fires in paving way for Dendroctonus brevicomis attack on yellow pine forests in California, checked and mapped all trees attacked in the burned area, and measured the cubic mass of the trees. By repeating this procedure several years in succession, he was able to ascertain the amount of damage caused by the beetle. His method was designed to estimate the amount of injury caused by the bark beetle, but not aimed at a calculation of the absolute number of the beetle population.

Trägårdh and Butovitsch (1938) devised the 'Strip survey' method to estimate the density of bark beetle populations in storm-swept forest in Sweden. With the help of a compass, sample strips were laid across the area to be investigated in such /

such a way that representative cross-sections were obtained through all the varying conditions of the area. Bark samples, 20 by 40 cm. in area were taken from trees within the strips, and the number of beetles in the samples counted. From the data obtained, the investigators were able to assess the density of bark beetle population in the storm-swept areas. Knight (1958) used essentially similar method in surveying infestation of the Black Hills beetle in Ponderosa pine in Colorado, although the number of infested trees per strip was estimated rather than the number of beetles. Crooke (1955), carrying out a survey in the gale-damaged woodlands of north-east Scotland in 1953-1954, used as an index of pine shoot beetle population the number of mother galleries found in one foot of inner surface of bark exposed. Windblown trees were sampled by removing one foot sections of bark at heights of 5, 10, 20 feet etc. along the stems. Reid (1957) studied the manner in which _Ips pini_ was distributed in slash left after logging operation in Lodgepole pine forest in Alberta, by carrying out slash sampling in plots of 50 feet in diameter, taking one linear foot of slash as his sampling unit. Knight (1960) got basic information on number of Engelmann spruce beetles /

beetles attacking spruce in Colorado, by estimating the number of beetle attacks per one square foot sample of bark over the entire bole of numerous trees. From his data, he was able to relate beetle attacks to the diameter of infested trees. Nagel et al (1957) used similar method in measuring the population density of the same bark beetle, but took his samples at 8-foot intervals along the bole of the sample trees, instead of at 5-foot intervals as done by Knight (l.c.).

Population studies on _Ips cembrae_ at the Ord were carried out with the objects of revealing the manner of its distribution, and the effects of bark thickness and heights of trees at points of infestation on this distribution, as well as the relationship between air and subcortical temperature of larch trees infested by _Ips cembrae_.

Methods employed in population studies on _Ips cembrae_.

Sampling procedure.

The sampling areas for the study were compartments 64 to 68 of the Ord Wood, Cawdor Estate, in Nairnshire. The areas have been described in Chapter 2.

Before proceeding with the sampling programme, some preliminary investigations were carried out to /

to select sample size. Sample size should be related to the frequency, abundance and size of the beetle to be collected. The sample unit taken at the beginning of the work was larger than necessary.

Bark sampling was carried out in the five compartments (64 to 68). Within each compartment, 10 windblown trees were selected by drawing numbers. The sample unit was one square foot of bark. Sampling in one compartment and one date consisted of taking 5 bark samples, each one square foot in area, from 2 sample trees. The samples were taken at 5-foot intervals along the bole of the tree starting from its base, and the number of larvae, pupae and adult beetles in each bark sample was minutely counted and recorded. Bark thickness at points of sampling was also measured with a bark gauge and recorded, and the total length of each sample tree was recorded as well. The sampling programme was carried out on consecutive days between 14th of April and 8th of May 1963, before the emergence of the beetles.

Additional samples were taken shortly after the emergence of the beetles, and the data collected from these samples formed the basis for the determination of the nature of the bark beetle distribution. /

distribution. As a result of quick extraction of windblown larch in the wood, comparatively small number of infested trees was available. Therefore, 2 sample trees were selected from each of the 5 compartments by the same method as above. The sampling unit was reduced to 6 x 6 square inches of bark in order to take adequate number of samples. Sampling in one compartment and one date consisted of taking 25 samples, each 6 x 6 square inches in area, from one sample tree. The samples were spaced at 2-foot intervals along the bole of the tree, starting from its base, and the number of beetles per sample was counted and recorded. The sampling programme was conducted on consecutive occasions between 30th of May and 8th of June 1963. Details of the sampling data are given in the appendix.

Field techniques for study of subcortical temperatures of trees infested by Ips cembrae.

Procedure.

Temperatures under bark of infested trees were measured with a sensitive thermistor, which is essentially a Wheatstone's bridge. The very sensitive point of the thermistor is placed at the end of a glass rod about 6 cm. long.

The method consisted of inserting the sensitive /

Fig. 23. Measurement of bark temperature with a thermistor.

sensitive point of the thermistor into the exist holes of the bark beetles, and pressed a little further into the holes for measurements of bark temperatures (fig. 23). In this way the point was in close contact with the inner surface of bark. By switching the current on, the temperature under bark was indicated on the dial scale of the thermistor, and this was read from the prepared graph.

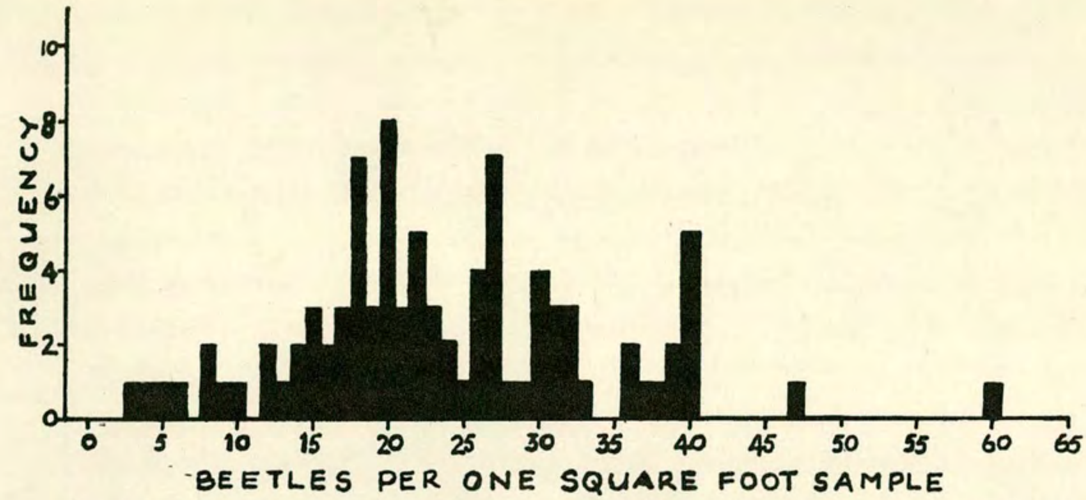
Subcortical temperature readings were taken on both north and south sides of selected trees, and corresponding air temperatures were recorded with a Centigrade thermometer. Bark thickness at points of insertion of the thermistor was also recorded. Readings were taken at 30 minutes interval one day each in April, May and June, from 8 a.m. to 8 p.m.

During the investigations, fifteen pairs of 6 x 6 square inches bark samples were taken on both north and south sides of each of the six trees used for studies, and the number of entrance holes per sample was recorded as an index of beetle attacks per sample. The data were analysed to show if there was significant difference in beetle attacks on both north and south sides of the trees.

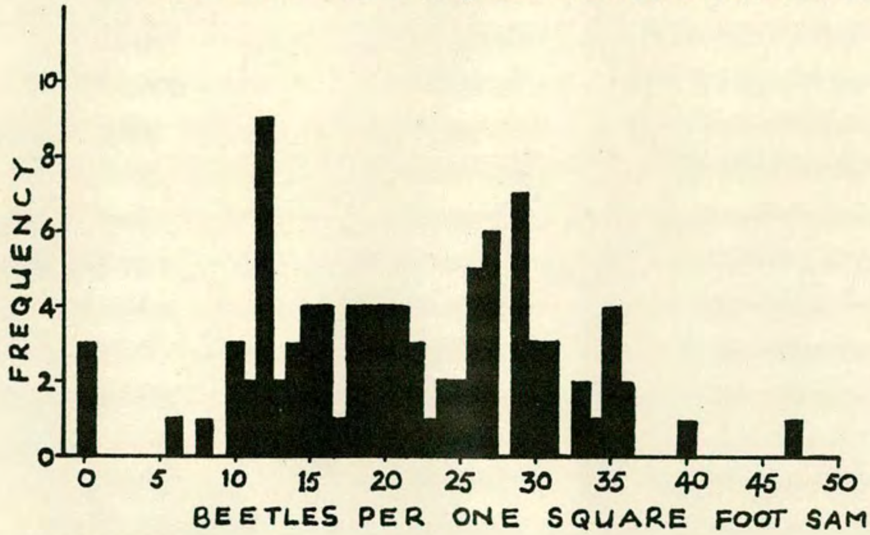
Chapter 6.

Analysis and Results.

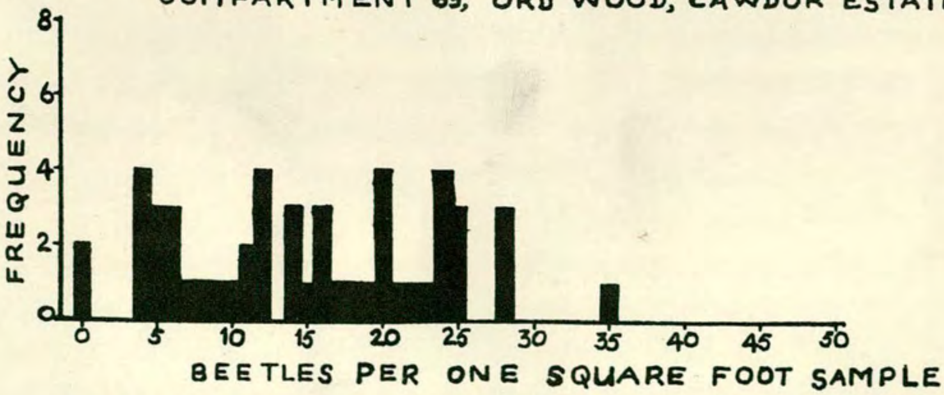
The frequency distributions of the populations of Ips cembrae, found in one square foot of bark samples taken in compartments 64 to 68 are shown in Figs. 24 to 28, and Fig. 29 is an histogram of frequency distribution of the bark beetle in the five compartments together. The figures indicate the skewness of the beetles distribution in all the compartments. In order to determine a suitable form of transformation that should be applied to the data to render them susceptible to multiple regression analysis, standard deviations of Ips cembrae counts were plotted against the means (Fig. 30), as well as variances against the means (Fig. 31). Figure 30 shows that the standard deviation tends to increase with the mean but not proportionally, while variance tends to increase proportionally with the mean. The appropiate transformation is thus the square root. Quenouille (1950) states that the most suitable form of transformation, is given by $\sqrt{(x + \frac{3}{8})}$, where x represents the count. The transformed data are shown in Table 6.



FIG·24· HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENT 64, ORD WOOD, CAWDOR ESTATE.



FIG·25· HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENT 65, ORD WOOD, CAWDOR ESTATE.



FIG·26· HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENT 66, ORD WOOD, CAWDOR ESTATE.

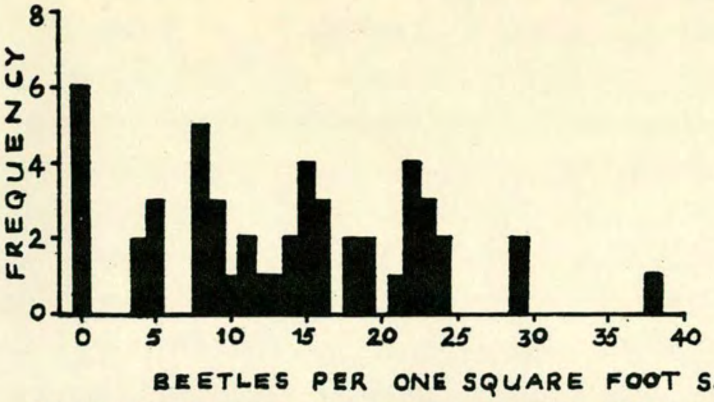


FIG. 27. HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENT 67, ORD WOOD, CAWDOR ESTATE.

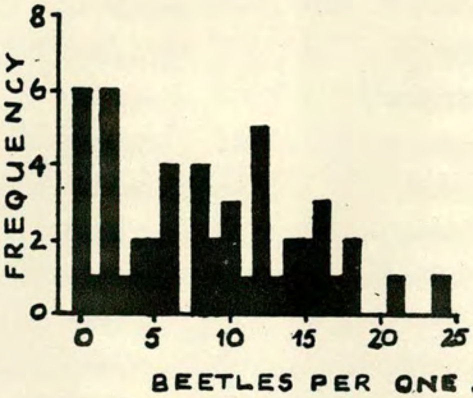


FIG. 28. HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENT 68, ORD WOOD, CAWDOR ESTATE.

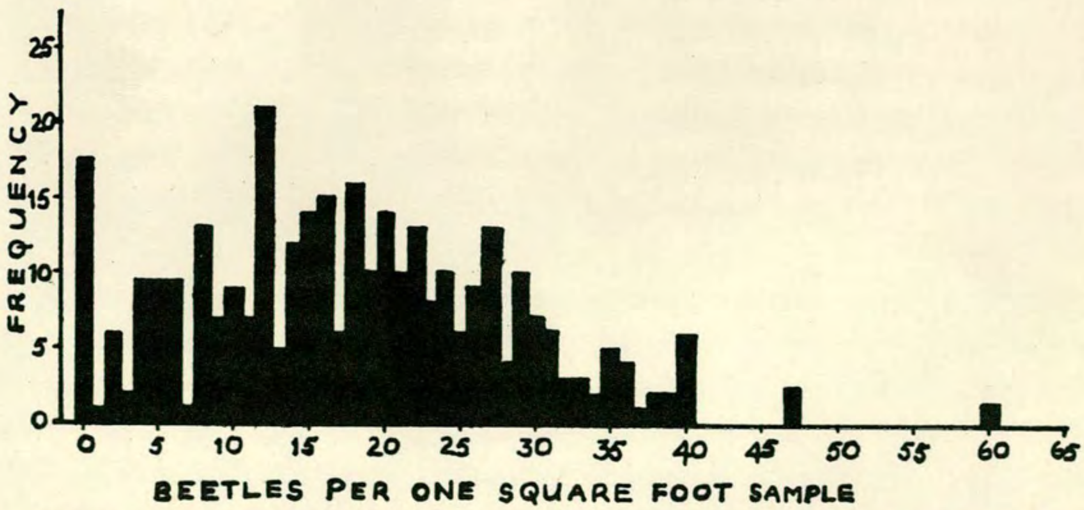
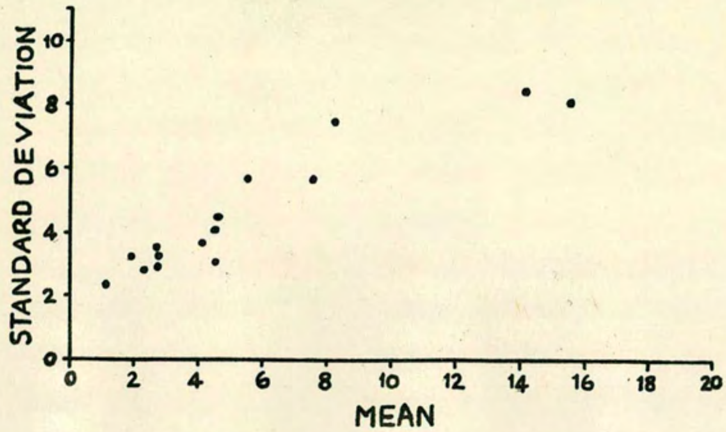
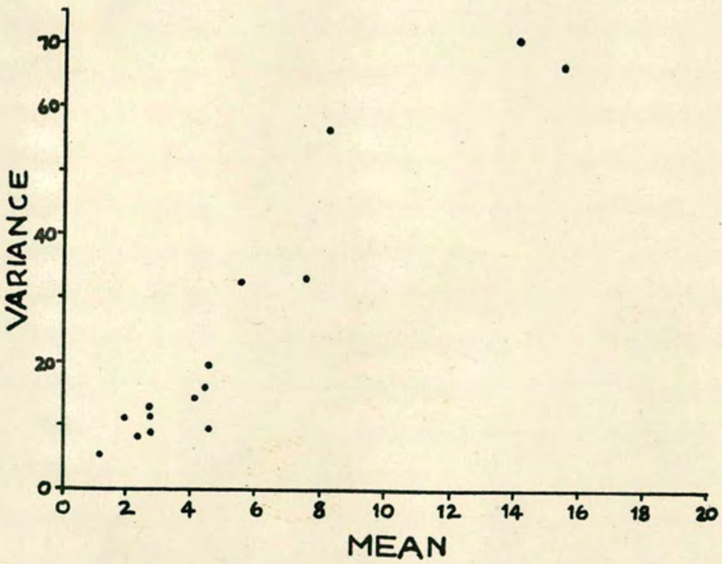


FIG. 29. HISTOGRAM OF FREQUENCY DISTRIBUTION OF IPS *cembrae*, COMPARTMENTS 64-68, ORD WOOD, CAWDOR ESTATE.



FIG·30·PLOT OF MEANS AND STANDARD DEVIATIONS OF IPS *cembrae* COUNTS, ORD WOOD, CAWDOR ESTATE.



FIG·31·PLOT OF MEANS AND VARIANCES OF IPS *cembrae* COUNTS, ORD WOOD, CAWDOR ESTATE.

Table 6.

Original data of <u>Ips cembrae</u> counts in one square foot of bark samples taken from compartments 64 to 68, Ord Wood, and subjected to square root transformation ($\sqrt{x + \frac{3}{8}}$).

No.	Compartment 64	Compartment 65	Compartment 66	Compartment 67	Compartment 68
1.	4.29	4.94	5.04	5.42	2.52
2.	5.60	5.13	4.84	5.42	2.09
3.	4.94	3.37	5.33	4.05	1.54
4.	5.60	4.05	3.37	3.52	1.17
5.	4.29	3.52	2.32	2.89	0.61
6.	5.51	3.52	4.94	4.84	2.89
7.	6.28	4.29	2.52	3.92	1.54
8.	4.73	5.04	2.32	3.37	1.54
9.	3.92	3.52	2.09	2.89	1.84
10.	5.23	4.62	2.09	2.89	1.54
11.	3.66	5.23	2.52	4.73	4.29
12.	3.79	5.60	4.05	4.73	3.79
13.	4.51	5.13	3.52	3.79	2.89
14.	5.51	4.62	4.05	3.22	2.52
15.	4.05	3.79	2.52	3.06	1.54
16.	4.29	5.23	4.62	4.29	3.52
17.	4.51	4.51	3.22	3.92	3.37
18.	5.23	4.17	2.32	3.06	3.06
19.	4.51	3.52	3.52	2.32	2.89
20.	2.89	3.52	2.09	0.61	2.32
21.	2.32	4.84	5.95	4.05	4.17
22.	2.09	6.03	4.94	4.62	4.05
23.	4.29	5.95	3.37	2.89	3.22
24.	2.89	4.73	3.79	2.09	3.52
25.	2.52	5.23	0.61	0.61	0.61
26.	5.13	5.95	4.40	0.61	2.89
27.	4.51	5.78	3.52	2.89	3.06
28.	3.79	5.42	2.72	3.06	0.61
29.	4.40	6.35	3.79	4.40	2.52
30.	4.05	5.23	3.92	4.73	2.09
31.	6.03	5.23	4.73	3.92	4.29
32.	6.20	5.42	4.51	4.40	4.05
33.	5.33	5.13	4.51	3.92	3.22
34.	5.23	5.42	2.09	2.09	2.09
35.	1.84	0.61	4.05	0.61	1.54
36.	5.69	4.29	5.04	4.84	4.05
37.	4.62	3.52	4.94	4.84	3.92
38.	6.88	4.05	4.94	4.73	3.66
39.	6.11	4.40	4.17	0.61	3.52
40.	4.73	0.61	0.61	0.61	0.61

Table 6. (Continued)

No.	Compartment 64	Compartment 65	Compartment 66	Compartment 67	Compartment 68
41.	4.84	4.05	5.33	6.20	4.62
42.	5.13	2.89	5.33	4.29	3.22
43.	4.51	3.22	5.04	3.79	2.32
44.	3.52	4.29	4.29	2.32	0.61
45.	3.06	4.73	3.06	2.32	0.61
46.	4.29	4.29	4.51	4.94	4.94
47.	4.73	3.52	4.51	4.94	3.92
48.	5.13	3.37	3.79	4.05	3.79
49.	4.51	3.66	2.89	3.66	3.52
50.	3.52	5.13	3.52	3.37	3.52

The negative binomial distribution was fitted to the data from 6 x 6 square inches bark samples taken shortly after the beetles emergence. The procedure used for computing the negative binomial and for testing its fit is described by Bliss and Fisher (1953). The estimate of the parameter K was computed using the first formula of Bliss and Fisher (l.c.), where K was determined from the mean $\bar{x}$ and variance S^2 of the sample as $K = \frac{\bar{x}^2}{S^2 - \bar{x}}$.

The observed data compared with the calculated data for the negative binomial distribution are shown in Table 7. In Table 7, f is the observed frequency, Ø the calculated frequency for the negative binomial. The observed and expected frequencies were compared by X^2 test, where X^2 has three fewer degrees of freedom than the number of ratios summed. The calculation of X^2 for the discrepancy between the observed and expected frequencies is shown in the last column of Table 7, pooling the frequencies for $x \geq 5$ so as to avoid expectations of less than Ø = 5.

Table 7.

Fitting the negative binomial distribution to counts of Ips cembrae in compartments 64 to 68, Ord Wood. Beetles per 6 x 6 square inches sample of bark.

No. of beetles per sample x	Observed frequencies f	Expected frequencies ø	$\frac{(f - ø)^2}{ø}$
0	25	15.9	5.208
1	21	19.5	0.115
2	20	20.3	0.004
3	17	19.7	0.370
4	19	18.8	0.002
5	13	17.4	1.113
6	14	15.9	0.226
7	12	14.4	0.400
8	10	13.0	0.692
9	12	11.6	0.014
10	10	10.3	0.009
11	10	9.2	0.070
12	7	8.1	0.149
13	7	7.1	0.001
14	5	6.3	0.268
15	6	5.5	0.045
16	5	4.8)	
17	4	4.2)	0.386
18	3	3.7)	
19	3	3.2)	
20	5	2.8)	0.805
21	3	2.4)	
22	2	2.1)	
23	2	1.8)	0.639
24	2	1.6)	
25	3	1.4)	
26	2	1.2)	
27	2	1.0)	
28	2	0.9)	0.111
29	1	0.8)	
30^+	3	5.1)	
Total	250	250.0	$10.627 = X^2$

$\bar{x} = 8.3$, $S^2 = 56.1$, $K = 1.442$

The resulting X^2= 10.627 with 17 degrees of freedom is not significant at the 5 per cent level, indicating a good agreement with the negative binomial distribution.

An attempt was made to fit the negative binomial to the data from the one square foot bark samples by the same method. A satisfactory fit was not got. This point is referred to in the section on discussion.

The transformed data in Table 6 were analysed by the application of multiple regression. With this statistical method, the effect of heights of trees at points of infestation, and bark thickness on the bark beetle density of attack was revealed. The results of the analysis are laid out in Tables 8 to 11. In the tables, y represents the height at which samples were taken, and z the bark thickness.

Table 8.

Summary of analysis of variance for multiple regression on <u>Ips cembrae</u> population in compartments 64–68, Ord Wood, Cawdor Estate.

Variation	Compartment 64				Compartment 65				Compartment 66			
	D.f.	S.s.	E.v.	V.r.	D.f.	S.s.	E.v.	V.r.	D.f.	S.s.	E.v.	V.r.
Ascribable to y and z	2	7.22	3.61		2	8.24	4.12		2	28.15	14.08	
Residual	47	52.69	1.12	3.22	47	57.61	1.22	3.36	47	45.68	0.97	14.49
Total	49	59.91	1.22		49	65.85	1.34		49	73.83	1.51	

Table 8. (Continued)

Variation	Compartment 67				Compartment 68			
	D.f.	S.s.	E.v.	V.r.	D.f.	S.s.	E.v.	V.r.
Ascribable to y and z	2	41.72	20.86		2	35.66	17.83	
Residual	47	55.22	1.17	17.76	47	35.87	0.76	23.36
Total	49	96.94	1.98		49	71.53	1.46	

In Table 8, D.f. is Degrees of freedom, S.s. is Sum of squares, E.v. is Estimated variance and V.r. is Variance ratio.

The Variance ratio with 2 and 47 degrees of freedom in each of the 5 compartments is significant at the 5 per cent level, and compartments 66-68 are also significant at the 0.1 per cent level. Thus, height of tree and bark thickness have significant effects on the beetles density of attack.

In order to test the effects of height of tree and bark thickness on the beetles density of attack in the whole area, the data for ~~each of~~ the 5 compartments were massed together and subjected to analysis. The result is presented in Table 9.

Table 9.

Summary of analysis of variance for multiple regression on <u>Ips cembrae</u> population in the 5 compartments together.

Variation	Degrees of freedom	Sum of squares	Estimated variance	Variance ratio
Ascribable to y and z	2	100.805	50.4025	33.26
Residual	247	374.272	1.5153	
Total	249	475.077	1.9079	

The variance ratio 33.26, with 2 and 247 degrees of freedom is significant at the one per cent level. This indicates significant effects of height of tree and bark thickness on the beetles density of attack in the whole area.

An overall analysis was carried out to test whether the differences between the regressions for the 5 compartments were significant. The analysis is as shown in Table 10.

Table 10.

Overall analysis of variance on <u>Ips cembrae</u> population.

Variation	Degrees of freedom	Sum of squares	Estimated variance	Variance ratio
Ascribable to overall regression.	2	100.805	50.4025	
Ascribable to differences between regression coefficients.	8	20.185	2.5231	2.40
Ascribable to sum of regressions.	10	120.990	12.099	
Residual	235	247.070	1.051	
Total	245	368.06	1.502	

The variance ratio, $\frac{2.5231}{1.051} = 2.40$ with 8 and 235 degrees of freedom is significant at the 5 per cent level. This shows that the differences between the regressions for the 5 compartments are significant. Coefficients of regression for each compartment are presented in Table 11.

Table 11.

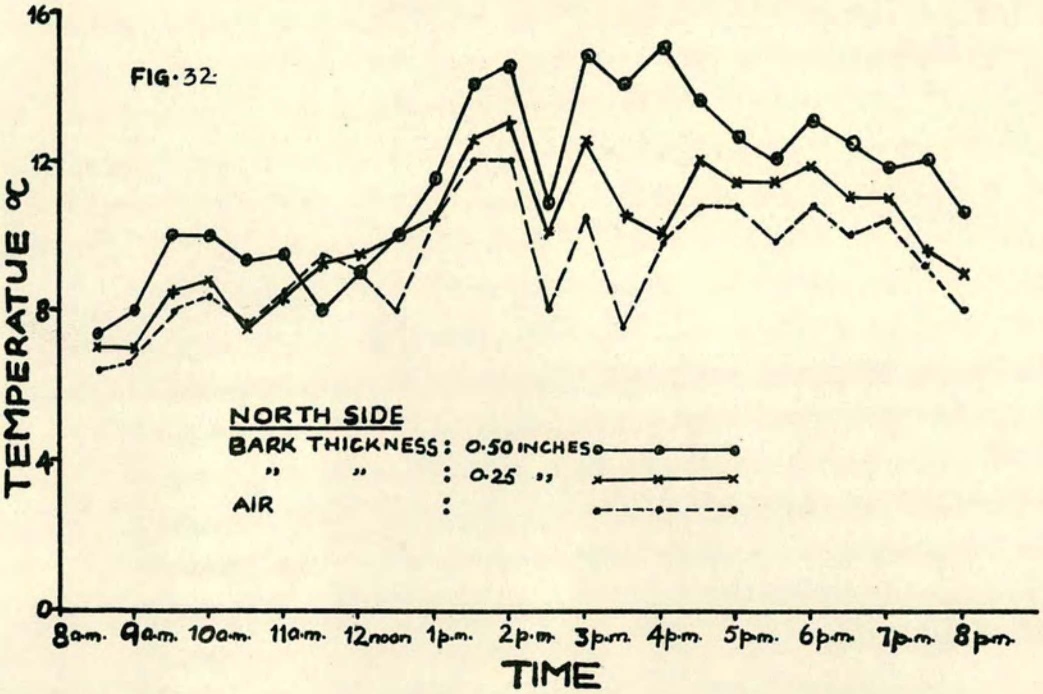
Regression coefficients, compartments 64 to 68.

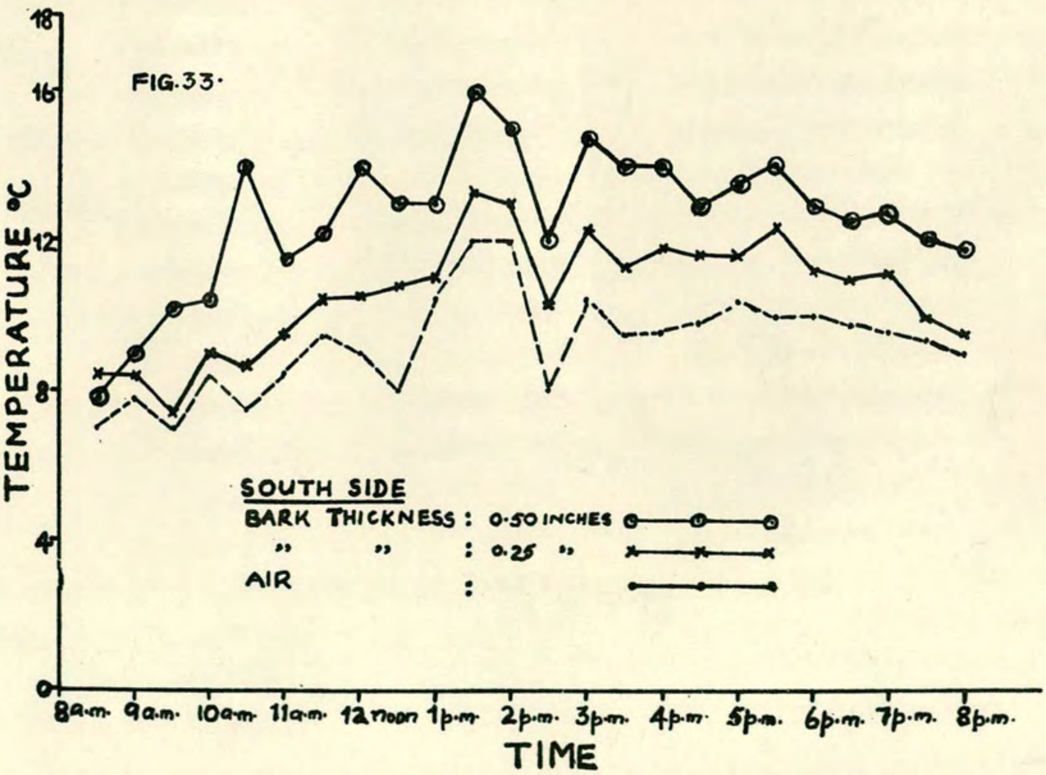
Compartment	Regression coefficients	
	by	bz
64	-0.035	1.525
65	-0.016	3.311
66	-0.104	0.401
67	-0.133	1.077
68	-0.096	3.068

Subcortical temperature investigations.

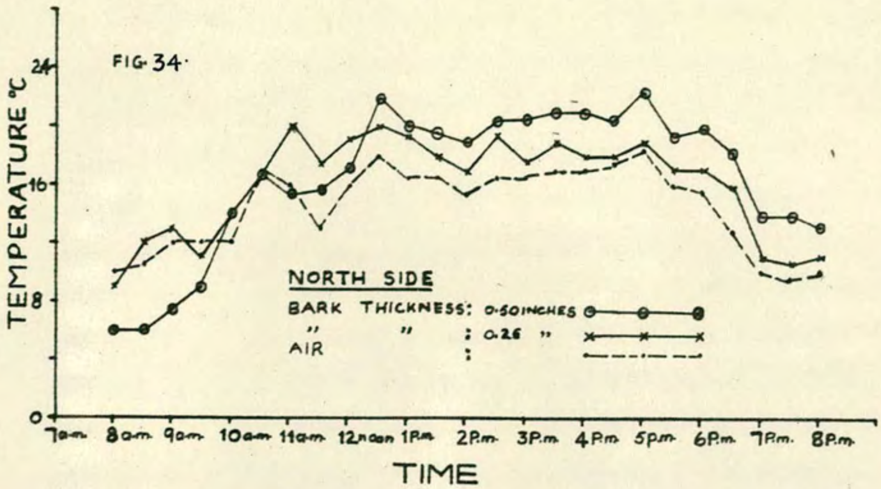
Results from the bark temperature investigations are presented in Figs. 32 to 37. An analysis of subcortical temperatures, as expressed in the figures shows that there is variation in bark temperatures on the north and south sides of the same tree. The south side of the tree warms up rapidly when the sun is shining directly on the bark. Heat is then absorbed rapidly and subcortical temperatures rise higher than those on the north side of the same tree. Bark temperature is the most important single factor which determines the relationship between air and subcortical temperatures of trees in the field. A study of the figures (32-37) shows that temperatures in thin bark follow closely the trend of air temperatures. Thin-barked trees cool rapidly with falling air temperatures, and warm up quickly as temperatures

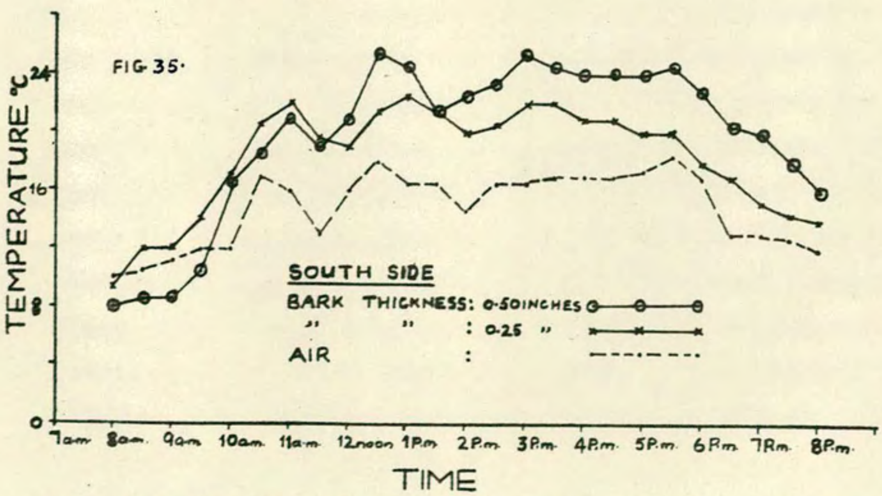
rise, /



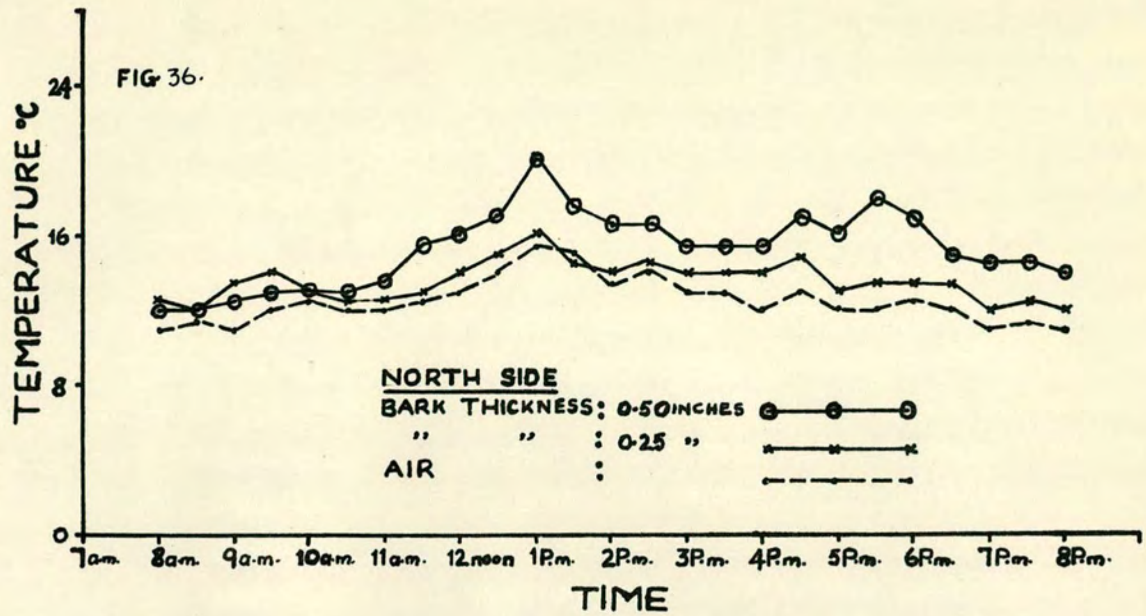


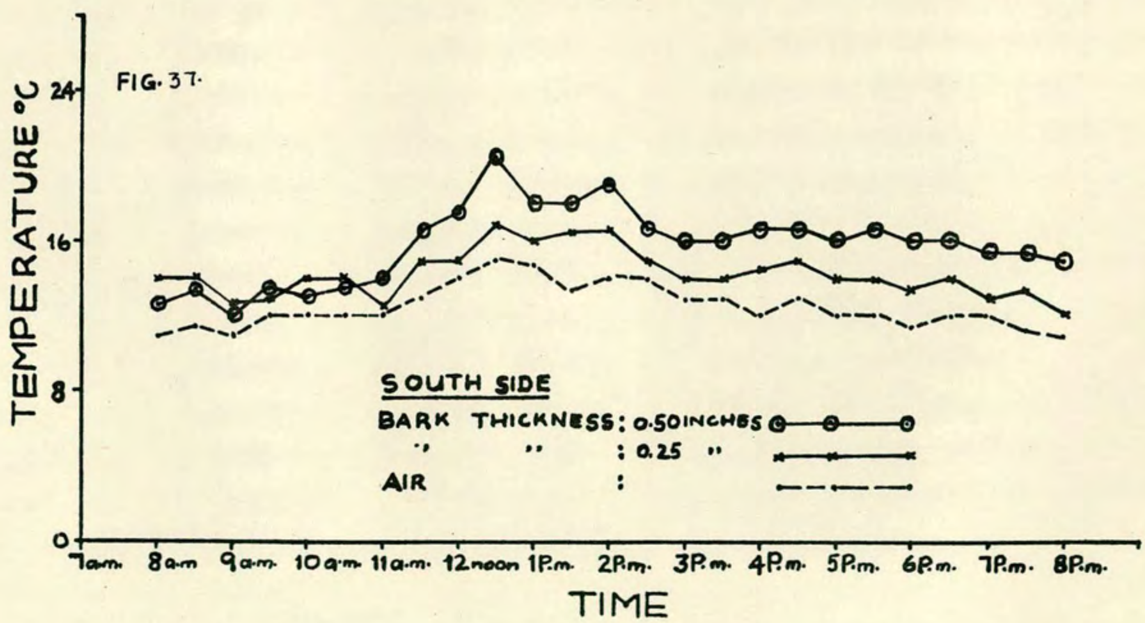
FIGS. 32-33. RELATION OF AIR AND BARK TEMPERATURES OF EUROPEAN LARCH INFESTED BY IPS *cembrae*, ORD WOOD. APRIL 9TH, 1963.





FIGS. 34-35. RELATION OF AIR AND BARK TEMPERATURES OF EUROPEAN LARCH INFESTED BY IPS *cembrae*, ORD WOOD. MAY 9TH, 1963.





FIGS. 36-37. RELATION OF AIR AND BARK TEMPERATURES OF EUROPEAN LARCH INFESTED BY IPS *cembrae*, ORD WOOD. JUNE 9TH, 1963.

rise, while thick-barked trees respond more slowly to changes in air temperature, but attain higher temperatures than thin-barked trees. A sharp change in the trend of air temperature produces corresponding change in subcortical temperatures. A lag exists between bark temperatures and air temperatures, and the time of this lag increases with bark thickness.

The data shown in Table 12 illustrate the differences between the mean number of attacks by *Ips cembrae* per 6 x 6 square inches of bark samples on both north and south sides of infested trees. The data for the table were taken from the six trees used in the subcortical temperature studies.

Table 12.

Mean number of *Ips cembrae* attacks per 6 x 6 square inches of bark samples taken on the north and south aspects of infested trees.

No.		Aspect on tree		t-test
		North	South	
1	Mean number of attacks per sample.	2.4	6.2	4.033
2	"	5.7	9.4	3.105
3	"	2.3	3.9	2.820
4	"	4.7	6.5	3.414
5	"	5.1	6.8	2.699
6	"	1.5	3.6	3,178

Significant differences in number of *Ips cembrae* attacks on the north and south sides of infested /

infested trees are apparent by t-test. With 14 degrees of freedom, numbers 3 and 5 are significant at the 5 per cent level, and 1, 2, 4 and 6 at the one per cent level. This indicates that south aspects of the trees exhibiting higher subcortical temperatures than the north aspects are more attractive to *Ips cembrae*.

Discussion.

The reason for applying the square root transformation to the original data collected from one square foot bark samples, was based on the relationship of variance to the mean of the beetles counts (Fig. 31), rather than the skewness of the beetles distribution in each compartment or skewness over all compartments (Figs. 24-29). As shown in Fig. 31, the variance increases proportionally with the mean. To this end, the square root transformation as suggested by Quenouille (1950) was appropiate because it reduced the skewness of the distribution and gave rise to a near normal form of distribution, which made the data amenable to analysis of variance.

The analysis of the transformed data using multiple regression (Quenouille, 1952) revealed the significance of heights of trees at the points of attack, and bark thickness on Ips cembrae number. The significant nature of the results (Tables 8 &9) indicates that the bark beetle density of attack in the five compartments decreases towards the tops of the infested trees, which is due to gradual decrease in bark thickness. The density of attack in the five compartments is not the same (Tables 10 & 11), although the behaviour of the bark beetle with /

with regard to height of tree at point of attack, and bark thickness follows the same direction. The variability in extent and degree of attack in the five compartments could be explained by the fact that the degree of susceptibility of the windblown larch to the bark beetle infestation varies from one compartment to the next. Windblown trees which have been lying in the wood for a while are more heavily infested by the bark beetle than fresh windblows which can still exhibit resistance to attack by exudation of resin.

The fact that the data collected from one square foot bark samples did not satisfactorily fit the negative binomial distribution indicate that that sample size was not sufficiently refined to define the distribution of the bark beetle,and was thereby liable to exceed in size many of the beetles aggregation. On the other hand, the data from the 6 x 6 square inches samples gave a good fit to the negative binomial distribution (Table 7). The contagious aspect of this type of distribution implies that where one beetle is found, there is a likelihood that some more will be found. A successful attack by Ips cembrae indicates that a tree or log has satisfied the bark beetle requirements and is suitable for the establishment of brood. It follows /

follows that the requirements for other bark beetles will be similarly satisfied by the tree or log or adjacent tree with the same favourable features. Bliss and Fisher (1953), Waters (1955) and others have shown that the negative binomial distribution is applicable to many insect problems of this type.

A number of workers have drawn attention to the great differences in temperature which may occur between ambient air and subcortical regions of the bark of trees. Many of these workers have also illustrated the effect of high subcortical temperatures on the behaviour of bark beetles. Graham (1924) illustrated a relationship between subcortical temperatures and the distribution of certain bark and wood-inhabiting insects on various aspects of slash. Beal (1934) has studied the relationship of air to bark temperatures of infested Ponderosa pine during sub-zero weather, and indicated the considerable protection from extreme low temperature given by the bark to beetles.

Results from the air and subcortical temperature investigations (Figs. 32-37) on larch trees infested by _Ips cembrae_ indicate that bark thickness is an important factor which determines the relation of air temperature to subcortical temperature /

temperature of infested trees in the field. Temperature under thin bark follows the trend of air temperatures, while thicker bark responds more slowly but attains higher temperature. The spread between air and bark temperature is governed chiefly by bark thickness and rate of temperature change. The lag in reaction of bark to air temperature changes depends principally on bark thickness. Subcortical temperature varies according to aspect, south sides of trees warm up rapidly for a short period during the day than the north sides, and subcortical temperatures rise higher than those on the north side of the same tree.

Analysis of data (Table 12) from bark samples on north and south sides of trees, which reached known temperatures in the field shows that south aspects of tree exhibiting higher subcortical temperatures than north aspects of the same tree are more attractive to adults of Ips cembrae.

Conclusions.

The results from population studies on the larch bark beetle, Ips cembrae, at the Ord Wood, Cawdor Estate, have thrown some light on the nature of the bark beetle distribution, and the effects of tree height and bark thickness on the beetle density of attack.

The contagious aspect of the bark beetle distribution is best described by the negative binomial distribution, which implies that the presence of one beetle in a bark sample increases the chance of finding others in the same sampling unit.

Analysis of sampling data for the effects of tree height and bark thickness on Ips cembrae population, indicates that the beetle density of attack decreases as the height of tree increases, also, the beetles infestation decreases in density with reduction in bark thickness of infested trees. This suggests that Ips cembrae prefers the thicker bark portions of trees at lower heights for breeding purposes, to the thinner bark portions towards the tree crown. Although the effects of tree heights and bark thickness on the beetles number follow the same general direction in the five compartments studied, there is apparent variation in the beetle density of attack in different compartments, /

compartments, as a result of differences in the state of susceptible trees. Future sampling programme in the area should be very intensive, so as to collect data that will reveal the relationships of different states of susceptible larch to incidence of attack by *Ips cembrae*.

The results from subcortical temperature investigation show that the relationship between bark and air temperatures is governed by bark thickness. The temperature under thin-barked trees tends to follow the trend of air temperature, but thick-barked trees attain higher temperatures than thin-barked trees.

It is apparent from the results of the investigations that there is variation in bark temperatures on the north and south sides of the same tree. The south side of the tree warms up rapidly during the day when the sun is shining on the bark, and subcortical temperatures rise higher than those on the north side of the tree. The south side, exhibiting higher subcortical temperature than the north side of the same tree is more attractive to *Ips cembrae*.

Appendix A.

The following is a list of insects found in association with Ips cembrae. The insects were identified using the keys of Joy (1923) and Brauns (1953).

A. Coleoptera

Cleridae : Thanasimus formicarius, L.
Predatory on adult Ips cembrae, usually found on bark of larch infested by the bark beetle.

Colyiidae : Rhizophagus depressus, F.)
Rhizophagus dispar, F.)
Small numbers were regularly found in the tunnel systems of Ips cembrae, destroying the eggs.

Nitidulidae : Epurea pusilla, III.
A few were found in the tunnel systems of Ips cembrae and have been observed feeding on the eggs.

B. Diptera.

Lonchaedae : (Lonchaea spp.))
Cecidomyiidae)
A large number of these dipterous larvae were observed in the tunnels of Ips cembrae in the winter period; they were predatory on the overwintering larvae, pupae and adult beetles.

APPENDIX B

Sampling data of *Ips cembrae* population at the Ord Wood, Cawdor Estate. Sampling unit : one square foot of bark.

Compartment 64.

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of Pupae per sample	No. of adults per sample	Total
0.35		5	4	-	14	18
0.75		10	2	4	25	31
0.55	41.5	15	4	2	18	24
0.50		20	6	5	20	31
0.40		25	2	2	14	18
0.80		5	2	-	28	30
0.75		10	4	10	25	39
0.65	44.5	15	2	4	16	22
0.35		20	-	2	13	15
0.50		25	5	2	20	27
0.30		5	3	-	10	13
0.35		10	8	-	6	14
0.45	44.0	15	12	4	4	20
0.40		20	15	2	13	30
0.25		25	6	5	5	16
0.50		5	10	-	8	18
0.55		10	8	-	12	20
0.40	41.0	15	12	5	10	27
0.35		20	6	8	6	20
0.30		25	2	2	4	8
0.55		5	-	-	5	5
0.65		10	-	-	4	4
0.70	47.5	15	5	-	13	18
0.45		20	6	-	2	8
0.70		25	-	-	6	6
0.65		5	-	4	22	26
0.65		10	-	1	19	20
0.55	43.0	15	-	2	12	14
0.45		20	-	3	16	19
0.40		25	8	-	8	16
0.50		5	8	-	28	36
0.45		10	6	4	28	38
0.35	46.0	15	4	2	22	28
0.40		20	3	6	18	27
0.55		25	-	-	3	3

Compartment 64. (Continued)

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.45		5	4	-	28	32
0.40		10	-	-	21	21
0.80	37.0	15	-	8	39	47
0.75		20	8	4	25	37
0.60		25	2	2	18	22
0.35		5	5	-	18	23
0.50		10	6	-	20	26
0.50	35.0	15	3	4	13	20
0.25		20	4	2	6	12
0.25		25	5	-	4	9
0.30		5	5	-	13	18
0.30		10	4	4	14	22
0.25	41.0	15	2	9	15	26
0.25		20	6	10	4	20
0.25		25	8	2	2	12

Compartment 65.

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.50		5	-	-	24	24
0.60		10	-	-	26	26
0.45	48.0	15	-	-	11	11
0.40		20	6	2	8	16
0.30		25	8	-	4	12
0.60		5	-	-	12	12
0.40		10	-	-	18	18
0.45	45.0	15	-	1	24	25
0.35		20	-	-	12	12
0.30		25	4	-	17	21
0.65		5	1	-	26	27
0.45		10	6	-	25	31
0.50	51.0	15	2	12	12	26
0.25		20	5	8	8	21
0.25		25	10	4	-	14
0.45		5	1	1	25	27
0.35		10	1	-	19	20
0.40	39.5	15	4	-	13	17
0.30		20	-	-	12	12
0.25		25	2	-	10	12
0.40		5	4	-	19	23
0.45		10	6	-	30	36
0.50	45.5	15	8	2	25	35
0.30		20	4	6	12	22
0.25		25	5	4	18	27
0.50		5	10	-	25	35
0.45		10	5	-	28	33
0.35	38.0	15	8	5	16	29
0.40		20	8	8	24	40
0.40		25	5	4	18	27
0.45		5	5	-	22	27
0.45		10	5	-	24	29
0.35	39.0	15	8	8	10	26
0.35		20	10	4	15	29
0.25		25	-	-	-	-
0.45		5	-	-	18	18
0.45		10	-	-	12	12
0.50	38.0	15	5	4	7	16
0.35		20	6	5	8	19
0.25		25	-	-	-	-

Compartment 65. (Continued)

Bark thick-ness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.45		5	-	8	8	16
0.45		10	-	8	-	8
0.50	41.5	15	5	5	-	10
0.35		20	6	-	12	18
0.50		25	7	-	15	22
0.50		5	6	-	12	18
0.50		10	6	-	6	12
0.40	41.5	15	5	1	5	11
0.35		20	4	1	8	13
0.50		25	1	10	15	26

Compartment 66.

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.35		5	-	-	25	25
0.35		10	-	-	23	23
0.40	48.0	15	-	-	28	28
0.35		20	-	-	11	11
0.35		25	-	-	5	5
0.60		5	12	-	12	24
0.55		10	6	-	-	6
0.50	42.0	15	5	-	-	5
0.60		20	-	-	4	4
0.55		25	-	-	4	4
0.45		5	6	-	-	6
0.30		10	12	-	4	16
0.50	41.5	15	-	-	12	12
0.55		20	8	-	8	16
0.50		25	-	-	6	6
0.45		5	12	-	9	2
0.30		10	-	4	6	10
0.30	36.5	15	-	-	5	5
0.25		20	8	-	4	12
0.25		25	-	-	4	4
0.75		5	12	5	18	35
0.70		10	8	4	12	24
0.60	37.0	15	5	2	4	11
0.65		20	-	4	10	14
0.25		25	-	-	-	-
0.55		5	5	8	6	19
0.50		10	8	4	-	12
0.40	47.5	15	5	-	2	7
0.45		20	4	5	5	14
0.30		25	6	-	9	15
0.25		5	4	5	13	22
0.30		10	8	-	12	20
0.40	42.5	15	6	6	8	20
0.40		20	-	-	4	4
0.50		25	-	8	8	16
0.50		5	8	4	13	25
0.50		10	8	8	8	24
0.30	37.5	15	13	6	5	24
0.40		20	5	-	12	17
0.35		25	-	-	-	-

Compartment 66. (Continued)

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.45		5	12	8	8	28
0.40		10	9	6	13	28
0.35	35.0	15	8	5	12	25
0.30		20	6	4	8	18
0.40		25	5	-	4	9
0.80		5	-	6	14	20
0.50		10	12	8	-	20
0.70	41.0	15	-	4	10	14
0.75		20	-	-	8	8
0.60		25	-	-	12	12

Compartment 67.

Bark thick-ness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.50		5	1	-	28	29
0.40		10	2	-	27	29
0.45	41.5	15	-	-	16	16
0.25		20	-	-	12	12
0.35		25	-	-	8	8
0.45		5	5	-	18	23
0.40		10	5	-	10	15
0.35	39.5	15	-	4	7	11
0.45		20	2	-	6	8
0.25		25	-	-	8	8
0.50		5	6	-	16	22
0.40		10	4	-	18	22
0.50	41.5	15	7	-	7	14
0.55		20	8	-	2	10
0.45		25	5	-	4	9
0.45		5	-	-	18	18
0.55		10	5	4	6	15
0.60	47.5	15	4	-	5	9
0.40		20	5	-	-	5
0.50		25	-	-	-	-
0.40		5	8	-	8	16
0.40		10	5	8	8	21
0.60	47.0	15	-	4	4	8
0.50		20	4	-	-	4
0.55		25	-	-	-	-
0.40		5	-	-	-	-
0.45		10	8	-	-	8
0.35	40.0	15	9	-	-	9
0.30		20	12	-	7	19
0.25		25	14	-	8	22
0.70		5	6	5	4	15
0.50		10	7	-	12	19
0.30	44.0	15	-	8	7	15
0.60		20	4	-	-	4
0.25		25	-	-	-	-
0.60		5	-	9	14	23
0.35		10	5	10	8	23
0.45	48.0	15	6	5	11	22
0.40		20	-	-	-	-
0.25		25	-	-	-	-

Compartment 67. (Continued)

Bark thick- ness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.30		5	5	8	25	38
0.50		10	6	4	8	18
0.60	41.5	15	7	-	7	14
0.40		20	5	-	-	5
0.45		25	-	5	-	5
0.80		5	12	12	-	24
0.70		10	10	4	10	24
0.60	40.5	15	8	-	8	16
0.30		20	5	8	-	13
0.50		25	-	-	11	11

Compartment 68.

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.45		5	-	-	6	6
0.50		10	-	-	4	4
0.35	41.5	15	-	-	2	2
0.25		20	-	-	1	1
0.25		25	-	-	-	-
0.50		5	-	-	8	8
0.45		10	-	-	2	2
0.30	37.0	15	2	-	-	2
0.25		20	-	-	3	3
0.40		25	-	-	2	2
0.30		5	8	4	6	18
0.50		10	6	3	5	14
0.60	42.0	15	4	2	2	8
0.40		20	2	4	-	6
0.25		25	-	-	2	2
0.40		5	5	-	7	12
0.35		10	8	-	3	11
0.25	37.0	15	4	-	5	9
0.40		20	-	-	8	8
0.30		25	-	5	-	5
0.45		5	8	-	9	17
0.50		10	10	-	6	16
0.60	42.5	15	6	-	4	10
0.35		20	7	-	5	12
0.30		25	-	-	-	-
0.50		5	2	5	1	8
0.25		10	4	-	5	9
0.25	45.5	15	-	-	-	-
0.40		20	-	-	6	6
0.30		25	-	-	4	4
0.30		5	5	-	13	18
0.60		10	-	8	8	16
0.50	42.5	15	-	-	10	10
0.40		20	6	-	-	6
0.40		25	-	-	2	2
0.55		5	8	-	8	16
0.60		10	-	-	15	15
0.60	42.0	15	-	4	9	13
0.50		20	-	-	12	12
0.25		25	-	-	-	-

Compartment 68. (Continued)

Bark thickness (ins.)	Length of tree (ft.)	Height of sample from tree base (ft.)	No. of larvae per sample	No. of pupae per sample	No. of adults per sample	Total
0.45		5	8	5	8	21
0.60		10	10	-	-	10
0.35	42.0	15	-	-	5	5
0.40		20	-	-	-	-
0.40		25	-	-	-	-
0.40		5	8	8	8	24
0.25		10	10	-	5	15
0.25	47.0	15	-	9	5	14
0.55		20	-	-	12	12
0.60		25	6	-	6	12

Sampling data of Ips cembrae population at the Ord Wood, Cawdor Estate. Sampling unit : 6 x 6 square inches of bark.

Compartment 64	Compartment 65	Compartment 66	Compartment 67	Compartment 68
No. of beetles per sample	No. of beetles per sample	No. of beetles per sample	No. of beetles per sample	No. of beetles per sample
23	5	17	4	3
30	1	1	7	13
22	16	-	2	5
20	9	7	6	8
22	11	-	20	6
24	13	-	3	2
20	8	5	10	6
27	7	2	14	2
10	16	4	3	4
23	6	6	9	12
16	13	6	5	2
16	20	-	-	30
24	4	18	7	13
28	8	10	9	-
18	15	11	26	7
6	2	-	12	-
-	9	7	25	3
5	19	19	3	6
-	2	2	12	1
4	4	5	9	2
11	9	1	15	12
1	-	7	3	6
8	2	4	10	-
3	9	-	13	19
2	1	-	3	1
2	1	4	8	3
1	17	9	3	10
10	1	13	26	6
4	5	5	3	25
21	7	11	2	20
1	1	7	3	1
-	4	4	15	3
28	6	10	5	15
-	16	21	2	1
-	9	5	14	17
5	11	4	2	2
27	8	14	-	4
11	-	5	14	18
1	4	4	12	3
6	11	30	1	1

Data (Continued)

Compartment 64	Compartment 65	Compartment 66	Compartment 67	Compartment 68
No. of beetles per sample	No. of beetles per sample	No. of beetles per sample	No. of beetles per sample	No. of beetles per sample
-	11	8	17	14
4	21	4	2	2
2	9	7	-	3
8	8	5	12	1
7	29	6	3	25
15	10	10	-	1
4	11	2	4	-
10	8	7	1	-
12	9	9	-	6
15	11	3	1	13

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