BULLETIN No. 41
O.D.C. 453

Commonwealth of Australia

Department of National Development
Forestry and Timber Bureau

# Sirex Noctilio and the Physiology of Pinus radiata

*Some studies of interactions between the insect, the fungus, and the tree in Tasmania*

By

M. P. COUTTS

FOREST RESEARCH INSTITUTE
CANBERRA, 1965

*Issued under the Authority of the Hon. David Fairbairn,
Minister for National Development*

G 78114—1

COMMONWEALTH OF AUSTRALIA

## DEPARTMENT OF NATIONAL DEVELOPMENT

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# FOREWORD

The woodwasp, *Sirex noctilio*, is a European insect which was introduced to New Zealand about sixty years ago, and became parasitic on a number of plantation conifers, including *Pinus radiata* from California. In the latter part of the decade 1940-1950, dry seasons were experienced in New Zealand and the Sirex wasps multiplied to epidemic proportions in the extensive plantations of *Pinus radiata* in that country. This caused concern among Australian foresters, entomologists and plant quarantine authorities, the fear being that if one of several species of Sirex wasps became established in Australia damage could be done to Australian coniferous plantations. The frequent occurrence of dry periods in Australia was thought to make the danger more real. In 1951 the Commonwealth Government, acting on representations made by the Australian Forest Services and other authorities, established a " Special Committee on whether precautions being taken against Sirex woodwasp should be intensified, maintained or relaxed ". This Committee took evidence on the question of Sirex wasps in all parts of Australia and New Zealand. Its report recommended the strengthening of quarantine regulations and the undertaking of research work on the problem by the Forestry and Timber Bureau.

In 1952 *Sirex noctilio* was observed in plantations of *Pinus radiata* near Cambridge airport in Tasmania. It is now realised that the insect must have been present in these plantations for several years before 1952. Studies of the infestation were commenced by the Forestry Commission of Tasmania and the State Department of Agriculture. Parasites of *Sirex noctilio* were introduced from New Zealand, and these have proved a most useful control measure in recent years. Efforts to prevent the spread of the wasp by quarantine measures were also undertaken with the co-operation of the Department of Health.

*Sirex noctilio* extended its range in Tasmania in spite of the local quarantine measures undertaken, and this caused further concern in mainland Forest Services and among Australian entomologists.

Early in 1961 the Forestry and Timber Bureau obtained approval for a tree-breeding research group to be attached to the research unit of the Bureau which had operated in Tasmania for many years in collaboration with the Forestry Commission. The functions of this group were the breeding or selection of strains of *Pinus radiata* which might be resistant to attack by Sirex.

In December 1961, the occurrence of *Pinus radiata* attacked by *Sirex noctilio*, in a suburb of Melbourne, was brought to the attention of the Forests Commission of Victoria. This discovery was considered to be a threat to the large area of pine plantations on the Australian mainland. A meeting of State and Commonwealth Ministers proposed that a National Sirex Fund be set up to provide funds for the early eradication of the Victorian occurrence, the ultimate eradication of the Tasmanian occurrence, and for research into the behaviour of the Sirex insect, control methods, and other aspects of the wasp in relation to forestry practice.

A National Sirex Fund was set up under the control of a National Sirex Fund Committee, with sub-committees to make recommendations on eradication and research respectively. The Research Sub-committee recommended that different aspects of the research programme could most appropriately be handled by three existing organizations which were equipped to do so, viz., the Division of Entomology, C.S.I.R.O., the Forest Research Institute of the Forestry and Timber Bureau and the Waite Agricultural Research Institute.

Early in 1962, the Forestry and Timber Bureau sought the acquisition of a site for a research station to act as local headquarters for work on Sirex and other research projects already being undertaken in co-operation with the Forestry Commission of Tasmania. The logical location was close to the Pittwater plantation (managed by Forestry Pulp and Paper Company of Australia Ltd.) and the Department of Civil Aviation agreed to grant permissive occupancy of an area on Hobart airport. Design and construction were put in hand and the building was occupied by the end of November, 1962. In the meantime, staff had been appointed by the Bureau or seconded by the Forestry Commission of Tasmania. Until the research building was available the staff occupied temporary quarters at Cambridge airport by courtesy of the Department of Civil Aviation.

Three phases of the problem are being attacked simultaneously:—

(1) the physiology of the pine in relation to the insect and its symbiotic fungus;
(2) the investigation of resistance aiming at the breeding of resistant strains of '*P. radiata*';
(3) the relationship between the pine, and the insect and the pathogenicity of the fungus.

This bulletin reports the work to date on the physiological phase which is being conducted by the Forest Research Institute and the Forestry Commission of Tasmania.

At the same time the Division of Entomology, C.S.I.R.O. is engaged on a large-scale programme of biological control, and on behavioural studies, while the Waite Institute is covering insecticides, attractants and lures, and the detail of the fungus itself.

D. A. N. CROMER,
Director.

Canberra, August, 1964.

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# SIREX NOCTILIO AND THE PHYSIOLOGY OF PINUS RADIATA

## Some studies of interactions between the insect, the fungus, and the tree in Tasmania

by

M. P. COUTTS *

## 1. INTRODUCTION

### (i) PREVIOUS WORK

*Sirex noctilio* is a native of Europe, where it is a comparatively uncommon insect. About sixty years ago, it was introduced to New Zealand, where it has been found in several tree species besides *P. radiata*, including *P. taeda*, *P. elliottii*, *P. echinata*, *P. muricata*, *P. ponderosa*, *P. patula* and *P. nigra*. It has also emerged from *Picea sitchensis* and *Larix decidua* (Rawlings and Wilson, 1949), and has been observed ovipositing on Douglas Fir, Rimu, Miro, Kauri and *Eucalyptus globulus* (Rawlings, 1948).

It is generally held to be a secondary insect, attacking weakened or dying trees, but between 1946 and 1950, it reached epidemic proportions in New Zealand. This has been attributed to overcrowding of the forest stands and a succession of droughts which followed several years of high summer rainfall (Rawlings and Wilson, 1949). The widespread mortality was partly attributed to Sirex and although the greatest proportion of deaths occurred in the lower crown classes, dominant trees were also killed and in a few places stands were left badly understocked.

In New Zealand, the habits of the insect, the damage it has done and its general forest relationships have been described chiefly by Rawlings (1948), Rawlings and Wilson (1949) and Jackson (1955). The important early observations on the habits of woodwasps and their parasites were made by Chrystal (1928, 1930), in England.

The literature on Sirex and its symbiotic fungus was surveyed at a recent conference at the Waite Institute at Adelaide (Warcup and Morgan, 1963), so only the bare outline will be given here. Buchner (1928) demonstrated that female siricids have a fungus in intersegmental sacs at the base of the ovipositor and Clark (1933) found this in S. noctilio. Parkin (1942) described the hypopleural organ on the first abdominal segment of the female larva, which also contained particles of fungus. The transference of the fungus from larva to adult has been studied by Franke-Grosman (1957).

Eggs and fungal arthrospores are injected into the tree, in tunnels drilled with the ovipositor. It is generally thought that the fungus kills the tree, and in some way helps to nourish the larva, but conclusive evidence is lacking.

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### (ii) PITTWATER PLANTATION

The Pittwater plantation, where the research is being done, is twelve miles east-north-east from Hobart in south eastern Tasmania. The plantation, and the first occurrence of Sirex there, have already been described by Gilbert and Miller (1952).

The plantation consists of trees a little over thirty years old (planted in 1929-35), and an area of dense regrowth about seven to nine years old, which developed after a fire. Most of the plantation is on stabilized sand dunes. The annual rainfall is approximately 24 inches.

Sirex was first found in 1952, but by then it was well established. After a few years it reached epidemic proportions and there are many reports of it buzzing around trees like swarms of bees. These may mostly have been males, but there are also reports of truck loads of logs being " black with Sirex ", as they were driven from the plantation to the local sawmill, and the females are a blue-black colour.

By 1962, when this work was started, the population had decreased to a low level. The increase and decline in the population followed a similar pattern to that in New Zealand and the causes are not well understood. The trees have been thinned by the insect (badly overthinned in places), and Sirex is now common only in the regrowth, where the trees are in a state of strong competition. Changes in the weather from year to year may be equally important, because the mating and flight habits of the insect are affected, as well as the condition of the trees. The parasites, *Rhyssa persuasoria* and *Ibalia leucospoides*, were first introduced in 1957 and 1959 by Mr. L. W. Miller, Government Entomologist.

### (iii) ASPECTS COVERED

Much of the research described in this paper is still in the early stages. Some of the experiments were only pilot tests designed to seek out the best methods of approach to problems about which very little is known. The work is concerned with techniques for physiological measurements, fundamental studies of the relationship of the insect and its associated fungus to the tree, and some more empirical field experiments designed to solve definite practical problems.

The work described here has been done on *Sirex noctilio* and *Pinus radiata*, so unless otherwise stated, every mention of Sirex and trees or logs refers to these species. For the sake of brevity, the phrase " Sirex females " will frequently be shortened to " Sirex ", and the associated fungus, which has recently been identified as an Amylosterium (Warcup and Morgan, 1963), will be referred to as the " Sirex fungus ".

## 2. MOISTURE CONTENT

### (i) MOISTURE CONTENT, CROWN CLASS AND THE SURVIVAL OF TREES

The death of trees from Sirex attack is known to be connected with suppression and drought (Rawlings and Wilson, 1949; Jackson, 1955; Rawlings, 1957). Stands most seriously affected by the New Zealand epidemic were often on the better sites; trees on normally moist sites are more severely affected by unaccustomed drought. Rawlings thought Sirex were unable to attack vigorous trees successfully, because the moisture content of their wood was too high for the Sirex fungus.

In 1963, counts were made in a 30-year-old stand at Pittwater, the dead and living trees being tallied by their crown classes. The dead trees were not felled for stem analysis, and some of them were certainly killed a few years before, so the estimation of their crown classes at time of death was rather difficult; but the following figures do give some idea of the distribution of Sirex attack in one compartment.

TABLE 1

THE DISTRIBUTION OF SIREX-KILLED TREES AMONG DIFFERENT CROWN CLASSES AT PITTWATER

| Crown Class | Number of Trees per Acre | | |
|---|---|---|---|
| | Living Trees | Dead Trees with Sirex emergence holes | |
| | | No. | Per cent. in each crown class |
| Dominant | 115 | 8 | 6 |
| Co-dominant | 49 | 15 | 23 |
| Sub-dominant and suppressed | 59 | 242 | 80 |
| Total | 223 | | |
| Gaps | 75 | | |
| Stumps of Thinned Trees | 90 | | |
| TOTAL | 388 | 265 | |

Some of the suppressed trees would have sickened anyway and were probably attacked by Sirex when they were dying, but it is clear that the dominant trees are the ones which survive best. The figures in table I refer to one of the least affected areas of the plantation.

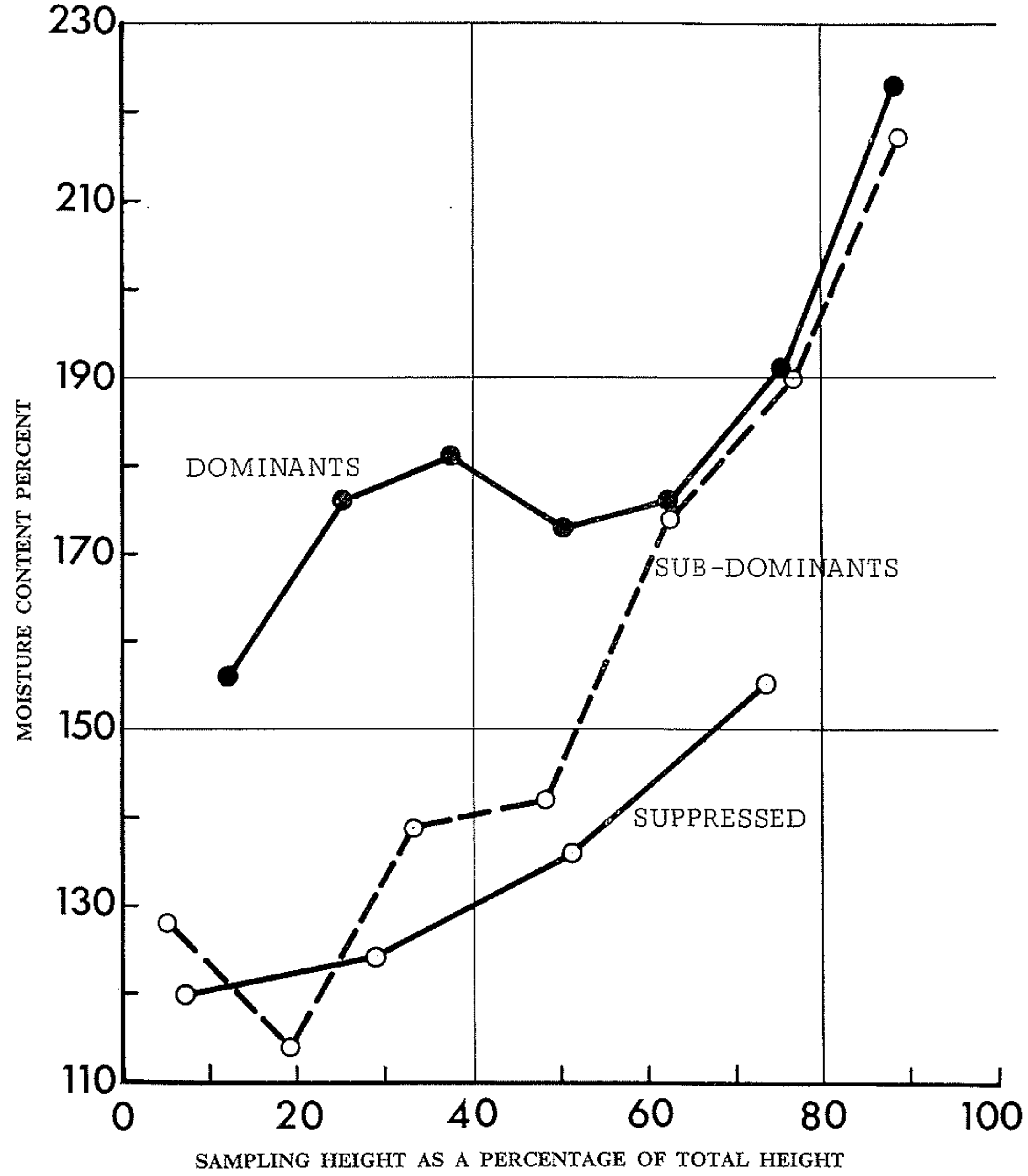

**Figure 1.**—Variation of moisture content (in the outer half inch of wood) with height, of trees of different crown classes.

Each line represents the mean of three trees, aged seven years

One factor connected with dominance is moisture content, suppressed trees often having a slightly lower moisture content than dominants (Hughes and Mackney, 1949; Fielding, 1952).

Nine trees were felled in the regrowth at Pittwater in November, 1962. The outer half inch of the wood was sampled when the diameter under bark was more than one inch. The moisture content generally increased with height, but for any height or any diameter, the dominants were wetter than the suppressed trees. Unfortunately, wood density was not measured. The results are shown in Figures 1 and 2.

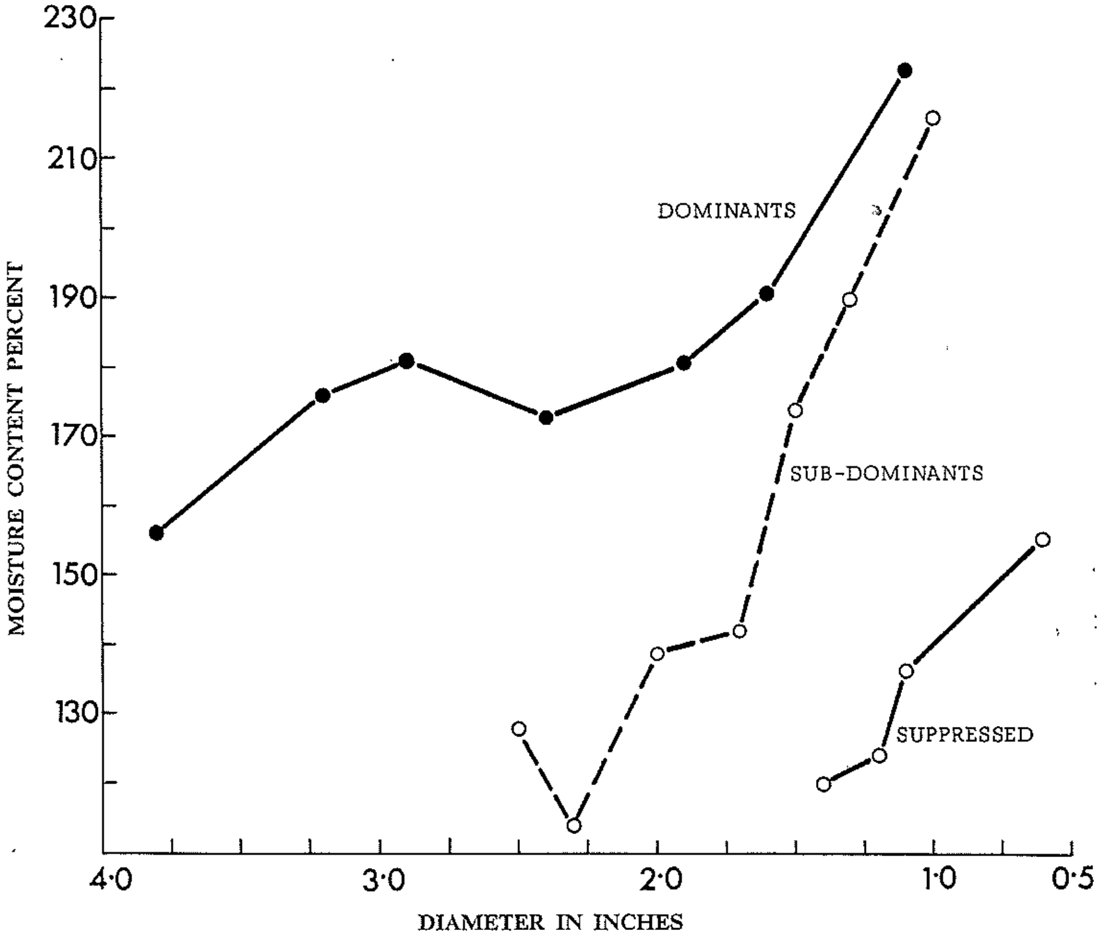

**Figure 2.—Variation of moisture content (in the outer half inch of wood) with diameter of trees of different crown classes.**

**Each line represents the mean of three trees, aged seven years.**

The moisture content of the outer annual ring of the tree may be more important in connection with Sirex attack than the outer half inch. In a 30 year old co-dominant, there was a steep moisture gradient in the outer layers. The outer annual ring, which was two to three mm. wide was much wetter than the outer quarter of an inch of wood (Figure 3).

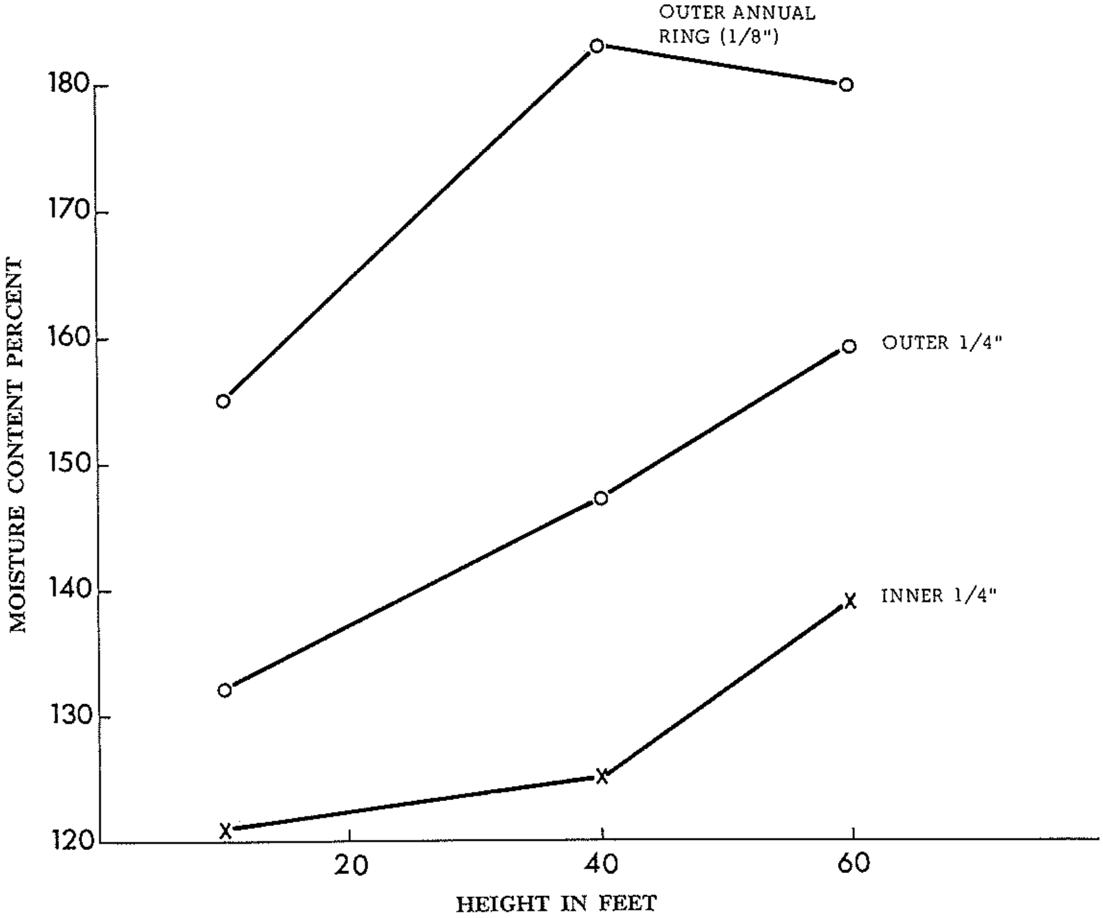

**Figure 3.—Variation in the moisture content of the outer layers of wood, at three different heights on a co-dominant tree aged thirty years.**

## (ii) TECHNIQUES FOR MEASURING MOISTURE CONTENT

Because of the supposed connection between Sirex attack and moisture content, various techniques for its measurement were tried.

When the female Sirex drills her oviposition tunnel it only penetrates the bark and the outer layers of the wood of the tree. The outer layers are often very much wetter than the inner sapwood. Various methods of sampling logs for moisture content were tried and the most satisfactory one is described as follows. Logs a foot long are cut in the forest with a chain saw, and sampled the same day in the laboratory. Discs one inch thick are cut with a bow saw—a chain saw gave inaccurate moisture content results for this. They are quartered with a butcher's chopper and a mallet. The outer layers of wood are then cut away from each quarter separately with a length of bandsaw blade with the teeth filed off and one side sharpened like a knife. It is held in a slotted wooden handle in which it can be adjusted to fit the curve of the log (Plate 1).

In this way annual rings can be cut cleanly from logs from quite eccentrically grown trees. The samples are weighed to ·001 gram on a Mettler H4 balance and oven dried at 100 degrees centigrade for three days. They are then cooled in desiccators and reweighed.

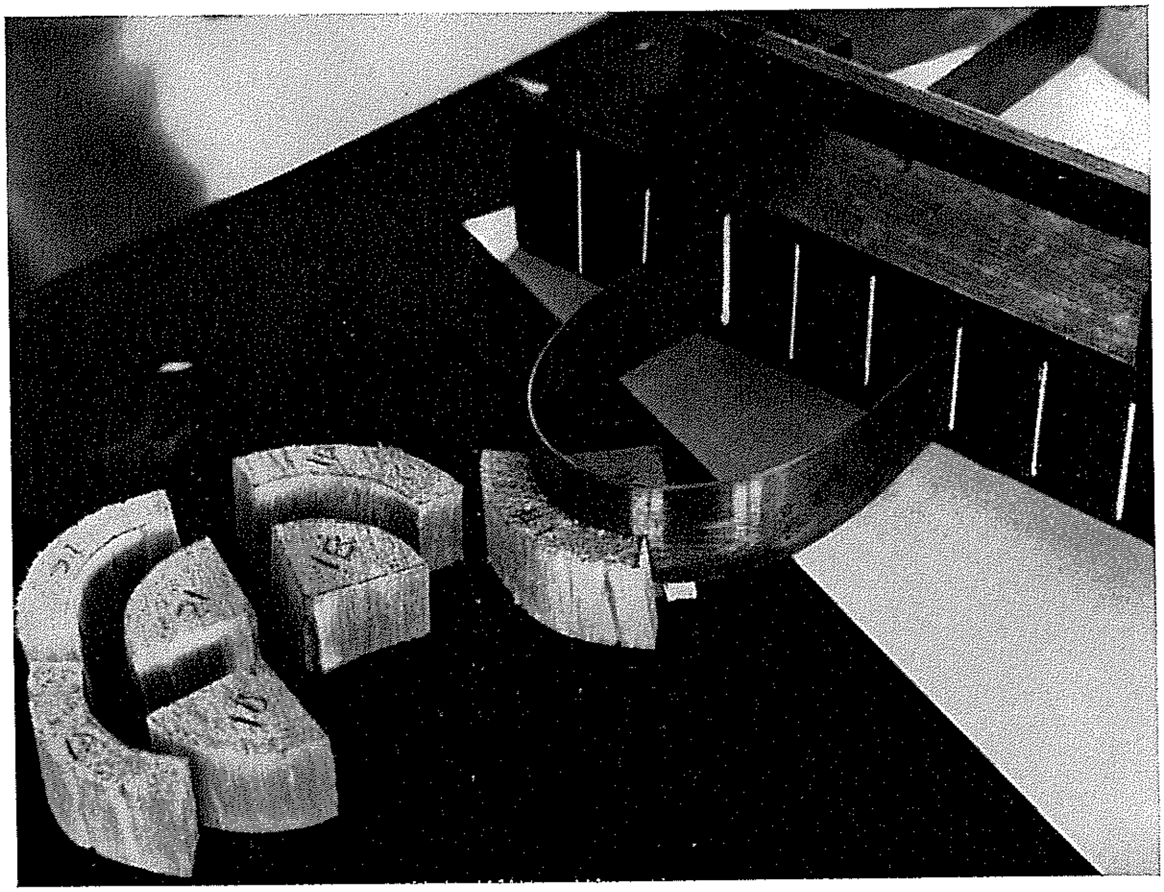

Plate 1.—The apparatus used to separate layers of wood along the annual rings.

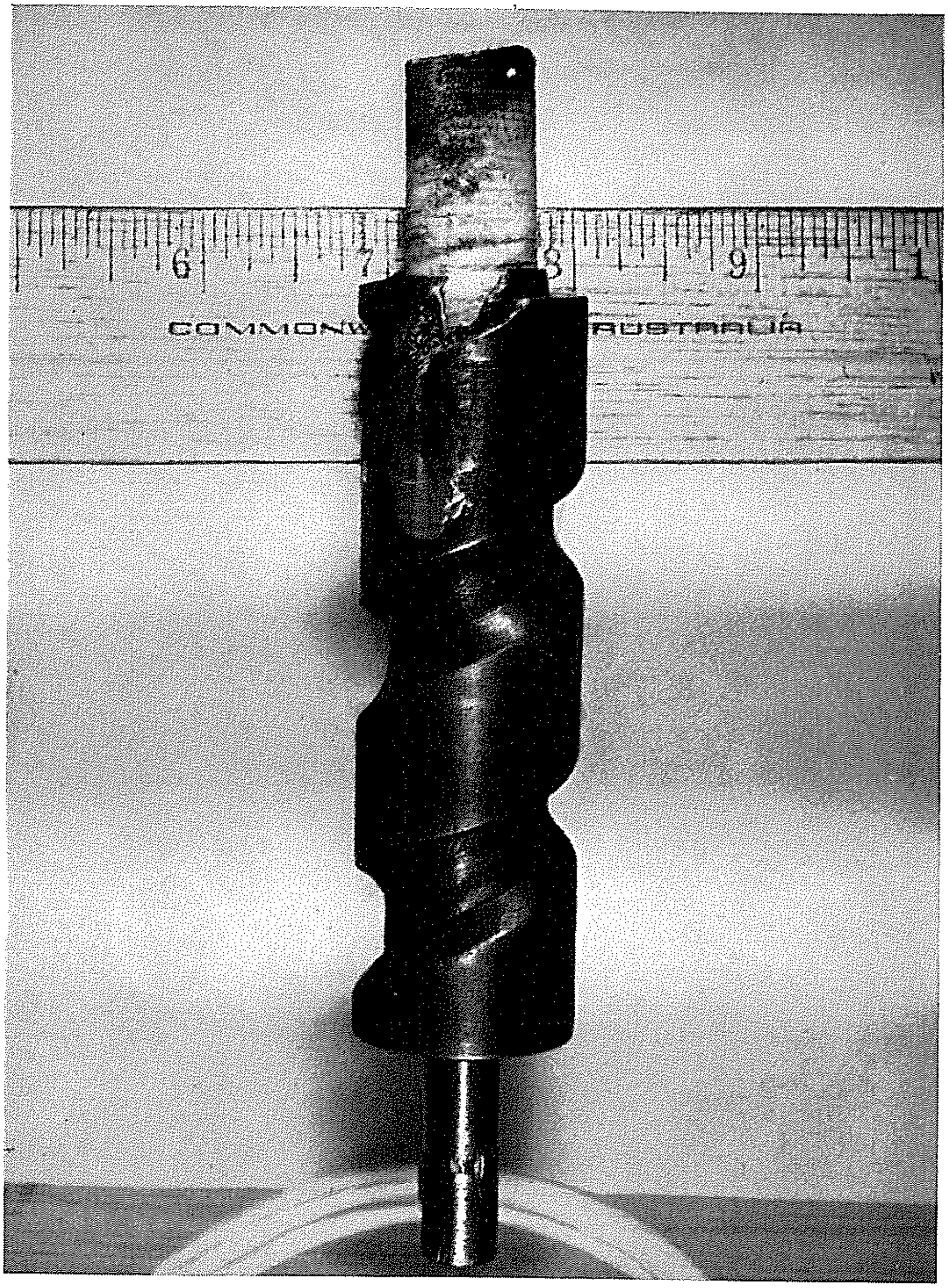

Plate 2.—Special bit designed to cut cores about ¾-inch diameter.

For more accurate results, more discs are cut from the sample log. After the first disc has been sampled, an inch is sawn from the log to get rid of the exposed surface which will have dried in the meantime and another disc cut. If the outer half inch of the log is sampled, the difference between the moisture contents of two discs, one inch apart, is usually less than 4 per cent., for corresponding quarters.

The moisture content of standing trees is much more difficult to measure, if the trees are not to be badly injured. Electric moisture content meters can only be used effectively at low moisture contents. An increment borer was used with some success by Huckenpahler (1936), but when it was tried at Pittwater the method gave erratic and generally low results compared with the samples taken by cutting discs. Gibbs (1957) sampled twigs using double cutters to prevent water loss through sap tension. He also tried banging a metal punch into the tree to extract a core. With *P. radiata* a punch compressed the wood and squeezed water out of the sample.

A power tool for cutting cores was suggested by Dr. D. A. N. Cromer as being the most promising approach. Yelft (1962) describes a power increment borer, but it is a cumbersome apparatus and the cutting bit would heat the core too much for moisture content work. The requirements of a good core-cutting tool are that it must cut above and below the core more or less simultaneously to avoid water loss by sap tension; it must not heat the core by friction, and it must not squeeze it or get jammed with sawdust. It must be light enough to use near the tops of trees.

After several failures a suitable bit was developed (Plate 2).

Some of the earlier efforts were satisfactory at low moisture contents, but large inaccuracies appeared when they were used in wet wood (the outer half inch of *P. radiata* often has a moisture content of more than 200 per cent. of its oven-dried weight). The tool now used makes a hole in the tree $1\frac{1}{4}$ inches in diameter and cuts a core with a diameter of $\frac{11}{16}$ of an inch. (It will cut quite long cores, but normally only the outer quarter inch or outer half inch have been sampled in experiments connected with Sirex.) The curved cutting teeth cut a kerf for the bit to revolve in, slightly wider than the body of the tool. The chisel tooth is set at an angle so that it cuts the inside of the shaving before the outside, turning it out into the spiral. The inside of the bit is reamed out to give a small clearance round the core. It is used in an electric drill supplied from a petrol-driven 240-volt generator through 100 feet of flex. The bark is removed from the cores which are put in weighed bottles with plastic stoppers.

Another method involving the interception of gamma rays was suggested by Dr. B. I. H. Scott, Lecturer in Biophysics, University of Tasmania. A radio-active source was held on one side of the tree and gamma rays were picked up by a geiger counter on the other side. The amount of interception is related to the density of the body and hence to the moisture content of the tree. The method appeared quite promising but was discontinued after the bit described above was made. It would not have been possible to sample the outer layers. The method could only give a mean moisture content figure for the whole thickness of the tree.

## (iii) MOISTURE CONTENT AND THE SURVIVAL OF SIREX EGGS AND LARVAE IN LOGS

### (*a*) Methods Used

Two experiments have been carried out using logs in an insectory. For the *first experiment*, in February, 1962, fifty six-foot logs were collected from Stoodley plantation in Northern Tasmania. They were not collected locally from Pittwater to avoid any previous Sirex attack. They were taken from the tops of trees thinned between October, 1962, and February, 1963, to give a range of moisture content and two trees were freshly felled to give the wettest logs. The logs were sampled at both ends by the disc method. They ranged from 20 to 204 per cent. moisture content in the outer half inch. The logs were put in an insectory with female Sirex. It was hoped to find out if the Sirex would attack logs of certain moisture contents in preference to others and 500 female Sirex were required. When the logs were put in the insectory, only a small number of Sirex were available, so chance attack outweighed any preference the insects might have shown.

The ends of the logs were greased to prevent rapid drying out, but blue stain appeared in some of them, so instead of keeping all of them to find how many Sirex would emerge the following year, some of the oviposition tunnels were dissected to see how many eggs and young larvae had survived.

Cores were cut from the logs with a hole saw with modified teeth. The cores need to be one inch wide, so that when the outer end of a slanting oviposition tunnel is in the middle, the inner end will not extend beyond the edges of the core.

The *second experiment* was started in March, 1963. Short logs about four inches in diameter were cut from vigorous trees about eight years old. They were sampled for moisture content and the ends of the logs were flamed off before they were greased, to keep out blue stain. To get a range of moisture contents, trees were cut and stood up complete with branches, against a fence for various lengths of time to dry. To get very dry logs, some trees were brought indoors and dried with a hot fan. The moisture content ranged from 10 to 215 per cent. The logs were placed singly in a cage, each with about six small to medium sized, freshly emerged Sirex females.

Some of the logs were sampled at intervals to find how long it would take for the eggs to hatch and some observations were made on the development of the eggs.

### (*b*) EARLY DEVELOPMENT IN THE OVIPOSITION TUNNEL

The egg is about 1 mm. long and is usually placed well down towards the end of the oviposition tunnel. If two eggs are laid in a tunnel (see 3 (iii)) they are normally a millimetre or more apart. Sometimes the outermost egg is laid right at the beginning of the tunnel and can be seen as soon as the bark is removed.

The new laid egg is a bag of fluid. The fluid thickens to a jelly and eventually the larval segments and head become visible under the microscope. Before hatching, the head and anal spine darken.

Fine white hyphal threads of the symbiotic fungus become visible criss-crossing the tunnel a few days after oviposition. By the time the egg is ready to hatch, the shell often appears to be invested with a network of strands continuous with the fungal hyphae.

The egg is laid so that the anterior end of the larva is facing to the outside of the tree. Some newly hatched larvae have been found facing outwards, but soon after hatching the larva is found in the oviposition tunnel facing inwards, so presumably it turns a somersault in the tunnel. If the mature egg is burst with a needle, the larva sometimes pops out with its body arched over backwards. Soon after hatching the larva starts to tunnel, either upwards or downwards. Less than the whole eggshell seems to be present in the oviposition tunnels at this stage. The larva probably eats part of it, but it has not been seen doing this.

In warm summer weather the eggs hatch in about two weeks. (Zondag (1959) found they took at least nine days to hatch, at 20° C. in New Zealand.) In the first moisture content experiment, when the mean temperature was 61° F. (mean maximum 71°, mean minimum 51°), hatching took three to four weeks. In the second experiment, done in the colder weather of March, at a mean temperature of 55° F., but with some low night temperatures, the first eggs took two months to hatch and some took nearly three months. Soon after the young larva begins to bore its way out of the oviposition tunnel it sheds its skin, which is pushed back towards the tunnel or right into it.

### (*c*) THE SURVIVAL OF EGGS AND LARVAE AT VARIOUS MOISTURE CONTENTS

In the first experiment, 344 oviposition tunnels were dissected in which 192 eggs had been laid. Some were examined before hatching, but most a week or two after hatching. Nineteen eggs (10 per cent.) died before hatching and of the 173 young larvae, eight had died during their first instar. At the time of writing (March, 1964), Sirex are emerging from most of the logs.

In the second experiment, 697 tunnels were dissected, in which 442 eggs had been laid. Thirty-three per cent. of the eggs died before hatching and, of larvae 23 per cent. died at first instar, usually before leaving their oviposition tunnels. Of the larvae which had reached or passed second instar by the time they were dissected out, only four per cent. died; three at second instar and one at fourth instar. Thus about half the eggs laid developed into larvae at or beyond second instar, after which there was very low mortality (see 5 (i) also). The much higher mortality in the logs used in this second experiment, compared with the one in which the tops of trees were used, may be connected with the lower temperatures and the longer time taken for hatching and development in March and April.

In both experiments, the moisture contents of the logs, both at the time of oviposition and at the time of dissection for eggs and larvae, showed no correlation with survival at any moisture content above 30 per cent. All the eggs laid in a log with a moisture content of 26 per cent. died before hatching. At moisture contents below 20 per cent. no eggs were laid. Logs dry very slowly, if their ends are greased. The following figures are for three logs used in the second experiment. The later samples were taken well away from oviposition holes. The ends of the logs were re-greased after each sampling.

*The change in moisture content per cent.* (*outer half inch of wood*) *of three logs, with time*

| *First Sample* | *After* 56 *days* | *After* 122 *days* |
|---|---|---|
| 220 | 186 | 167 |
| 138 | 118 | 86 |
| 32 | 26 | 23 |

The wood of a tree felled in November containing Sirex larvae felt very dry and was sampled for moisture content in the neighbourhood of the larvae. It was 26 per cent. The larvae were small, but appeared healthy. This is in close agreement with the findings of Clark (1933) in New Zealand. He measured the moisture content of the wood near larval galleries and it varied from a minimum of 27·3 up to 41·6 per cent.

One attempt made to discover the lowest moisture content at which larvae can survive failed. Logs nine inches in diameter and containing large larvae were collected in November, 1963. They were cut into four foot lengths and left with a fan heater for four weeks to dry out from the ends. The logs were then sawn into discs inch by inch, to find the region containing living larvae, it being supposed that they would have died in the very dry ends. Larvae which had been boring towards the ends had turned around and worked back into the middles of the logs, where the moisture content was 26 per cent. No dead ones were found. The middles of the logs were then cut out and left to dry, but the larvae promptly pupated.

### (*d*) THE EFFECT OF BLUE STAIN ON SURVIVAL

Blue stain fungi grow quickly and if the wood around an oviposition tunnel becomes infected, the egg dies. If the blue stain enters a log some time after oviposition, and the Sirex fungus has time to develop, the blue stain is often unable to spread, and long narrow islands of whitish wood with an oviposition in the centre of each can be found in a sea of blue stain. The eggs may hatch under these circumstances and the larvae would probably perish on tunnelling into the contaminated wood, but this has not been demonstrated. If Sirex is well established in a log, blue stain may be kept out indefinitely. Sirex was allowed to oviposit heavily on one side of a log, the other side being protected by aluminium foil. The log was left with its cut ends exposed and blue stain soon spread through the side where there was no oviposition, from end to end of the log. After two months, it had still failed to penetrate the half of the log which had been oviposited. This has also been noticed in the tops of felled trees (see 2 (iv, *e*)).

If a log which has been oviposited is peeled a week or so afterwards, blue stain is often seen spreading from oviposition punctures. Spores from the bark are probably carried into the wood on the ovipositor. To see if larvae will tunnel and survive in wood with blue stain, logs from a young tree which had been killed by Sirex were squared off and encased by slabs of wood full of blue stain, planed to fit closely. They were then wrapped in polythene to prevent excessive drying. None of the larvae left their parent log and ventured into the blue stain. Several of them pupated and the adults had to tunnel through the blue stained wood in order to get out. This they did apparently without ill effects. Several Ibalia emerged in the same way. The blue stain did not spread from the slabs of wood into the logs to which they were nailed.

## (iv) THE DRYING OF TOPS AND SIREX ATTACK

### (*a*) GENERAL

The tops of felled trees provide suitable material for Sirex to breed in. The population can build up more or less unnoticed and then turn to living trees. Experiments are being done to find the rate of drying of tops under clear felling conditions at Pittwater and to give information on the amount of attack on tops and the survival of Sirex in them. The tops are all from trees about thirty years old.

### (*b*) SAMPLING METHODS

Eighty-four tops from trees felled in December, 1962, were marked on the days when the trees were felled. Nine tops were sampled for moisture content the day they were felled. At various numbers of days after felling, groups of six other tops were sampled (i.e., different tops were used each time, because they were spoilt by sampling). This was repeated in the months which followed.

The tops had an average diameter of 6.4 inches at the butt end and an average length of twenty-five feet.

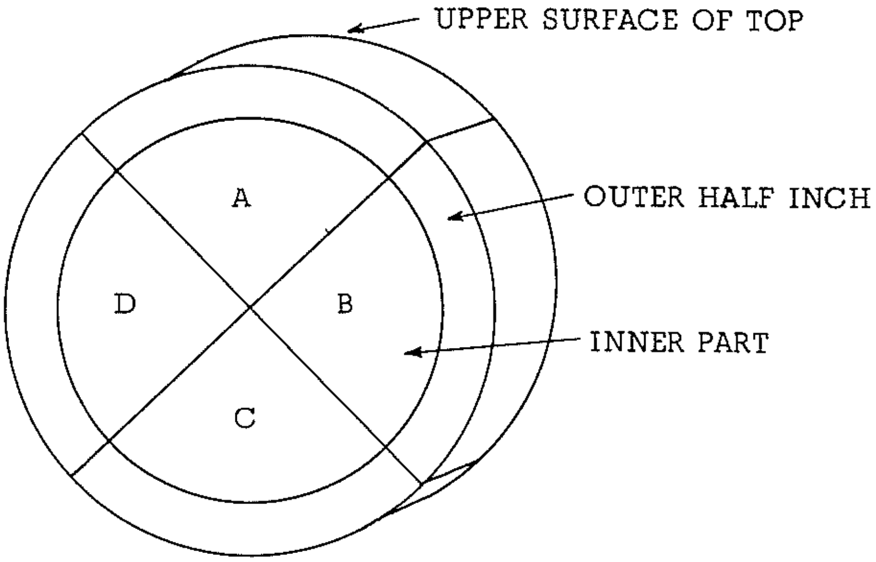

**Figure 4.—Diagram to show how discs were sampled when measuring the moisture content of tops.**

They were sampled for moisture content by the disc method in three places:—

(1) Butt sample, taken two feet from the cut end;

(2) Tip sample, taken where the diameter was 3 inches;

(3) Middle sample, half way between (1) and (2).

The upper side of each sample log was marked and the discs divided as shown in Figure 4.

### (*c*) RATES OF DRYING

The mean rates of drying of groups of tops from trees felled in different months, are shown as curves of decreasing moisture content against time, in Figure 5.

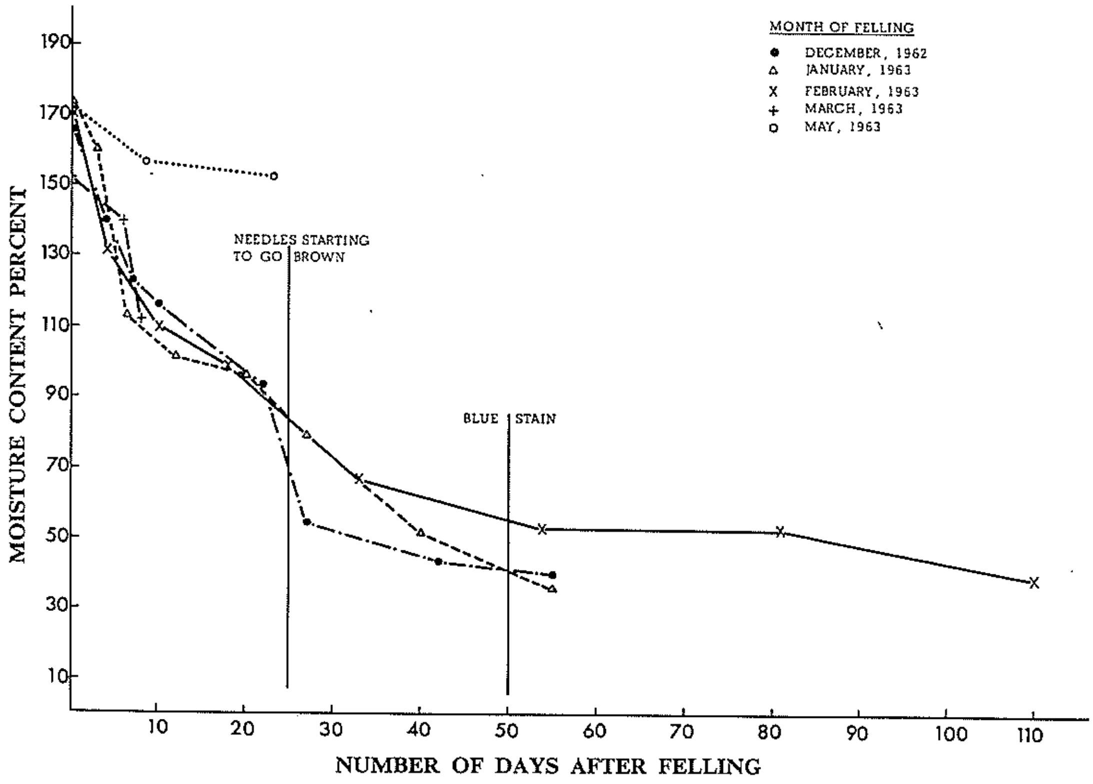

**Figure 5.—The moisture content of the outer half inch of wood, two feet from the butt end. Each point is the mean for six or more tops**

Drying is very rapid to begin with in the summer months, and gradually slows up as the top dries out. The tip of a fresh top is rather wetter than the butt, on average, but it dries more quickly and soon falls below the butt in moisture content.

The middle dries at a rate intermediate between that of the butt and tip. The upper side of the top dries more quickly than the underside, but by the time the moisture content reached about 50 per cent., they become equal again. The outer half inch is wetter than the inner part to start with, but these two become about equal when the moisture content reaches 50 per cent.

During the winter, the moisture content fluctuates between 30 and 50 per cent., depending on the weather. By the time Sirex emerge the following summer, the moisture content is usually about 20 per cent.

Tops of six trees felled early in September, 1962, were sampled in mid-January, 1963. Their mean moisture content was 41 per cent. The wettest top was 61 per cent. and the driest, 23 per cent. None of them was attacked by Sirex.

*Sources of variation*

The method of sampling by taking discs is accurate on fresh tops, and several discs cut close together give very similar results; this also applies to very dry tops of 30 per cent. moisture content or below. But when drying is in full swing, the tops are often wet in patches and quite a lot of variation is encountered, especially near branch whorls and where the bark is bruised or broken.

The original moisture content varies from top to top. Some of this variation is shown in Table I. There were nine tops in each monthly sample.

TABLE I

THE RANGE OF MOISTURE CONTENT AMONG THE TOPS OF FRESHLY FELLED TREES

| Date of Felling | Mean Moisture Content of Outer half inch, when freshly felled. Mean for 9 tops. | Driest Top | Wettest Top |
|---|---|---|---|
| December, 1962 .. .. | 172 | 141 | 178 |
| January, 1963 .. .. .. | 181 | 159 | 217 |
| February, 1963 .. .. .. | 176 | 169 | 198 |
| March, 1963 .. .. .. | 165 | 156 | 195 |

There is some variation in moisture content on different sides of a tree. The wettest side, as sampled by the method of cutting discs into quarters is usually opposite the driest side. In freshly felled tops, the average difference between the wettest and driest sides in the outer half inch at the butt is 15 per cent. and varies from 2 per cent. to more than 30 per cent.

After drying has started, the greatest source of variation between tops is exposure. Tops which are shaded by trees dry out much more slowly, which could be important for thinning (see Table II). Tops which are covered over by other tops also dry out very slowly. Most of the water loss in the early stages of drying takes place by transpiration through the needles; the density of the branches and foliage also appear to affect the rate of drying.

TABLE II

THE MOISTURE CONTENTS OF TOPS FROM A SECOND THINNING AT STOODLEY PLANTATION, MEASURED IN FEBRUARY, 1963. THE FIGURES ARE THE MEANS OF BUTT AND MIDDLE SAMPLES

| Date of Felling | No. of days after felling | No. of tops sampled | Mean Moisture Content | | No. of tops with blue stain |
|---|---|---|---|---|---|
| | | | Outer half inch | Inner Part | |
| 22-2-63 | 1 | 6 | 181 | 168 | 0 |
| 19-2-63 | 2 | 4 | 166 | 170 | 0 |
| 13-2-63 | 8 | 4 | 160 | 153 | 0 |
| 11-2-63 | 10 | 6 | 160 | 153 | 0 |
| 30-1-63 | 23 | 4 | 139 | 123 | 0 |
| 19-12-62 | 73 | 5 | 72 | 66 | 3 |
| 6-11-62 | 107 | 4 | 72 | 67 | 1 |
| 16-10-62 | 123 | 2 | 53* | 67* | 2 |

* The mean is misleading here. One top was 25 and 30 per cent. M.C. in the outer and inner parts respectively and the other was 81 and 104 per cent. Both had patches of blue stain.

The diameters of the Stoodley tops varied from three to four inches at the butt ends. The figures for tops felled in January and February lie well above the lines on Figure 5 for clear felling at Pittwater.

Diameter showed no relation to the rate of drying within the range encountered at Pittwater, but any correlation could be masked by the other sources of variation.

### (*d*) OVIPOSITION

The C.S.I.R.O. co-operated in this experiment by examining the sample logs cut for moisture content determinations, for Sirex attack. Counts of oviposition tunnels were made and converted to figures per square foot.

The first ovipositions found on tops for each month of felling at Pittwater were as follows :—

| *Date of Felling* | *First ovipositions found* |
|---|---|
| December, 1962 | 22 days after felling |
| January, 1963 | 5 days after felling |
| February, 1963 | 12 days after felling |
| March, 1963 | 5 days after felling |
| April, 1963 | 3 days after felling |

Quite heavy attack was recorded a week after felling on several tops, by which time the mean moisture content lay between 110 and 130 per cent. However, the first tops of any month of felling to be attacked, generally had moisture contents below the means of the groups from which they were taken. Very wet tops were not attacked.

The number of tops attacked is shown in Table III.

TABLE III

THE NUMBERS OF TOPS ATTACKED, FROM DIFFERENT MONTHS OF FELLING

| Date of felling | No. of tops sampled a week or more after felling | No. Attacked | Percentage |
|---|---|---|---|
| December, 1962 | 36 | 7 | 19 |
| January, 1963 | 48 | 17 | 35 |
| February, 1963 | 65 | 30 | 46 |
| March, 1963 | 15 | 3 | 20 |
| April, 1963 | 36 | 3 | 8 |

The figures are conservative. Other tops could have been lightly attacked, the Sirex having missed the parts of the logs which were sampled.

A fire in March, 1963, destroyed all but the February felled tops.

The low percentage of December felled tops which was attacked would be due mostly to the emergence of Sirex increasing later in the summer. Of the tops felled in December and sampled in January (i.e., excluding those sampled during December), seven out of twenty-four (29 per cent.) were attacked. The fellings mostly took place in the first week in each month. The large number of February felled tops which were attacked may be accounted for by their proximity to the regrowth where Sirex were plentiful.

During April there were few Sirex about in the felling area. None of the tops felled in September, 1962, or May, 1964, were attacked.

The heaviest oviposition is at the butt ends of the tops. The figures in Table IV are percentages of the mean density of oviposition tunnels per square foot, for the three positions of sampling.

TABLE IV

DISTRIBUTION OF OVIPOSITION TUNNELS ALONG THE LENGTHS OF TOPS ATTACKED BY SIREX

| Month of Felling | | Butt | Middle | Tip |
|---|---|---|---|---|
| December . . . . | Mean number of oviposition tunnels per sq. ft. . . | 173 | 70 | 15 |
| | Ratio . . . . | 11·5 | 4·7 | 1 |
| January . . . . | Mean number of oviposition tunnels per sq. ft. . . | 55 | 28 | 5 |
| | Ratio . . . . | 11·0 | 5·6 | 1 |

In later months, sampling the middles of the tops was discontinued.

Most of the oviposition is on the undersides of the tops, shown by the counts on the A, B, C and D quarters of the sample logs.

TABLE V

PERCENTAGE OF OVIPOSITION TUNNELS COUNTED ON SAMPLES FROM TOPS FELLED BETWEEN DECEMBER, 1962 AND MARCH, 1963

| A<br>Upper Quarter | B<br>Side | C<br>Under Side | D<br>Side |
|---|---|---|---|
| 3 | 14 | 56 | 27 |

The upper surface of the logs does dry out more quickly than the underneath, but the difference is not likely to be great enough to affect Sirex eggs or larvae, with their wide tolerance of moisture content. On hot summer days, the upper surfaces of logs in the open becomes so hot, it can be painful to rest one's bare arm on them. Temperatures in the outer layers of wood have not been measured. Sirex which have been observed on tops, run straight underneath; they do not attempt to maintain a vertical position on the sides of the logs, with head going upwards or downwards as they do on trees, but generally drill their oviposition tunnels while facing approximately along the axis of the top. When they walk out on the side of the top, they rarely walk above the half way mark; the ovipositions on the B and D samples are mostly on the parts curving underneath.

The light oviposition on the narrow ends of the tops as opposed to the butt ends may be a reaction of the insect to diameter. It is not unlike the pattern found in standing trees. The proportions of single and multiple tunnels (see 3 (i)) were not recorded.

The actual amount of attack is generally much lighter than on standing trees of comparable size. On the tops felled between December and March and attacked by Sirex on the undersides at the butt ends, the mean density of oviposition tunnels was only 62 per sq. ft. Because of their rapid rate of drying the tops probably pass quite quickly through an attractive stage (see 3 (viii)).

Most emergence from tops takes place from the underneath and sides. Emergence from tops felled and attacked in February, 1963, started at the end of January, 1964, and plenty of Sirex were still emerging in mid-March. The tops often have between 100 and 300 flight holes in them.

### (*e*) BLUE STAIN IN TOPS

Blue stain becomes abundant in summer-felled tops at Pittwater about seven weeks after felling, when the mean moisture content is about 50 per cent. According to Da Costa (1959), blue stain fungi cannot attack very wet wood, nor can they grow in wood below 25 per cent. moisture content. They grow quickly in an intermediate moisture content range.

The blue stain generally comes in on the undersides of the logs. Bark is usually damaged most underneath. It also enters at the cut end, at branch whorls and at the broken tips. All tops are attacked by it. If Sirex becomes well established in the underside of a top before it is invaded by blue stain, the blue stain is prevented from spreading. The blue stain eventually invades the upper half of the top, and a cross section often shows the upper part blue and the lower part yellow, with a sharp dividing line between. Most tops from trees felled some months before Sirex emerges, if they are still attractive from the point of view of freshness or moisture content, would probably be unsuitable on account of blue stain. Many of the tops of trees felled in September and sampled the following February had so much blue stain that the survival of Sirex in them would be impossible.

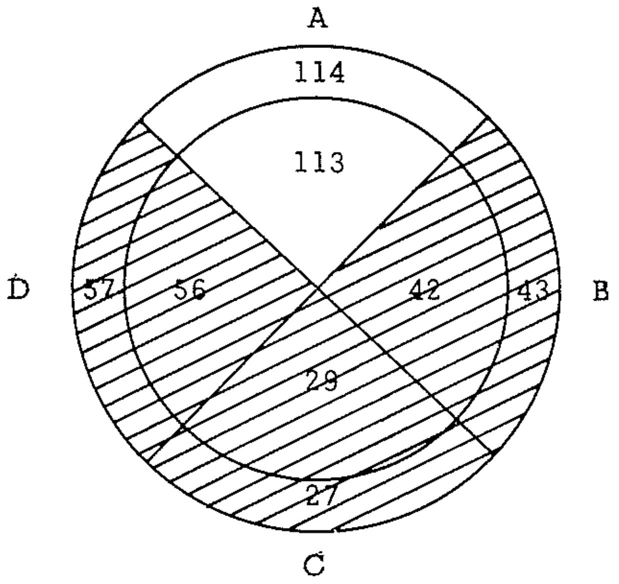

FIGURE 6 A SAMPLE DISC CUT IN FEBRUARY FROM A TOP FELLED IN DECEMBER. THE FIGURES ARE MOISTURE CONTENT PERCENT. THE SHADED PART WAS FILLED WITH BLUE STAIN.

Wood samples filled with blue stain are often much drier than surrounding, uninfected wood. A typical example, from a December top sampled eight weeks after felling, is shown in Figure 6.

Bethge and Lindgreen (1962) mention that during the seasoning of wood, fats are hydrolized and unsaturated fats and resin acids are oxidized. They found that the dry weight of a spruce log increased from 56·5 to 85·1 per cent. during six months' storage in a cool dry room. Fats can be split by lipase which is produced by blue stain fungi. This may help to dry the wood. Of wood filled with blue stain fifty-seven per cent. has been the highest moisture content found.

Blue stain fungi live in the phloem as well as in the wood and the bark flakes and peels off, whereas the bark of the parts of logs attacked by Sirex sticks closely to the wood.

### (v) Oviposition and the Drying of Wood

If the bark is peeled off some time after Sirex has oviposited in a tree or log, narrow streaks of pale coloured wood will be exposed, running with the grain above and below the oviposition sites. When double and treble oviposition tunnels are made (see 3 (i)), separate streaks can sometimes be seen coming from each individual tunnel in the early stages, but they soon combine. These streaks are often overlaid on the surface of the wood by a brown stain which is also present in the bark. The pale streaks appear to be drier than the rest of the wood, but they are rather small to sample for moisture content determinations. It was supposed that the drying might be caused by evaporation through the oviposition hole in the bark, so the following experiment was carried out.

A log from a young dominant tree was cut into three short lengths and discs cut between them for moisture content sampling. The outer half inch was sampled. The moisture content was 200 per cent. and quite even all round the log. The ends of the logs were greased and one side of each log was covered with aluminium foil. Sirex were allowed to oviposit heavily on the exposed sides of two of the logs in a cage. The exposed side of the third log (taken from between the other two) was punctured all over to a depth of half an inch with a No. 80 drill, which is slightly thicker than a Sirex ovipositor. The tinfoil was removed and after two weeks the bark was peeled from two of the logs. The log which had been artificially drilled had minute white streaks with a small speck of brown stain round each drill hole. The log oviposited by Sirex had the brown stain over most of the surface on the side which had been attacked. It had not spread laterally to the protected side of the log. Discs were cut for moisture content sampling, and the drilled or oviposited sides and protected sides were sampled separately. The side of the log which had been drilled and its protected side, both gave values close to their original moisture content of 200 per cent. and the side which had been protected from oviposition on the other log also had a moisture content of 200 per cent. The outer half inch of the side which had been oviposited, however, had a moisture content of 119 per cent. Four days later the third log was sampled. On the oviposited side the outer half inch had been reduced to 101 per cent. moisture content and on the protected side it was a little below 200 per cent. The outer quarter inch was sampled. On the oviposited side it was 58 per cent. and on the protected side 171 per cent.

Having given such an unexpected result, the experiment was followed up by a study of the rate of fall of moisture content in a very wet log from another evenly grown, vigorous young tree. The ends of the log were greased and one side was protected and the other attacked by Sirex as before, the tinfoil being removed immediately after oviposition. It was then sampled by cutting discs, 5, 10, 14 and 35 days afterwards (Figure 7). It was kept indoors in warmer conditions than the previous experiment.

Other discs were cut and sampled to see the development of eggs and larvae. After fourteen days, by the time the eggs were hatching, the moisture content of the outer half inch was reduced from 224 to 67 per cent. The dried area was quite distinct from the wet wood on the cut end of the log. Figure 8 shows similar dried areas on a log with fissured bark.

The streaks of drying spread most rapidly below the surface of the wood and then out to the cambium. This may be because the fungus is injected down into the end of the oviposition tunnel.

On the half of the log oviposited, the bark soon shrank, due to the drying of the phloem. Depressions appear on attacked trees in the same way, often exaggerated by the subsequent growth of the living wood around them.

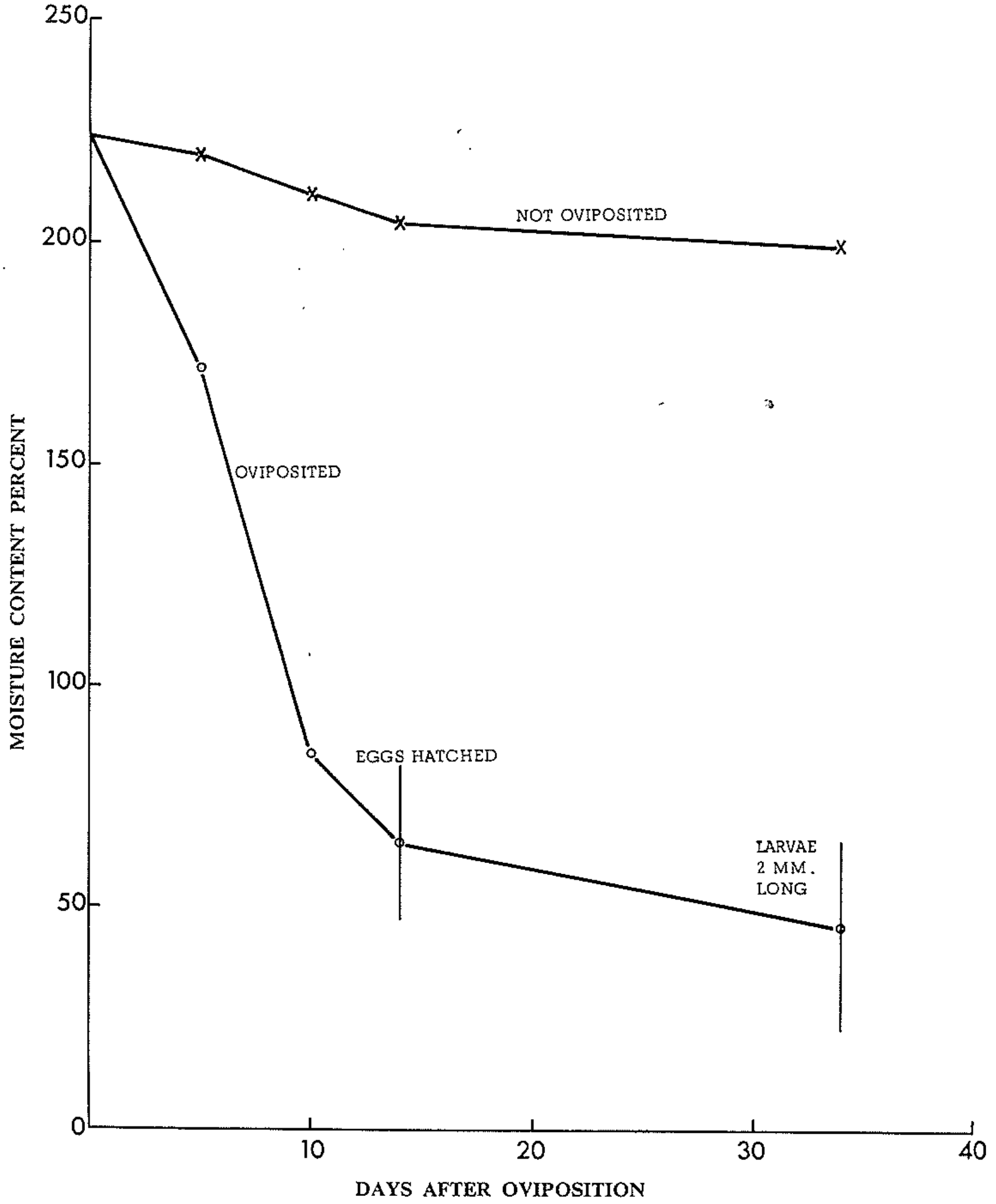

Figure 7.—Comparison of the rate of moisture loss from the outer ½ in. of wood of oviposited and non-oviposited sides of the same log.

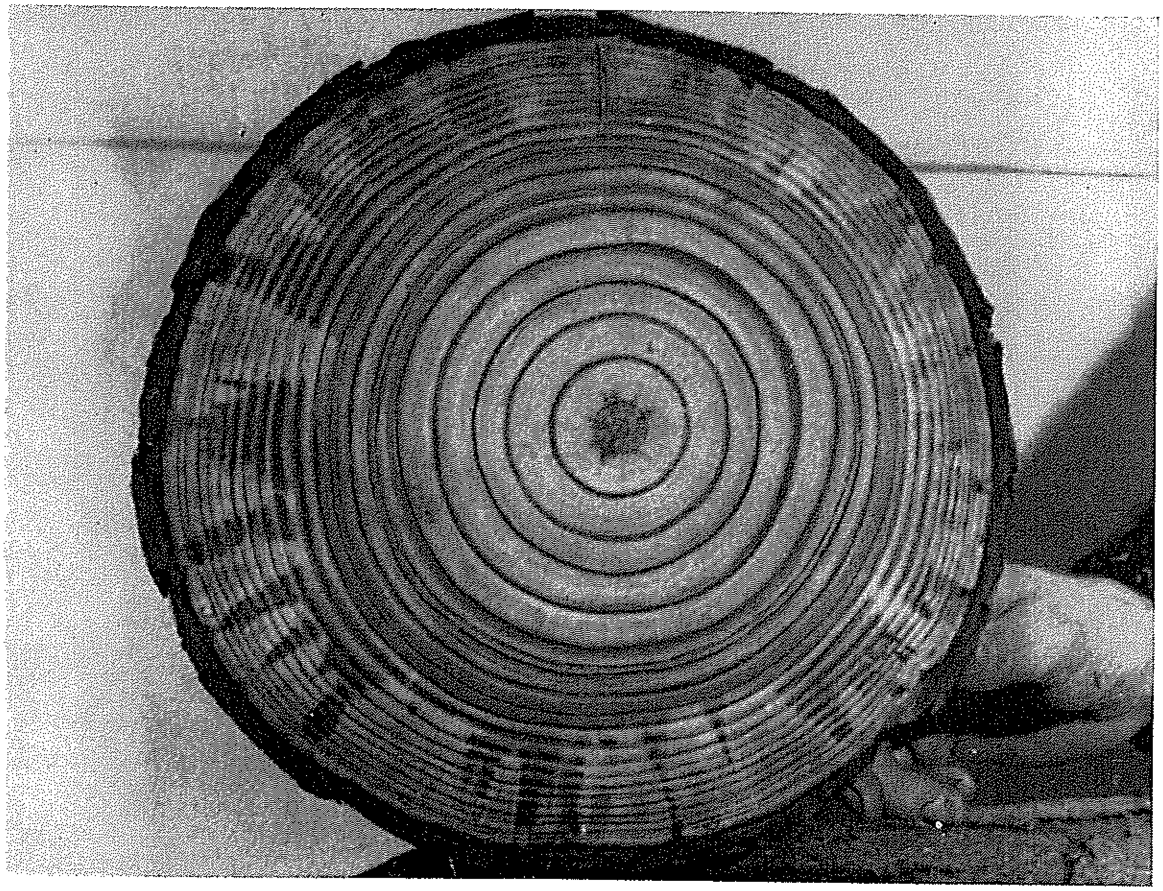

Plate 3.—The whitish areas show the inward spread of drying from moderate oviposition on a log with slightly fissured bark.

The rapid drying of wood after oviposition probably accounts for the lack of correlation found previously between the moisture content of logs and the survival of eggs and larvae. Even in the wettest logs, the moisture content will be reduced to a low level by the time the eggs hatch.

The loss of water is so large and sudden that until the experiment is repeated using logs in weighed airtight containers, and including measurements of wood density, the possibility of evaporation being somehow accelerated by the fungus cannot be ruled out. However, Yarwood (1947) studied the loss of water (as measured by loss in weight) from cultures of various fungi growing in petri-dishes, and found that they generally lost less weight than petri dishes of water. The Sirex fungus was not among the species studied.

Yarwood also found that various fungi can cause great increases in the permeability of cells in the leaves of herbaceous plants, such as beans and cucumbers, resulting in uncontrolled evaporation and wilting. How much of the water lost from Sirex attacked wood is due to increased permeability of the wood cells, resulting in increased evaporation through the oviposition tunnels or through the bark, has not been determined. The first local loss of water in attacked trees will be due to the ovipositor breaking the sap stream which is under tension (described below). Some water would then be used in hydrolysis caused by the fungus. But the bulk of water may evaporate. These aspects of drying are being studied.

The drastic drying of the sapwood should be sufficient to kill the tree. The sap being under tension, the tree cannot push water back into the tracheids, except possibly near the butts. Young trees die far more quickly from Sirex attack than from ringing an inch into the sapwood. The drying caused by the fungus must be equivalent to removing most of the sapwood all the way up the tree.

If the fungus does kill the tree by removing water from the wood, and thereby breaking the flow of sap to the crown, this adds another category to the vascular wilt diseases described by Dimmond (1955). Other vascular wilts may act by releasing toxins, by blocking vessels with hyphae or products of cell breakdown, or by obstructing them by causing tyloses. Dimmond also mentions the gas embolism theory of Tochinae, and the thickening of tracheal fluid caused by certain bacterial wilts. Hyphae of the Sirex fungus are often concentrated in the medullary rays. They grow along the tracheids, and move from one tracheid to another through pits and through fine bore holes in the tracheid walls. The fungus grows but sparsely in the wood, and is never plentiful enough to block tracheids. It has been observed growing most densely in the wood bordering larval tunnels. Tyloses have been found in infested wood, but not in sufficient numbers to affect transpiration.

The drying spreads very slowly tangentially and less slowly radially, though it seems to be held up by the late wood of the annual rings. In January, Sirex were put on a log from the base of a tree, one foot in diameter. They drilled oviposition tunnels in the bark crevices, and in cross section, the drying could clearly be seen as whitish areas inside the crevices spreading inwards through the darker wetter wood. Plate 3 shows a similar result of moderate oviposition, although the bark was not deeply fissured in this case. Ten weeks after oviposition, the drying had spread through five growth rings—a distance of about one inch. The larvae were in their sixth instar and had tunnelled into the second and third growth rings, one to two inches from their oviposition sites.

In a log from further up the tree, where the bark was thin enough to allow oviposition anywhere, the drying spread inwards in a complete ring. The sapwood was four inches wide. Trees can probably maintain a green crown as long as there is enough unaffected sapwood to keep them going. Although they dry out near the oviposition puncture, the cambium and phloem adjacent to the ends of the dry streaks often remain moist for some time. But eventually the drying spreads out to the surface of the wood and the cambium and phloem are killed.

### *Drying from oviposition on a living tree*

Two cages were fixed just below the crown of a co-dominant tree, encircling the stem one above the other. Female Sirex were put in one cage and six weeks later some more were put in the other. Three weeks after that, the tree was felled and the bark peeled. The streaks of drying from the oviposition tunnels were measured.

TABLE VI

THE DEVELOPMENT OF DRY STREAKS FROM OVIPOSITION ON A LIVING TREE

*Mean length of dry streak in centimetres*

| | *After Three Weeks* | *After Nine Weeks* |
|---|---|---|
| Above Oviposition .. .. .. .. | 3·4 | 12·1 |
| Below Oviposition .. .. .. .. | 2·2 | 6·4 |
| Total Length .. .. .. .. | 5·6 | 18·5 |

Enzymes are probably carried upwards in the sap stream. Drying has been seen 2 cm. beyond the limits of the spread of the fungus, above the oviposition tunnels, but in towards the centre of the tree, and to either side, the fungus spreads beyond the bounds of the dried wood.

If fine holes are drilled in a tree in the summer, faint streaks of drying a few millimetres long usually appear, either immediately or after a few hours. In some trees where this was tried, the streaks continued to lengthen for several days, until they were up to eight centimetres long. Other trees showed very little drying of this sort. The streaks are often larger above the hole than below it and are probably caused in the first place by sap tension dragging the water out of the broken tracheids. They are no wider than the holes drilled. It has not been thoroughly studied, but the withdrawal of sap from above and below the oviposition tunnel while it is being made may create favourable conditions for the symbiotic fungus. Drying caused by oviposition looks quite different. The streaks are wider and much more obvious and are associated with the brown stain.

### (vi) MOISTURE CONTENT OF WOOD AND SIZE OF SIREX WHICH EMERGE

Chrystal (1928) found that when logs containing *S. cyaneus* were allowed to become very dry in an insectory, the Sirex which emerged were very small. Zondag (1959) found the same thing with *S. noctilio* in New Zealand. These observations have been confirmed at Pittwater in small diameter logs. Yet Sirex which emerged in February, 1964 from the tops of trees felled in February, 1963 and left lying in the plantation were nearly all larger than average. The undersides of the tops absorb water from the ground during the winter.

Chrystal (1928) quotes Scheidter as having found an average of 400 eggs in *S. noctilio*, and Rawlings (1953) considered 400 to be an average figure in New Zealand and gives a graph of the weight of adults and the number of eggs they contained.

The Sirex at Pittwater are generally rather small. A number of females of various sizes were measured from the head to the end of the abdomen, not including the bit of ovipositor which projects beyond the end.

A curve was drawn and divided into three more or less equal lengths to give three size classes. Females at the limits of the size classes were preserved and 1,040 females were compared with these by eye and allotted to the size classes. (This was done for a cage experiment which is not yet complete.) The result was as follows:—

TABLE VII

THE SIZE DISTRIBUTION OF FEMALE SIREX AT PITTWATER

| Body length in mm. | Average No. of eggs per Sirex | January Emergence | | February Emergence | | Total | |
|---|---|---|---|---|---|---|---|
| | | No. Sirex in each size class | Percentage | No. Sirex in each size class | Percentage | No. Sirex in each size class | Percentage |
| 30-36 .. .. | 250 | 72 | 24 | 163 | 22 | 235 | 23 |
| 20-30 .. .. | 150 | 79 | 26 | 143 | 20 | 222 | 21 |
| 15-20 .. .. | 75 | 153 | 50 | 430 | 58 | 583 | 56 |
| Total .. | .. | 304 | .. | 736 | .. | 1,040 | .. |

More than half of them were in the smallest size class.

The average number of eggs allotted to each size class was probably too low. It was based on dissections made as soon as adult Sirex emerged in 1963 and later dissections have given a larger number of eggs for the various body sizes, especially in the largest size class. There was a lot of variation, especially among the larger insects, but few of them had more than 400 eggs.

## 3. THE NATURE OF THE TREE AND THE INSECT'S BEHAVIOUR

Although in the experiments described in Section 2 (iii), there was no connection between the survival of eggs and young larvae, and the moisture content of the wood (so long as it was above the minimum requirement), nevertheless moisture content did affect the egg-laying habits and general behaviour of the insect. Before dealing with this, the general pattern of oviposition must be described.

### (i) GENERAL OVIPOSITION BEHAVIOUR

When the female Sirex is about to oviposit on a tree (or a vertically placed log), it usually stands with its head pointing either up towards the top of the tree, or down towards the ground. The ovipositor and its sheath are lowered, until the tip of the ovipositor catches on some irregularity of the bark surface. Then the sheath flicks up and the serrated valves of the ovipositor start to work with reciprocal motion. It also rotates, first to one side, then the other. Rawlings (1951) mentions that the ovipositor rotates through 360 degrees.

The ovipositor may go in up to the " hilt " or only part of the way (see 3 (iii)). If an egg is laid, there is a slight pause and then a sudden rapid palpitation of the abdomen, after which the ovipositor is quickly withdrawn. It is often withdrawn so that its tip comes out into the bark; the angle of the insect's body is tilted to one side and a new tunnel is made. This may be repeated, so through one hole in the bark, the insect may drill one, two or three holes in the wood. Occasionally more than three are made, but four or five are comparatively uncommon.

Chrystal (1930) recorded one instance of two tunnels through one hole in the bark, made by Sirex gigas on larch in England. He considered this to be an interesting abnormality. He did not observe the same thing for *S. cyaneus* and it would scarcely have escaped such a keen observer. Stillwell (1960) figures oviposition holes on the outside of the wood, made by *S. cyaneus* and *Xeris spectrum*. They all appear to be single.

In this paper, the term "*oviposition site*" is used to denote one or more oviposition "*tunnels*" made through one hole in the bark. The terms *single tunnels*, *double tunnels* and *triple tunnels* will be used for the conditions described above.

The proportion of single, double and triple tunnels is called the "*oviposition pattern*".

Double and triple tunnels begin to diverge in the bark. If the bark is peeled away, they are usually about 2 mm. apart on the outside of the wood. They fan out sideways, sometimes at an angle of more than 45 degrees, so if the ovipositor is long (see 3 (iii)) the ends of the tunnels will be quite far apart in the wood of the tree. The tunnels are not always straight. If the ovipositor meets the hard late-wood of an annual ring, a sharply bending tunnel is sometimes made.

To dissect oviposition tunnels for eggs, cores three quarters of an inch in diameter, each with an oviposition site in the centre, were cut with a one inch hole saw. The teeth of the saw had to be deepened and given a wider set—when tunnels were opened for eggs after a first trial, the eggs had a peculiar appearance and it was found they had been cooked by the heat of the saw. The bark is removed from the core which is sliced away with a scalpel at an angle from the holes in the outside of the wood.

By observing the angle of the ovipositor and noting when eggs were laid, the order of oviposition was worked out. When single tunnels are made, eggs may or may not be laid. If two tunnels are made at one site, an egg is normally laid in the first tunnel, but not in the second. When three tunnels are made at one site, eggs are laid in the first and second tunnels, then the third tunnel is made between them and no egg is laid in it (Figure 8). When three tunnels are made, the middle empty tunnel is usually longer than the tunnels to either side.

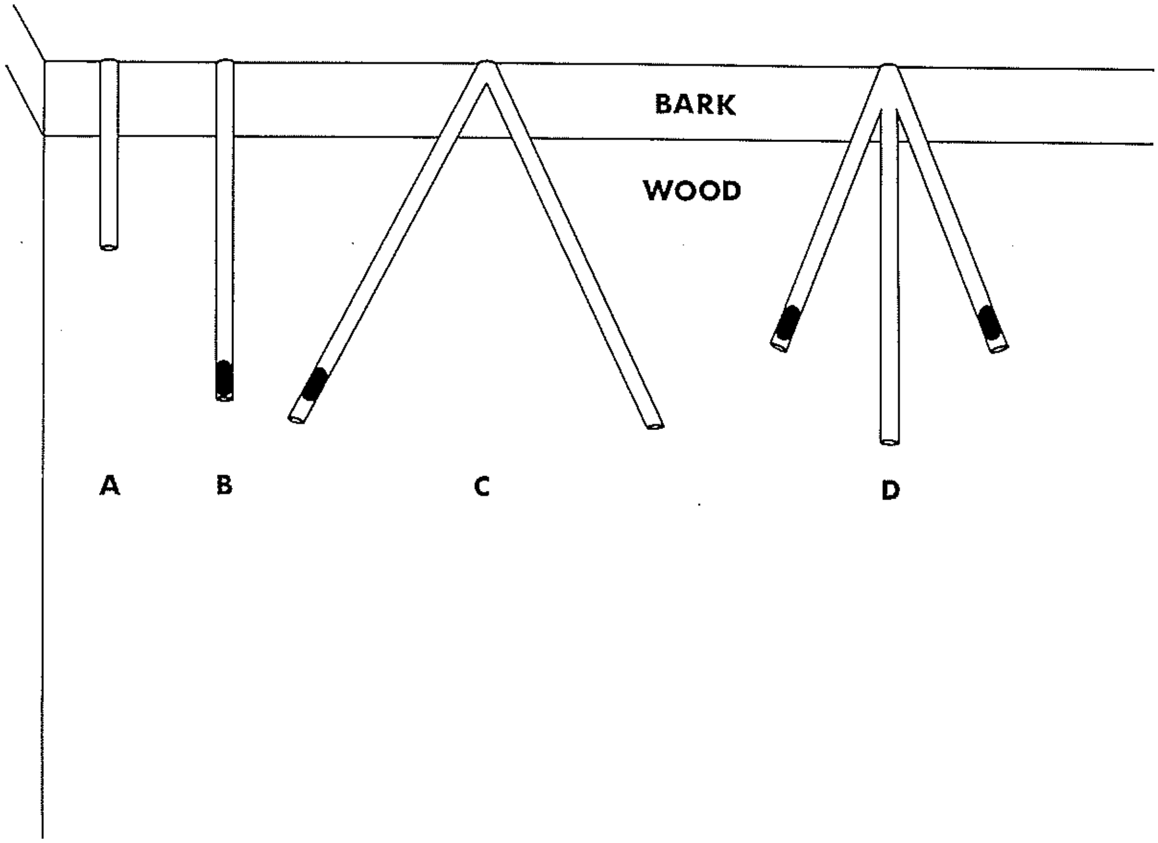

**Figure 8.—Diagram showing the typical conditions of oviposition tunnels and egg laying.**

**A.—Short single tunnel (about 5 mm. long); no egg.**

**B.—Longer single tunnels (about 9 mm. long) do sometimes contain eggs.**

**C.—Double tunnels. An egg is laid in the first tunnel, while the second tunnel to be made is empty.**

**D.—Triple tunnels. Eggs are laid in the first and second tunnels. The third tunnel, which is slightly longer, is empty.**

*Note:*—**The egg is about 1 mm. long, and the tunnels 0·5 mm. in diameter.**

## (ii) OVIPOSITION PATTERN AND MOISTURE CONTENT

At very high and very low moisture content, a large percentage of oviposition sites had only single tunnels and no triple tunnels were made. At intermediate moisture contents, the proportion of single tunnels decreases and the triple tunnels increase. The proportion of double tunnels is much more constant (Figure 9). These figures would not be universally valid, as other factors affect the oviposition pattern, but they do show that the behaviour of the insect is affected by moisture content.

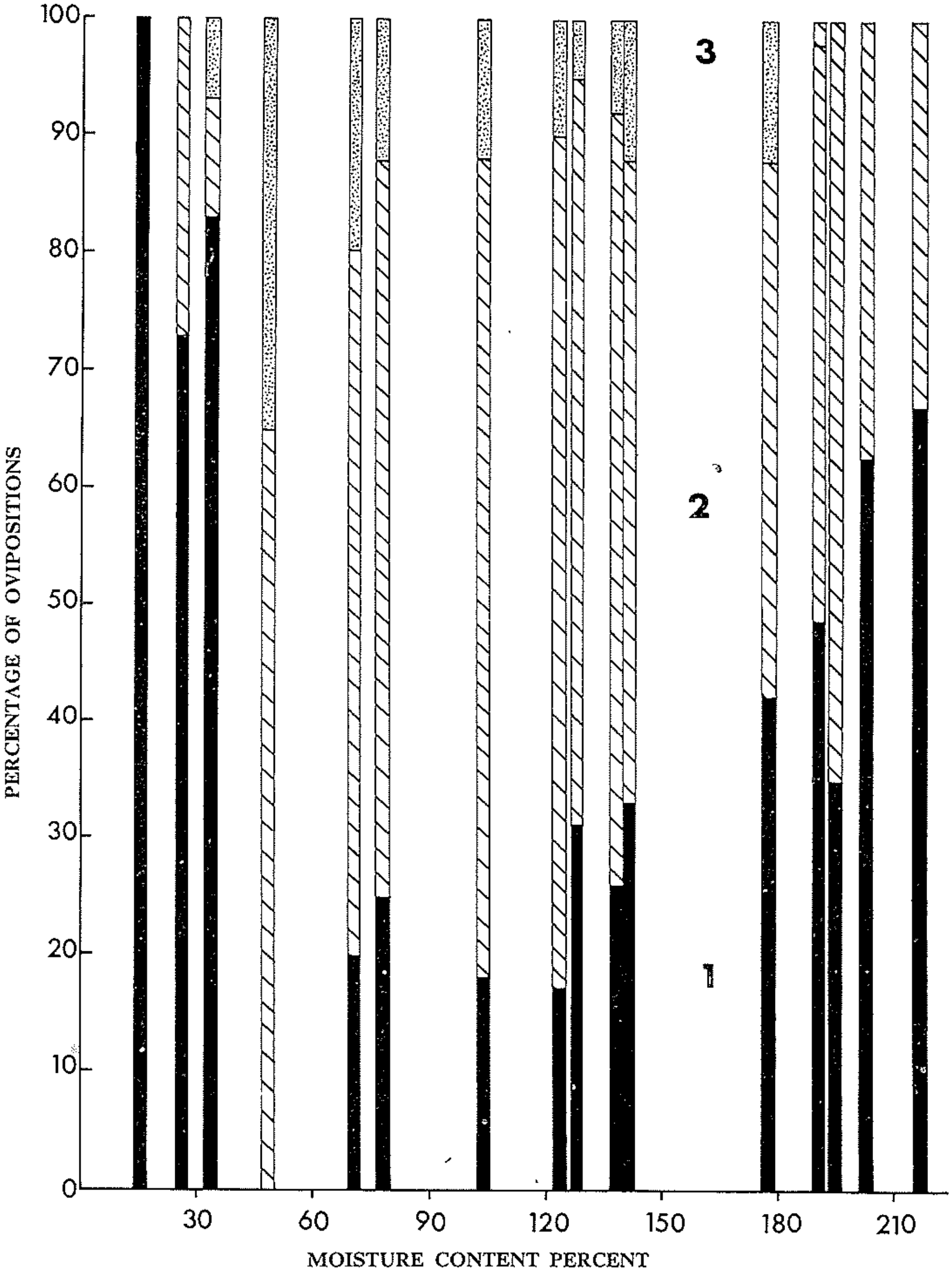

Figure 9.—The percentage of oviposition sites with one, two or three tunnels on logs of various moisture contents.

Table VIII shows the proportions of tunnels in the various oviposition types in which eggs were laid. It is a summary of the figures from the second moisture content experiment using logs from young dominant trees.

TABLE VIII

THE NUMBER OF TUNNELS AT AN OVIPOSITION SITE, AND EGG LAYING

*Figures from the experiment using logs from young trees over a wide moisture content range*

| Single Tunnels | | | Double Tunnels | | | Triple Tunnels | | | Total No. of tunnels | No. contg. Eggs | % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of tunnels examd. | No. contg. Eggs | % | No. of tunnels examd. | No. contg. Eggs | % | No. of tunnels examd. | No. contg. Eggs | % | | | |
| 159 | 52 | 33 | 424 | 186 | 44 | 114 | 69 | 61 | 697 | 307 | 44 |

When this experiment was done the order of egg laying was not known. (It was supposed that eggs were not laid in some tunnels only because conditions were unfavourable.) The figures in Table VIII, however, support what was found by the later observations. One could expect the percentage of double tunnels containing eggs, multiplied by 1·33 to equal the percentage of triple tunnels containing eggs.

*Percentage containing eggs*

| | |
|---|---|
| Triple tunnels .. .. .. .. .. | 61 |
| Double tunnels .. .. .. .. | 44 × 1·33 = 58 |

The result is almost the same.

The variation in the proportion of single, double and triple tunnels is sufficient in itself to relate the proportion of tunnels which contain eggs to the moisture content of the tree or log being attacked; in very dry and very wet wood, a larger proportion of single (more often empty) tunnels is made.

This is modified further within each oviposition type. At the highest moisture content at which triple tunnels are made these are often empty. At slightly lower moisture contents, one of the three tunnels may contain an egg. Then the typical condition is reached, with two out of the three tunnels having eggs; but at what appears to be the optimum condition for egg laying—between 30 and 80 per cent. moisture content—some sites with triple tunnels have an egg in each tunnel.

A large proportion of single tunnels usually have no eggs laid in them, but this also changes with moisture content. The figures become very small when sub-divided into tunnel types and percentages of these with and without eggs, so there is a lot of variation. The percentage of double tunnels with eggs scarcely follows a trend with moisture contents, between 26 and 200 per cent.: about 50 per cent. of the tunnels generally contains eggs.

The variation in egglaying in single, double and triple tunnels, with moisture content is summarised as follows :—

| Log No. | MC % | Single Tunnels | | | Double Tunnels | | | Triple Tunnels | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | No. | No. with Eggs | % | No. | No. with Eggs | % | No. | No. with Eggs | % |
| 5 | 215 | 8 | 1 | 12 | 8 | 3 | 37 | 0 | 0 | 0 |
| 6 | 203 | 4 | 1 | 25 | 2 | 1 | 50 | 0 | 0 | 0 |
| 7 | 202 | 15 | 4 | 27 | 18 | 10 | 56 | 0 | 0 | 0 |
| 118 | 194 | 12 | 4 | 33 | 44 | 22 | 50 | 0 | 0 | 0 |
| 127 | 179 | 14 | 2 | 14 | 30 | 17 | 57 | 12 | 6 | 50 |
| 107 | 139 | 16 | 6 | 37 | 48 | 23 | 48 | 18 | 7 | 39 |
| 117 | 138 | 9 | 0 | 0 | 46 | 25 | 54 | 9 | 4 | 44 |
| 107A | 127 | 17 | 8 | 47 | 68 | 27 | 40 | 9 | 6 | 67 |
| 16 | 123 | 5 | 3 | 60 | 42 | 14 | 33 | 9 | 6 | 67 |
| 108 | 104 | 2 | 1 | 50 | 6 | 3 | 50 | 9 | 6 | 67 |
| 109 | 77 | 4 | 2 | 50 | 20 | 10 | 50 | 6 | 5 | 83 |
| 111 | 71 | 2 | 0 | 0 | 12 | 6 | 50 | 6 | 5 | 83 |
| 10 | 51 | 0 | 0 | 0 | 26 | 16 | 61 | 21 | 14 | 67 |
| 15 | 32 | 24 | 15 | 62 | 6 | 3 | 50 | 6 | 5 | 83 |
| 4P | 26 | 22 | 0 | 0 | 16 | 10 | 62 | 0 | 0 | 0 |
| 7P | 15 | 11 | 0 | 0 | 0 | .. | .. | 0 | .. | .. |
| 6P | 10 | 3 | 0 | 0 | 0 | .. | .. | 0 | .. | .. |

The proportion of tunnels containing eggs, including all oviposition types examined on each log, is shown in Figures 10 and 11 for the two moisture content experiments.

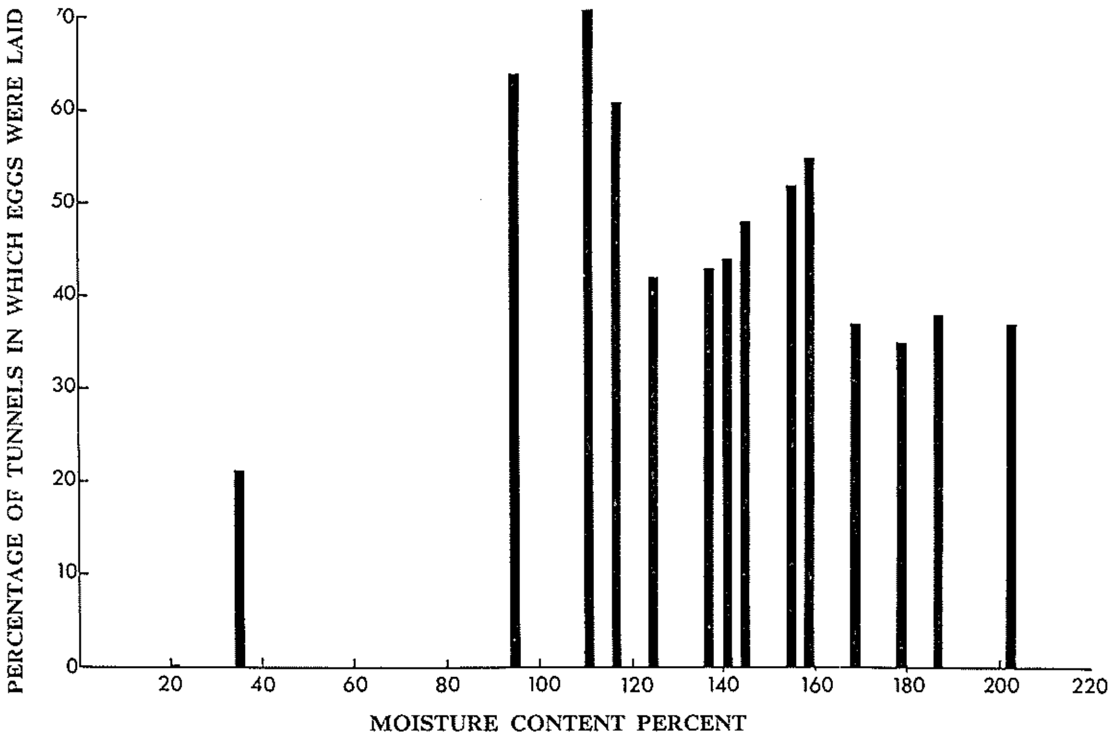

**Figure 10.—The percentage of oviposition tunnels in which eggs were laid at various moisture contents of tops.**

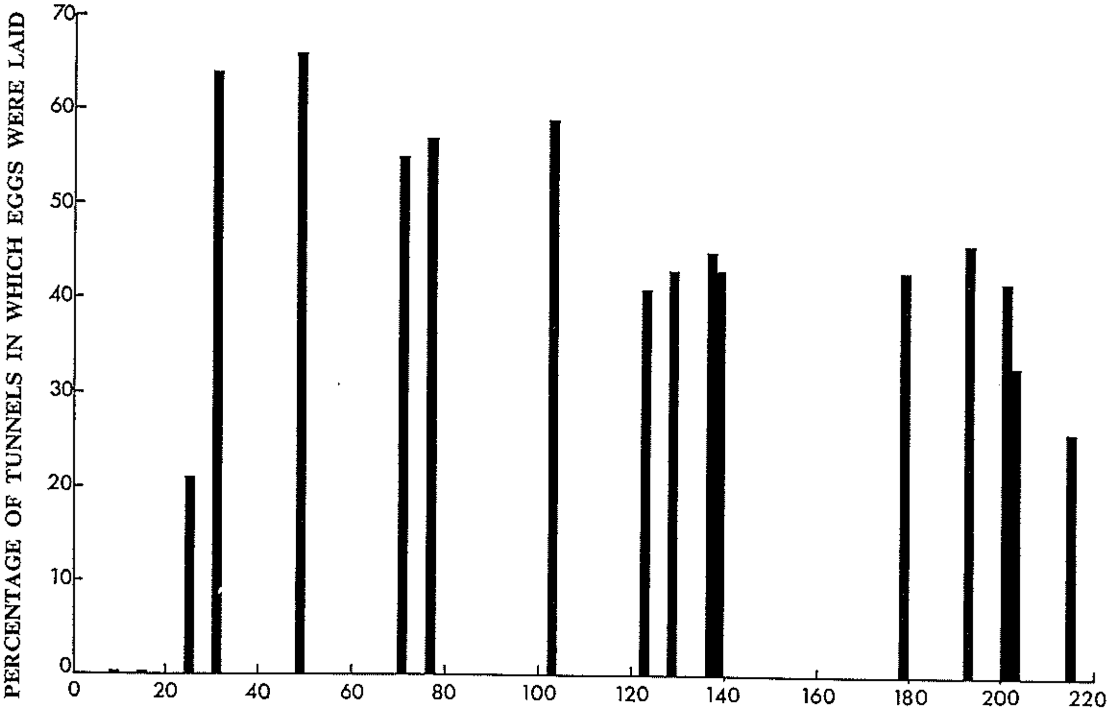

Figure 11.—The percentage of oviposition tunnels in which eggs were laid at various moisture contents of young trees.

In the first experiment, when tops were used, there were no logs between 35 and 96 per cent. moisture content. The log at 35 per cent. showed a large drop in the percentage of tunnels with eggs.

In the experiment with logs from young trees, the percentage only decreases below 32 per cent. The decrease is very sudden. The difference in the result may be due to blue stain in the dry tops or to the nature of the wood. The logs from young trees had outer annual rings about half an inch wide and were probably easier to drill at any moisture content. The Technical Assistant, Mr. J. Dolezal, who removed the cores with a hole saw, found that logs of intermediate moisture content were the easiest to cut.

Variation is very difficult to control in this type of experiment because, although moisture content measurements can be fairly accurate, no two logs are exactly alike in all other aspects.

It will be seen that survival of eggs cannot be considered at moisture contents below 20 per cent., because no eggs are laid in the tunnels, which are all single.

### (iii) OVIPOSITION TUNNELS WITH TWO EGGS AND TUNNEL LENGTH

Chrystal found that *S. cyaneus* more often than not laid two or three eggs in the same (single) tunnel, in a linear series. *S. gigas* sometimes laid as many as six or seven eggs (Chrystal, 1928).

In our first experiment using tops of thinned trees, 14 per cent. of the tunnels in which eggs were laid were found to have two eggs. In the second experiment, in which the wood of fast growing young trees was used, more than 40 per cent. of the tunnels containing eggs had two eggs. The presence of two eggs in a tunnel is connected with the type of oviposition and with the tunnel length. Single tunnels have the lowest proportion with two eggs, the double tunnels are intermediate and the triple tunnels have the most. The figures from the experiment using logs from young trees are shown in Table IX.

TABLE IX

THE FREQUENCY WITH WHICH TWO EGGS ARE LAID IN A TUNNEL, IN THE DIFFERENT OVIPOSITION TYPES

| Single tunnels in which eggs were laid | | | Double tunnels in which eggs were laid | | | Triple tunnels in which eggs were laid | | | Total No. of tunnels with eggs | Total No. with 2 eggs | % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| No. | No. with 2 eggs | % | No. | No. with 2 eggs | % | No. | No. with 2 eggs | % | | | |
| 52 | 17 | 33 | 186 | 76 | 41 | 69 | 38 | 55 | 307 | 131 | 43 |

The egg fits quite snugly in the oviposition tunnel, so it was supposed that when two were laid, the egg parasite *Ibalia leucospoides* might be unable to reach the second egg with its ovipositor or it might not know it is there. Whether this is true or not remains to be demonstrated, but Chrystal (1930) found that Ibalia frequently parasitized some or all of the three or four eggs laid by *Sirex gigas* in single tunnels. This may, in any case, be of limited practical importance, because the presence of two eggs in a tunnel is related to the tunnel length. Sirex vary greatly in size and the ovipositor may be less than 8 mm. to more than 20 mm. long (it equals about half the body length plus 1 mm.), but the full length is not always used. Three conditions for drilling have been recognised :—

(1) If the outer annual ring of the tree is wide enough for the ovipositor to be drilled full length into the wood without penetrating the hard late-wood of the next annual ring, the insect usually does this. Long tunnels are made and two eggs are commonly laid in a tunnel.

(2) If the outer ring is about 6 mm. wide, the Sirex usually drills only as far as the next annual ring and this seems to satisfy it. If the next ring is only lightly lignified, as in fast grown trees, the ovipositor often penetrates beyond it and goes in up to the hilt.

(3) If the outer rings are very narrow, the ovipositor penetrates two or three of them, but only a short tunnel is made, about three to five mm. long in the wood and usually only one egg is laid in a tunnel.

Trees which are successfully attacked by Sirex are mainly in the poorer crown classes and have fairly narrow annual rings, so except in the tops of felled trees, the percentage of tunnels containing more than one egg is usually rather low.

In one young tree, where there was little lignification of the annual rings in the upper part of the stem, tunnels containing two eggs only occurred in the upper part. In logs cut from young dominant trees with the outer annual rings more than half an inch wide, very long oviposition tunnels containing three eggs were sometimes found. Although triple tunnels more commonly have two eggs per tunnel than double tunnels, and the presence of more than one is related to tunnel length, the triple tunnels are not normally longer than double tunnels. However, double and triple tunnels are longer, on average, than single tunnels. Single tunnels often appear to be exploratory, especially in very dry and very wet wood, the ovipositor being quickly withdrawn.

When two eggs are laid in a tunnel and they both hatch, one larva may bore upwards and one downwards or they may both go in the same direction, making parallel borings, one near the surface of the wood and one slightly further in. In any case, the innermost larva is often better developed than the outer one and a typical example is shown in Figure 12.

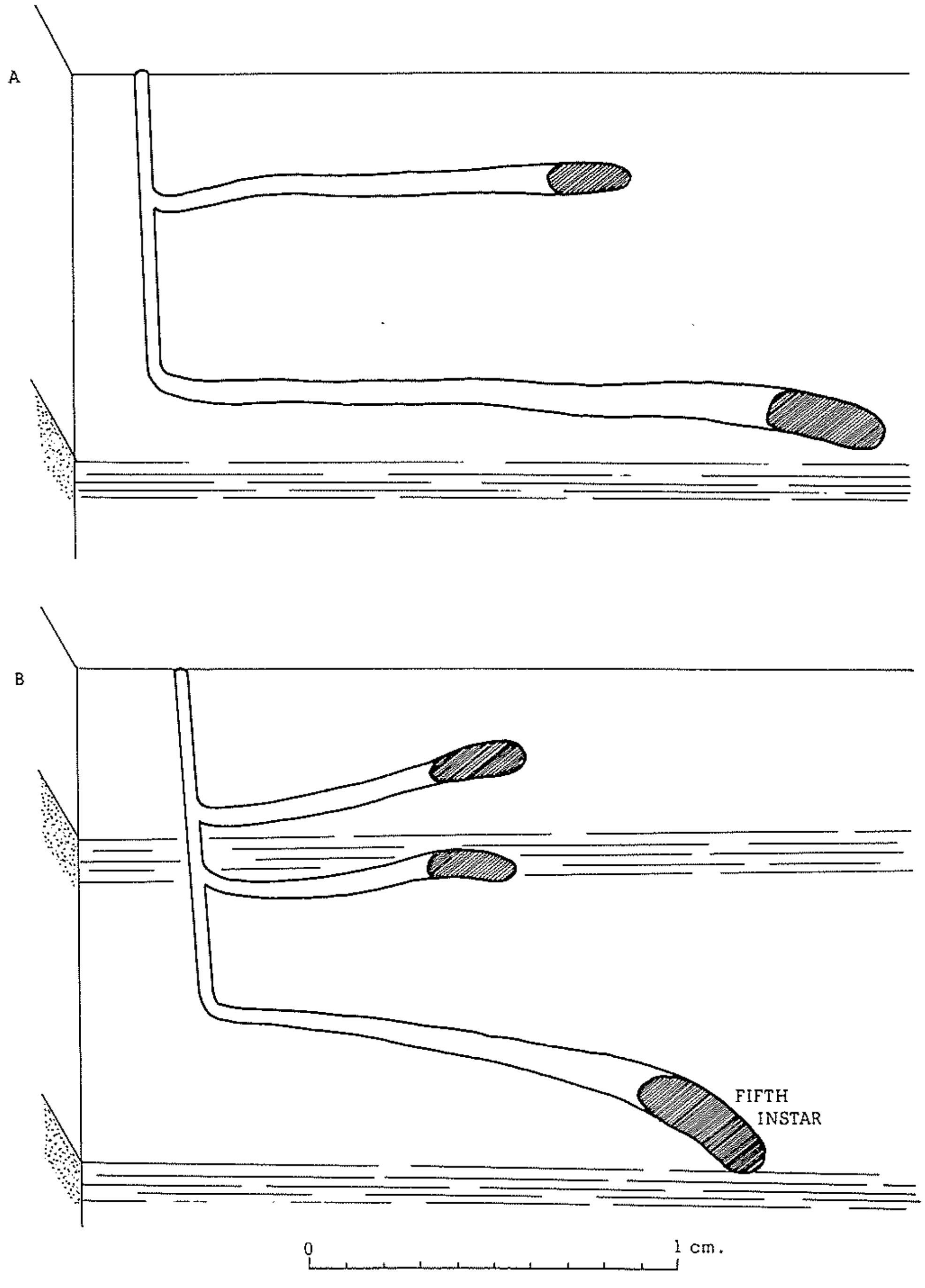

Figure 12.—Two examples obtained by dissection of oviposition tunnels and larval borings, showing diagrammatically the rapid development of larvae from the inner eggs (about ten weeks after oviposition). The horizontal lines represent latewood. The four unmarked larvae are fourth instars.

## (iv) OTHER FACTORS WHICH AFFECT THE OVIPOSITION PATTERN

Some thick lumps of bark were nailed on to one side of a smooth barked log nine inches in diameter, to leave crevices between them. Some female Sirex were put on the log and showed a strong preference for the part with the artificial bark. When the bark was removed and the oviposition tunnels marked, they could be seen massed beneath the artificial crevices, whereas they were thinly scattered over the rest of the log. There was a larger proportion of triple tunnels on the part of the log with the artificial bark.

The large Sirex seemed more attracted by the artificial bark than the small ones.

Subsequent experiments using large and small Sirex on logs with and without artificial bark have given variable results, partly because of variations in moisture content and diameter. Large females are at a disadvantage on very narrow logs; they seem to have difficulty in manipulating their long ovipositors so that they may be angled from side to side in the hole.

The way in which the proportion of single tunnels varies with diameter on some of the trees described in Section V is shown in Figure 19.

All but the young dominant show a sudden increase in the proportion of single tunnels right at the butt which is in no way related to diameter.

The foot of a tree may be unfavourable on account of bark thickness, hardness of the wood or reduced tension on the sap stream; or the pattern may be tied up with the behaviour of the insect which may start its boring at the foot of the tree.

Above the butt, the proportion of single tunnels rises as diameter decreases, but 50 per cent. of the oviposition sites had single tunnels on the 30 year dominant at a diameter of six inches and on the other trees at a diameter of about three inches. Possibly on very narrow stems, where the insect has difficulty in drilling, diameter has an overriding effect.

## (v) DISTURBED FEMALES

Franke-Grossman (1939) found that *S. augar* eggs are inoculated with oidia of the symbiotic fungus, in a mass of mucilage. The specimen observed laid from one to four eggs in single tunnels.

Clark (1933) induced female *Sirex noctilio* to lay eggs by stroking the ovipositor. He was unable to culture the symbiotic fungus from four cultures of three eggs each; only contaminants developed.

As *Sirex noctilio* nearly always drills an empty tunnel after it has drilled one or two containing eggs at any one oviposition site, it seemed possible that most of the fungus might be injected into the empty tunnels.

Considering the number of empty tunnels made on some trees (section 5), this is a matter of some importance. Two Sirex were put on a log where they began to drill. The log was such that most of the oviposition sites had two tunnels. As usual, eggs were laid only in the first tunnel of a pair. When the egg had been laid and the ovipositor was withdrawn to the bark before boring the second, empty tunnel, the Sirex were disturbed and forced to walk on up the log. (They were most relutcant to move on without first making an empty tunnel.) In this way a number of single tunnels containing eggs were obtained and a number of normal double tunnels. Some fine drill holes were made as well. After a week the log was peeled. The double tunnel ovipositions had produced the normal streaks of drying, often with the brown stain round the edges of the dry wood. The single tunnel ovipositions from which the Sirex were disturbed produced no more drying than the drill holes in most cases. Some of the double tunnel ovipositions had the dry streaks coming from one tunnel only. Two of these were dissected. The tunnel in the drywood was the empty one. Only small numbers of tunnels were examined in this small test and the result is not conclusive.

On another log, cores were taken containing tunnels from disturbed and undisturbed ovipositions as before. The normal double tunnel ovipositions were split to give two pieces of wood with a tunnel in each. They were sterilized in sodium hypochlorite and incubated in petri dishes at 22° C. After six days, the white mycelium of the symbiotic fungus grew up out of some of the oviposition tunnels and spread over the surface of the wood.

Two weeks after oviposition, four out of ten tunnels containing eggs and from which the female was disturbed before making a tunnel alongside, had failed to produce any fungus. The normal double tunnel oviposition did not make a very good control. Some of the tunnels were drilled more or less on the radius of the log and when the cores were split, some of the halves had sections of both tunnels in them. Nine oviposition sites were halved. Only one of the eighteen halves (one without an egg in it) failed to produce fungus.

It is possible that the fungus present in tunnels in which eggs are laid is merely contamination from the ovipositor or eggs and more fungus may be injected into the empty tunnels. The experiment is being repeated, using very large Sirex, so the ovipositions will be easier to handle.

### (vi) THE REJECTION OF FRESH LOGS BY FEMALE SIREX

In one of the experiments on the survival of larvae in logs at various moisture contents, the Sirex refused to drill oviposition tunnels in a very wet log (215 per cent. moisture content in the outer half inch), freshly cut from a young dominant tree. They ran about all over the log and sometimes probed the bark with their ovipositors, but they would not bore. The log was removed and put back twelve days later with some other Sirex which made several ovipositions. The log was again sampled for moisture content, but the wood was as wet as the day the tree was felled.

To study this further, two dominant trees, nine years old were selected as like one another as possible. One was cut through at the base and hung up against another tree for two weeks. The other tree was felled the day they were both used. The branches were cut off to reduce transpiration, leaving stubs about six inches long. The lower ten feet of each tree was sampled for moisture content by cutting discs at the ends and in the middle. The halves were joined up again, and the trees stood up on stands a few feet apart from one another in the laboratory. Female Sirex which had emerged the day before, but which had no chance to bore, were put on the trees and their behaviour observed. The temperature was maintained at 70° F. which allowed them to fly readily and the lighting controlled to prevent any unfair bias.

The freshly felled tree had a moisture content of about 200 per cent. and the tree which had been dried 100 per cent.

The Sirex were reluctant to attack the wet tree, especially when it was fresh. They would either fly off straight away or start to make oviposition tunnels but withdrew their ovipositors as soon as they penetrated the bark. In some instances resin flowed out which may have put them off. (Yet a Sirex has been observed continuing to bore in an old log, although resin was welling out around the ovipositor.) On the dry tree they started to bore without hesitation and carried on for hours.

Sirex which had been boring on the dry tree were transferred to the wet tree. They were then prepared to bore on the wet tree. (This method of conditioning the females has since been used when ovipositions were required on very fresh wet logs for experiments like the one described in Section 2 (v).

It is not yet clear whether the moisture content of the wood or bark is the important thing or whether there is some other factor which soon changes when a log loses its freshness.

The effect of bark moisture was studied, by peeling off the bark on a number of logs and soaking some of it and partially drying some and doing the same with the logs. The bark was nailed back in position to give dry bark on dry wood, dry bark on wet wood, etc. The logs were put in a cage with a number of female Sirex but so far results have been inconclusive.

### (vii) ARTIFICIAL ATTACK ON TREES, USING SIREX IN CAGES AND WITH GLUED WINGS

The study of the effect of Sirex attack on trees with various physiological characteristics is fraught with difficulty because there is no way of telling in advance which tree will be attacked (Jackson, 1955), so various ways of applying artificial attack have been considered.

An experiment has been started in which flywire cages, four feet long, were fixed below the crowns (i.e., at about 40 feet) of 30 year old trees of various moisture content, crown classes and resin pressures. Female Sirex were put in the cages in various numbers to give a calculated amount of attack per square foot of bark surface. The experiment was marred by the behaviour of the Sirex. They would sometimes begin to drill in the trees right away, but most of them ended up on the flywire, where they stayed until they died. Many of them were dissected and compared with a graph showing the number of eggs against body length. They had laid few of their eggs and only a few of the trees have started to die.

Because of the limited success of controlling attack by putting Sirex in cages on trees, new methods were tried. The wings of some females were clipped. Others had their wings stuck together with glue in the rest position folded over the insects' backs. They were put on trees in the regrowth. Some of the insects with clipped wings tried to fly and fell off. Those whose wings were glued settled down to their drilling and were able to wander about freely over the stems of the trees. When they were dead, seven of the females were dissected. Four had laid all of their eggs, two still had about a dozen and one, which had fallen off the tree, had all of its eggs left. Large Sirex stayed on some trees for nearly two weeks boring in all but cold or wet weather. Some with clipped or glued wings disappeared. Bits and pieces were found under one of the trees. Birds or mice or other insects must have taken them. A number of Sirex which had emerged and mated in a glasshouse and which were put on upright logs in a cage to produce females for experiments in the following year were eaten by mice.

If only the tips of the forewings are glued together, the insect can still spread its hind wings and attempt to fly. Sirex in this state were put on a vigorous young dominant tree. They drilled short single oviposition tunnels and then walked on up the tree buzzing their hind wings. After repeating this several times and failing to take off, they settled down to more normal drilling.

## (viii) THE ATTRACTIVENESS OF TOPS

Tops from various months of felling were moved into a clearing in an area of regrowth where Sirex were known to be plentiful. They were placed at random in a row, two to three feet apart. Their moisture contents were sampled with a core-drill along their sides (corresponding to the B and D samples of the previous tops experiment (see Figure 4)), at the butt and top ends.

In this way, each top could be sampled several times without much disturbance to the rate of drying. Sample areas were chalked on the sides of the tops and as far down underneath as it was possible to see. These were inspected regularly for oviposition holes in the bark. When oviposition holes were found, these were marked so that signs of new attack could be recognised. The first results of the experiment are shown in Table X.

The tops were free from Sirex attack before they were moved. All but the February tops were moved in the second week in January. The February ones were moved on the 7th February, 1964.

The fresh tops were very attractive to Sirex, but the older tops and one of the December felled tops with a low moisture content, had little or no attack. There was little attack at moisture contents below 50 per cent.

This shows the importance of the behavioural differences of the insect in the open and in the laboratory. In the laboratory 50 per cent. moisture content was more or less ideal for oviposition.

This experiment does not separate attractiveness from the suitability of the top for attack once the Sirex arrived. All the tops may have attracted Sirex, but only the fresher ones were attacked.

The fresher tops were very attractive to Sirex. Older tops had less attack. This may be on account of their moisture content—there was little attack below 50 per cent. moisture content. The August top with the high moisture content in Table X was from a tree burnt in March, 1963, when a fire swept through part of the plantation. Singeing of the needles may have checked transpiration. Female Sirex were seen running up and down this top, but no oviposition holes have been recorded.

## TABLE X

### Sirex Attack on Tops from Different Months of Felling, and with Various Moisture Contents

S = Sirex attack x = No. attack G = Needles green B = Needles brown.

| Date of Felling | Date Moved to Regrowth | Mean M.C. on 14-1-64 | Sirex attack between 10-1-64 and 20-1-64 | Mean M.C. on 12-1-64 | Sirex attack between 24-1-64 and 18-2-64 | Mean M.C. on 18-2-64 | Sirex attack between 18-2-64 and 3-3-64 | Sirex attack between 3-3-64 and 18-3-64 | M.C. on 18-3-64 |
|---|---|---|---|---|---|---|---|---|---|
| 1963— | | | | | | | | | |
| May .. .. | 8—13-1-64 | 25 | B x | 25 | B x | 23 | B x | B x | 23 |
| May .. .. | 8—13-1-64 | 34 | B x | 30 | B x | 26 | B x | B x | 20 |
| May .. .. | 8—13-1-64 | 33 | B x | 31 | B x | 25 | B x | B x | 20 |
| August .. .. | 8—13-1-64 | 39 | B x | 35 | B x | 20 | B x | B x | 19 |
| August .. .. | 8—13-1-64 | 37 | B x | 35 | B x | 26 | B x | B x | 25 |
| August .. .. | 8—13-1-64 | 143 | B x | 137 | B x | 50 | B x | B x | 33 |
| October .. .. | 8—13-1-64 | 30 | B x | 26 | B x | 23 | B x | B x | 23 |
| October .. .. | 8—13-1-64 | 49 | ¼B x | 41 | ¼B x | 24 | ¼B x | ½B x | 20 |
| October .. .. | 8—13-1-64 | 56 | ¼B S | 52 | ½B S | 47 | ¾B S | ¾B S | 41 |
| November .. | 8—13-1-64 | 58 | G S | 52 | G S | 38 | ¼B S | ¼B S | 24 |
| November .. | 8—13-1-64 | 49 | B x | 33 | B x | 28 | B x | B x | 24 |
| November .. | 8—13-1-64 | 56 | ½B x | 47 | ¾B x | 33 | B x | B x | 29 |
| December .. | 8—13-1-64 | 53 | B x | 34 | B x | 37 | B x | B x | 27 |
| December .. | 8—13-1-64 | 170 | G S | 71 | ¼B S | 37 | ¾B x | ¼B x | 44 |
| December .. | 8—13-1-64 | 153 | ¾B S | 39 | B x | 27 | B x | B x | 29 |
| 1964— | | | | | | | | | |
| January .. .. | 14-1-64 | 180 | G S | 145 | G S | 38 | G S | G x | 38 |
| January .. .. | 14-1-64 | 163 | G S | 123 | ½B S | 92 | ½B S | ¾B S | 49 |
| January .. .. | 14-1-64 | 170 | G S | 127 | ¼B S | 85 | ¾B S | ¾B S | 60 |
| February.. .. | 7-2-64 | .. | .... | .. | G S | 89 | ¼B S | ¼B S | 49 |
| February.. .. | 7-2-64 | .. | .... | .. | G S | 89 | ¼B x | ½B S | 46 |
| February.. .. | 7-2-64 | .. | .... | .. | G x | 111 | ¼B S | ¾B S | 71 |

None of the tops were attacked after all the needles had turned brown. The following figures are summarised from Table X, and show the waves of attack for all tops as found in the four assessments.

| | *Assessment* x *No. of Tops* | |
|---|---|---|
| | *Attack* | *No Attack* |
| Needles, green | 10 | 2 |
| ¼ brown | 7 | 3 |
| ½ brown | 6 | 3 |
| ¾ brown | 6 | 3 |
| completely brown | 0 | 41 |

The experiment is not yet complete, as some of the tops are still being attacked at the time of writing (March, 1964). It will be repeated with tops of smaller diameter in the shade of other trees. Cutting tops into shorter lengths may hasten drying or the onset of blue stain, and is being investigated.

## 4. SIREX AND RESIN

### (i) PREVIOUS WORK ON RESIN AND RESIN PRESSURE

The following notes were made from the large literature on resin in trees and only cover some aspects of it which might be of interest in this study.

Bordeaux and Schopmeyer (1957) describe the principle whereby resin pressure can be measured with manometer tubes made from capillary tubing and hypodermic needles. Using this method in *Pinus elliottii*, they found no pressure differences from ground level to 1·8 m. The pressure varied mostly with time of day—highest pressures were reached at dawn and with high humidity and low temperature. Pressure was low at noon on warm clear sunny days. So with high transpiration the resin pressure was low (the effect of shrinkage of tracheids on neighbouring epithelial cells). The mean pressure varied from tree to tree. Cuttings had similar pressure to their parents—there is rather strong genetic control. When wounded, the factors affecting resin flow are the number and size of resin ducts, and the pressure and viscosity of the resin. Duct size and number vary with stem age. Pressure and viscosity are probably unaffected by stem size above 5 cm. The ratio of pressure to viscosity is also under genetic control.

Harm (1953) measured the size and number per unit area of resin ducts in *P. nigra*, and the secretion pressure. All were hereditary.

Vite (1961) demonstrated the way in which resin pressure in *P. ponderosa* was related to site and soil moisture, as well as to atmospheric conditions affecting transpiration. It was not related to age or crown class. He stressed the dependence of resin pressure on the moisture condition of the tree. To produce high resin pressures it is essential for the tree to maintain the turgidity of the epithelial cells lining the resin ducts.

*P. radiata* resin can be extracted from the wood with ether (Buckland, Dalley and Mathieson, 1953) and the amounts expressed as a percentage of the oven dry wood. Most of the resin is near the pith in trees 25 years old (10 per cent.). In the rest of the sapwood, resin content is about 1·0 per cent. to 1·5 per cent. Higher up in the tree, the increase towards the pith is slighter. There is no marked increase in resin content with age, except where there is heart wood.

Berkel and Hus (1952) give the following figures for the resin contents of *Pinus sylvestris* and *Pinus pinea.*

| | | | | |
|---|---|---|---|---|
| *P. sylvestris* | Sapwood | 4·19 per cent. | Heartwood | 9·17 per cent. |
| *P. Pinea* | Sapwood | 3·47 per cent. | Heartwood | 14·16 per cent. |

There was no change laterally in the sapwood, but some lateral change in the heartwood. There was no change with height in the sapwood.

Wettstein (1952) states that the resin yield in *Pinus nigra* depends on the development of epithelial cells and secretion pressure. These can be used to select good resin yielders from seedlings one to three years old.

The resin content of the wood varies with the season. In *P. radiata* in New Zealand (New Zealand Forest Service, 1949), the butts of 20 year old trees had the most resin in spring. High up (at 10 inches to 7 inches dia.) it was highest in autumn and winter. Higher up still (6 inches to 4 inches dia.) it was higher in spring than in autumn.

In the sapwood the resin content decreased towards the bark. Towards the top of the tree, it is higher in summer than spring in the sapwood, but is still less than 2 per cent. This periodicity may be general. In Scots pine, from the 34th to the 57th ring, the number of resin ducts reaches a peak every two or three years.

In *Pinus nigra* the number of resin ducts is low every third year, from the 30th to the 45th growth rings (Vasiljevics, 1960).

Kanak (1956) found that the amount of resin in Scots pine varied with site, being less on marshy sites. The amount increased with age and d.b.h. Within the stem, the resin was at a maximum at the butt, decreasing to 21 or 36 feet, then increasing to reach a second maximum at the base of the crown.

The average size of the resin ducts decreases with the age of the ring in Slash pine (Mergen and Echols, 1955).

The chemistry of turpentine does not change when a tree is moved to a different habitat or with season. It is genetically fixed (Mirov, 1957). The interesting grafting experiments of Mirov (1945) demonstrated that the constitution of resin produced in the stem is somehow influenced by the crown of the tree.

Valentini (1958) applied Fusarium spore suspension to wounds of Virginia pine. It caused continuous resin flow for a season.

Messeri and Saya (1960) studied the modifications of resin canals after wounding in *P. pinea.* Turgor increased, causing the epithelial cells to swell up and block the canals. The secretion of resin increased and then stopped as the epithelial cells became dehydrated.

Schwerdtfeger (1948) found that bark-beetle attack of spruce was not related to moisture content but to resin flow. When a tree has been infested, resin flow is very much reduced. Trees with " small resin flow " are normally selected as breeding trees. When enough beetles are present, healthy trees with normal resin flow are attacked. Smith (1961) measured the toxicity of pine resins to *Dendroctonus brevicomis* and *D. jeffreyi.* Both species could tolerate the volatile fractions of the resins of their natural hosts (*Pinus ponderosa* and *P. jeffreyi* respectively), but neither could tolerate the resin of the other's host. Resin of a hybrid host was toxic to both.

Vite and Wood (1961) found that resistance of *P. ponderosa* to bark beetle attack was connected with resin pressure; trees with low resin pressure were susceptible. This fact, considering the lack of correlation between resin pressure and crown class, is puzzling. Person (1928) assessed trees in pairs and found that the average diameter growth rate of trees killed by bark beetles was 40 per cent. less than the check trees.

Schopmeyer and Larsen (1954) noticed that an increase in the width of the last annual ring was associated with increased resin production. The resin yield of *P. nigra* is related to mean monthly temperature (Gordeev, 1954).

## (ii) MEASUREMENT OF RESIN PRESSURE

Resin pressure was measured with manometers working on the principle described by Bordeaux and Schopmeyer (1957) for *P. elliottii.* Glass capillary tubing with a bore diameter of 0·5 mm. was ground to fit the sockets of No. 16 veterinary hypodermic needles with "leur" fitting. " Record " fitting is narrower and the tubing has to be ground so fine that it becomes too weak to use. The tubing was stuck into the needle sockets with a resin glue and the other end of the tube closed in a flame. The needles were cut off to leave a length of 8 mm. After removing most of the dead bark, holes $\frac{1}{16}$th of an inch in diameter were bored 12 mm. into the tree and cleaned by pushing in a $\frac{1}{16}$ of an inch rod. If this is not done, small particles of wood, from the drilling block the bore of the needle. The manometers are pushed in until the tapered socket is embedded in the bark. The resin flows in under pressure, compressing the air in the capillary tube. The bore of the hypodermic needles is wider than that of the capillary tube, so an adjustment is made to give the " corrected length " of the original air column. The air space left after the resin has risen in the tube is measured in millimeters and the pressure calculated. As a rule, the manometers can be measured at intervals for two or three days before the resin crystallizes. If they are inserted in the tree during wet weather and a small amount of water gets in, the resin may crystallize very quickly. Three manometers are used to give a mean reading for a tree. After use, the end of the capillary tube is broken off and the tube cleaned out with methylated spirits. It can then be resealed and used again. Various lengths of capillary tubing were tried. Long lengths should give accurate results, but often the volume of the resin is too small to give true readings in a long tube. Lengths of about 12 cm. are now used. They can be broken and resealed twice before becoming too short for accurate measurement.

## (iii) RESIN PRESSURE MEASUREMENT AT PITTWATER

Resin pressure in *P. radiata* varies with relative humidity as in other pine species studied by Bordeaux and Schopmeyer (1957) and Vite (1961). The pressure may be as high as twelve atmospheres in wet humid weather. On some trees very low pressures have been recorded, but this may be connected with past Sirex attack (see 4 (vi) ). Trees with low pressure usually have a rather variable pressure round the stem and the resin often fails to rise at all in the manometers.

No relationship has been found between resin pressure and crown class at Pittwater and there is no direct relationship between the moisture content of the sapwood of trees and their resin pressure, but factors which affect moisture content generally affect resin pressure as well (Vite, 1961).

Sirex epidemics have been connected with drought years in New Zealand. Rawlings and Wilson (1949) considered that in wet trees, the fungus would be drowned and that droughts dispose trees to successful attack by reducing moisture content. The sudden drying round the oviposition tunnel mentioned previously makes this seem unlikely, but drought would also reduce resin pressure and possibly the dominant trees with well developed root systems would be affected least. Nothing is known about this. The tops of trees make ideal material for Sirex to breed in at Pittwater. Resin pressure falls to zero very quickly when a tree is felled (Vite, 1961), but moisture content also decreases.

Sirex attack is usually concentrated at the base of the crown. Resin pressure at the base of the crown has been measured on only two trees. Manometers were inserted at breast height and at 40 feet on two 30-year-old trees. The pressures were lower at 40 feet, on one tree by one atmosphere; on the other by two atmospheres.

If resin pressure is connected with Sirex attack, it may be important at the time of oviposition, during the day when it could deter the insects from drilling; or the maximum pressures reached at night may harm the egg, larva or fungus. Rawlings (1951) observed that Sirex often withdraws its ovipositor if a resin duct is broken.

The fungus is often concentrated in the medullary rays, where the radial resin ducts occur.

A heavy attack by Sirex may reduce the resin pressure by bleeding through the oviposition tunnels, making the tree more favourable for later attack. Eight manometers were fixed in one tree which had a diameter of 15 inches, two, one above the other on each of the north, south, east and west sides. Circles of fine holes were drilled round four of them, at a radius of two inches from the manometers on the north side, and one inch on the south side.

tunnel walls when the drilling female rotates her ovipositor. Chrystal thought it was for lubricating the egg and ovipositor, but it may also help to keep resin out of the oviposition tunnel. The symbiotic fungus grows very rapidly in the oviposition tunnel and the mucilage might be the first nutrient medium for the germinating arthrospores. If the female Sirex is opened the mucilage can be drawn out of the gland in long strings, fine like a spider's web. In insects which had been dead for over a month, it had dried to a tough rubbery consistency.

## (v) TREES PARTLY KILLED BY SIREX

Sometimes the top or one side of a tree dies, but the rest survives (Plate 5).

The tree in Plate 6 was felled and cut lengthwise with a chainsaw. Between the narrow strip of living wood which rose up like a pipe to the green branches and the dead wood, there was a continuous layer of resin.

Sirex had emerged from the dead part of the tree. No emergence holes have ever been found in living wood at Pittwater. The larvae may avoid the resinous layer which separates the living from the dead wood, or they may attempt to tunnel through it and die. An adult was found which had attempted to bore its way out of the tree through the living wood. It had died on meeting the resinous layer.

Sometimes only a small part of a tree is killed—either a branch or an area of the stem. Plate 7 shows where Sirex have emerged from a tree. The rest of the tree is quite healthy.

When a tree is partly killed, the part which survives has generally had a lighter attack. It seems to be less a matter of one part of the tree having more resistance. In an experiment in which Sirex were used in cages encircling the stems of trees, there was most attack on the north east sides of the trees. This was both the sunny side and the side in the lee of the prevailing wind.

## (vi) TREES WITH RESIN BLOBS WHICH SURVIVED SIREX ATTACK AND THE MECHANISM OF RESISTANCE

Ten living trees were felled in the regrowth at Pittwater. They were eight years old. Three were dominants, two co-dominants and five were more or less suppressed. Their diameters varied from 1·4 to 5·8 inches at breast height. All these trees had lesions in the bark filled with hard resin. There are often big blobs of resin about the size of a cherry, in the lesions. A typical blob is shown in Plate 7 and lesions in Plate 8.

Resin blobs are usually gas filled, but sometimes contain a fluid smelling strongly of turpentine. The resin and bark were cut away on the ten trees examined. No Sirex ovipositions were visible, but when the annual rings were cut away, the trees were found to have been attacked one or two years previously.

In cross sections of the stems cut through the lesions, there were dark patches of resin in the outer parts of the annual rings where oviposition took place.

The late wood of the next ring within the one attacked was heavily impregnated with resin all round the tree. Growth below the lesions was slowed up and parts of some of the trees had been killed, giving a fluted stem. In some trees on which part of the stem had been killed, the living part had grown more quickly than before. The fluting often followed the spiral grain of the trees.

The density of attack varied from 170 tunnels per square foot in one of the suppressed trees to 580 tunnels per square foot on one of the dominants. The tunnels were counted on rather short lengths of stem which had lesions; the attack may not have been so heavy on other parts of the trees.

Plate 5.—The tree in the centre has been killed by Sirex, except for a few branches between ten and twelve feet up.

Plate 6.—On the left a pipe of living wood (from which the bark has been peeled) leads to a branch. It is separated from the dead wood, containing Sirex flight holes, by a dark layer of resin.

Plate 7.—An elliptical strip has been killed on an otherwise thrifty tree. Two Sirex emergence holes are visible, and between them on the border between the living and the dead wood, is a resin blob.

Plate 8.—A tree which has survived Sirex attack, with lesions full of hard resin.

Eighty-three tunnels were dissected. Eggs were found in all ten trees examined.

They were distributed among the ovipositions as follows :—

| *Type of Oviposition* | *Percentage of tunnels in which eggs were laid* |
|---|---|
| Single tunnels | 8 |
| Double tunnels | 39 |
| Triple tunnels | 50 |

As in the large bleeding trees described, there was a very large proportion of single tunnels and very few triple tunnels. The mean figures for all ten trees were as follows :—

| | |
|---|---|
| Single tunnels | 73 per cent. |
| Double tunnels | 26 per cent. |
| Triple tunnels | 1 per cent. |

The single tunnels were slightly shorter on average than the others.

| | *Mean Length in mm.* |
|---|---|
| Single tunnels | 4·33 |
| Double tunnels | 4·86 |
| Triple tunnels | 4·83 |

The mean lengths of the tunnels were shortest on the trees with the narrowest annual rings, but even on trees with wide rings the mean tunnel length did not increase beyond about 5 mm. as the following figures show :—

| *Tree No.* | *Annual Ring width (mm.)* | *Mean Length of oviposition tunnels (mm.)* |
|---|---|---|
| 1 | 1·5 | 3·8 |
| 2 | 2·5 | 4·4 |
| 3 | 3·5 | 4·6 |
| 4 | 3·5 | 4·9 |
| 5 | 5·0 | 5·0 |
| 6 | 5·0 | 5·1 |
| 7 | 7·0 | 5·0 |
| 8 | 7·0 | 5·1 |
| 9 | 8·0 | 5·0 |
| 10 | 8·0 | 5·1 |

Perhaps the resinous wood was not suitable for making long tunnels. Few tunnels penetrated into the next annual ring. The reason that many tunnels were longer than the ring width is because they slant at a steep angle in the wood. No tunnels were found containing more than one egg.

Of the eggs laid, 46 per cent. hatched, but all the larvae died. Many of them died before leaving their oviposition tunnels, but some had managed to bore a short distance—(up to 2 cm.).

The eggs and larvae were completely impregnated with resin and all the oviposition tunnels were filled with it.

The fact that eggs hatched and some of the larvae managed to start tunnelling shows that the oviposition tunnels cannot all have filled with resin as soon as they were drilled. The resinous layer outside the annual ring which was attacked often has no tracheids, being composed entirely of resin ducts and medullary rays. It is so weak that the inner part of the stem can often be knocked out of a short length of log, leaving the part of the tree which grew in the years after attack, as a hollow cylinder. Sometimes more than one ring of resin ducts is formed, with a few tracheids between. The early wood of the annual ring formed the year after attack also has many more longitudinal resin ducts than usual.

The wood in the neighbourhood of the oviposition tunnels which has been dried (presumably by the fungus), remains dry, even when it is completely surrounded by wet sapwood.

The mechanism whereby the Sirex-affected wood becomes impregnated with resin is probably akin to that described by Harris (1961) for the resinification of knots. When water is removed locally from the wood, resin is forced into the empty tracheids under pressure. The resin would escape from the resin ducts when the water is removed from the epithelial cells lining them.

The tracheids of the early wood of the ring attacked only become filled with resin near the oviposition tunnel. Resin is unable to spread far in the early wood tracheids because their pits become aspirated. It passes in radially to the late wood of the next annual ring, along the oviposition tunnel, or through radial resin ducts. It can then spread laterally in the late wood as few pits in the late wood tracheids become aspirated (Harris, 1961). The late wood may become so resinous that a complete barrier of resin is formed between the inner and outer parts of the tree.

In transverse section, the dried patches of wood resulting from Sirex attack in trees which have resisted it, are often bordered along their radial edges by a diffuse rosy stain. Sometimes there is a narrow band of stain just within the dried area, separated from the moist wood of the tree by a thin border of dry wood. Harris (1964) demonstrated that the red stained wood reacts with benzedine to give an intense rusty red colour, indicating that it is composed of phenolic substances. These would probably be produced by the medullary rays. Whether the red stain limits the spread of the fungus has not been demonstrated as yet, but phenolic substances are well known to be compounds toxic to fungi and apparently are produced by many host plants as a reaction to infection or injury. Allen (1954) observes that red and brown substances may not themselves be toxic, but are produced by the oxidation of phenols to quinones and by subsequent polymerization. The red stain in trees which have resisted Sirex attack sometimes seems to diffuse through the wood colouring large irregular areas.

Low temperature has a strong effect on the time taken for Sirex eggs to hatch (see section 2 (iii) (*b*)). The growth of the fungus and the action of its enzymes are likely to be slowed up in a similar way and may be affected more by low temperature than the defence reactions of the tree. Trees which have resisted a fair amount of attack usually appear to have been attacked at the end of the summer before producing late wood, when cold weather is expected. Trees may show individual variation in their ability to produce resins and phenolic substances and to form traumatic resin ducts quite apart from their growth rate.

The type of healing which would produce resin blobs has been observed. Some Sirex were put in a cage round the stem of a young vigorous tree in November, 1963. They bored a few oviposition tunnels. Two months later, the bark was peeled away. Broad flat cavities had formed under the bark about 3½ cm. long and 2 cm. wide and 3 mm. deep. They were full of liquid resin. The cavities had been formed by the death of patches of wood and the shrinkage of patches of bark which were dried out. They were accentuated by a raised lip of callous tissue gradually encroaching on the dead area, especially from above.

This form of healing would produce resin blobs or lesions later on.

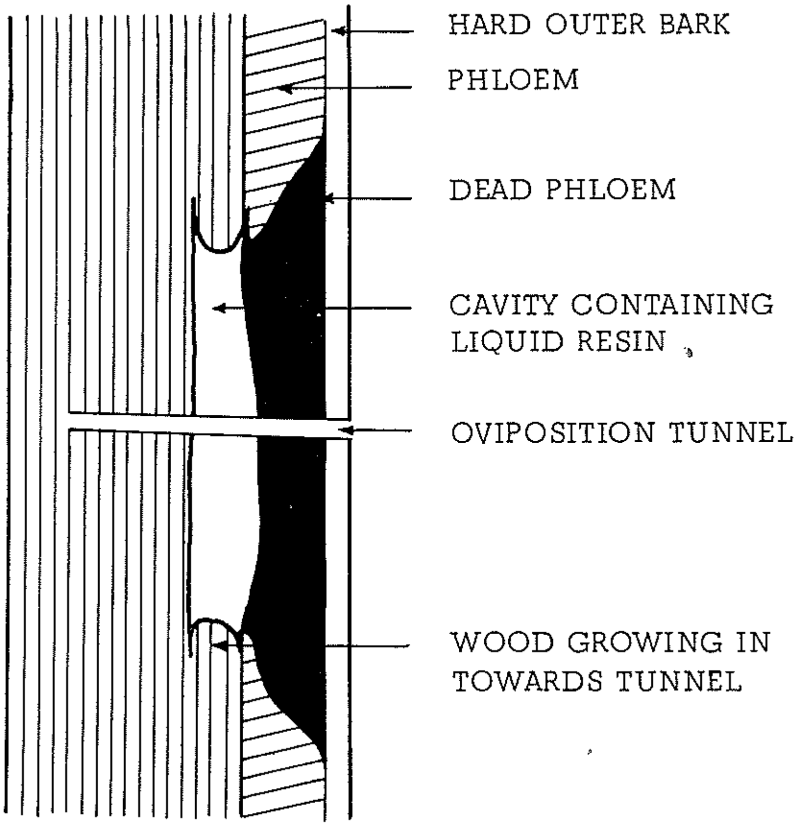

**Figure 13.—Diagram of radial section of a young tree, two months after attack.**

Oviposition does not always have such an effect on a healthy tree. More often the site is only marked by a small patch of brown cells in the phloem and bark, and the puncture in the wood which is quickly grown over. The annual rings can be cut away to find the small streaks of dried wood and the beginnings of the oviposition tunnels.

Trees with resin blobs and those which bleed a great deal of resin from oviposition punctures do not always survive, but few Sirex emerge from those which are killed.

Resin pressure measurements on trees with resin blobs have given low and erratic results so far, probably because the hypodermic needles on the manometers penetrate into dry streaks of wood, or into congealed resin. Measurements made nearer the tops of the trees above the parts attacked by Sirex might be more successful.

# 5. STUDIES OF TREES KILLED BY SIREX AND THE EFFECTS OF ARTIFICIAL ATTACK

It was hoped that by finding the regions in the tree with high and low survival of eggs or larvae and other details of attack, some clue might be given as to the physiological conditions in which Sirex succeeds or fails.

The following trees were dissected :—

(i) The largest dead dominant tree aged about 30 years, killed by Sirex in one compartment at Pittwater plantation.
(ii) A medium sized co-dominant, of the same age.
(iii) One of the smallest suppressed trees in the same compartment.
(iv) One of the largest dead dominant trees in the regrowth. It was killed when it was seven years old.
(v) A small suppressed tree from the regrowth, six years old.

The sixth part of this section deals with the effects of artificial attack on young trees.

### *Sampling methods*

The trees were felled, and sample logs one foot long cut at intervals. On large trees, samples were taken at every ten feet. On small trees the samples were taken much closer together.

The bark was peeled from the sample logs and ovipositions counted to give the number of ovipositions per square foot.

The dissection of oviposition tunnels is so time-consuming that it was not done on every sample log. The number of oviposition tunnels per square foot was plotted against tree height and they were sampled at certain heights, depending on this curve. Normally thirty tunnels were dissected for a sample, from five oviposition sites with three tunnels, five with two tunnels and five with one tunnel. (In some cases the sampling was doubled, but it gave similar results.)

To find the number of tunnels, eggs and flight holes for complete trees, the areas of the sections between sample logs were calculated and mean figures for the sample logs at either end of the sections were then applied to the sections.

## (i) A DOMINANT, KILLED WHEN IT WAS ABOUT THIRTY YEARS OLD

(FIGURF 14).

The tree was eighty feet tall, with a diameter of 12 inches under bark at breast height. Sample logs a foot long were cut at ten foot intervals up the tree.

The number of oviposition tunnels per square foot of stem reaches a maximum of 550 half way up the tree, in the lower part of the crown. The very low number at the base of the tree might be due in part to the small surface area available to the Sirex. Where the bark is fissured, oviposition only takes place in the fissures. Sirex rarely drills through more than 4 mm. of hard bark. On trees of this age at Pittwater, the layer of soft inner bark and phloem is usually one to three mm. thick. On cross sections of the stem, the amount of circumference taken up by thick bark and fissures was measured and the number of oviposition tunnels per square foot of available area calculated. The number of oviposition tunnels on the lower thirty feet of a tree is larger than at the lower part of the crown on this basis.

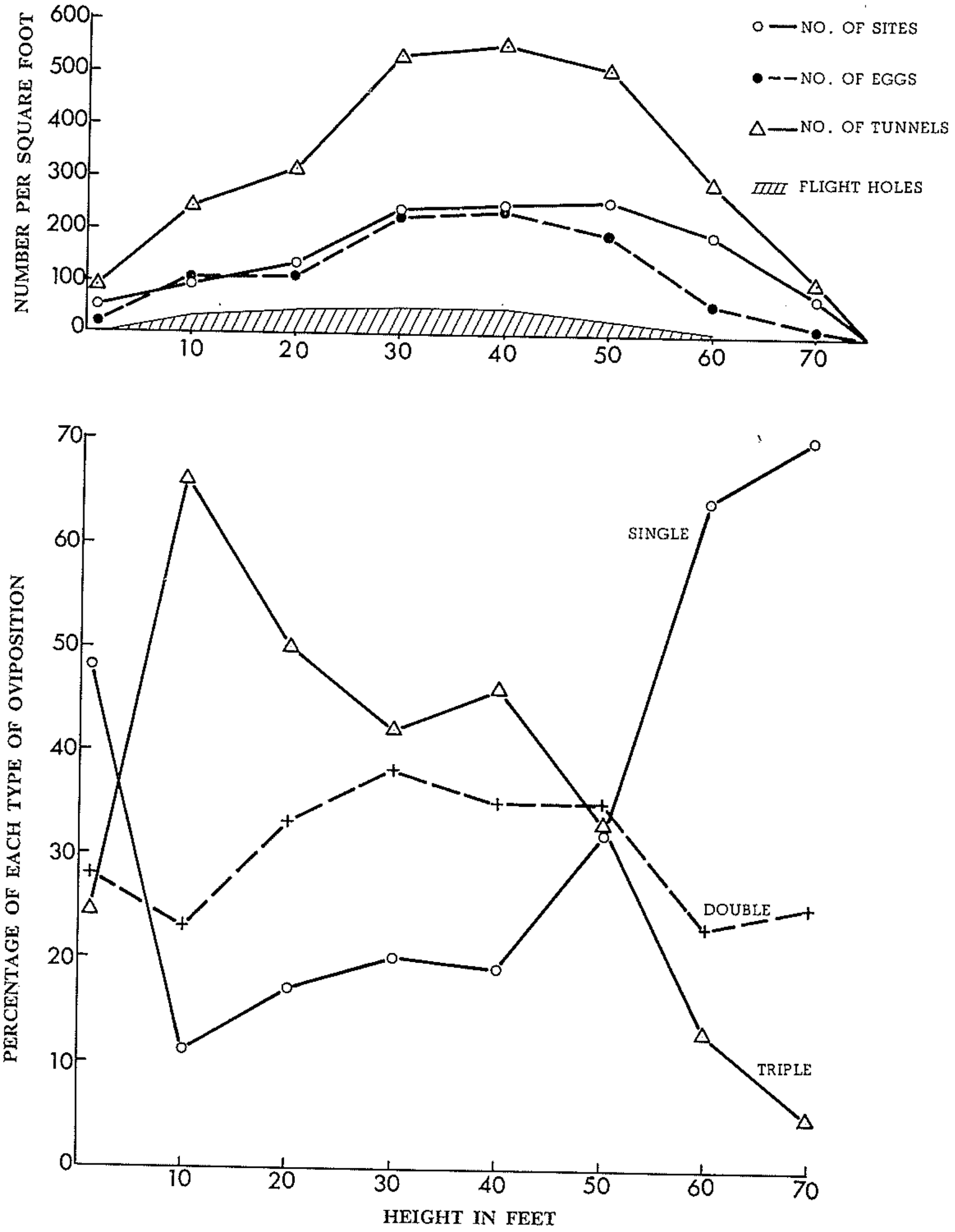

Figure 14.—Observations from a dominant tree killed by Sirex when it was thirty years old.

TABLE XIII

DENSITY OF ATTACK ON THE AVAILABLE AREA OF THE STEM

| Ht. of Sample (Feet) | Bark Thickness in in mm. | | Percentage of Bark Surface occupied by crevices | Oviposition Tunnels | | |
|---|---|---|---|---|---|---|
| | Thick Bark | In Crevices | | Amount in Crevices | No. per sq. ft. of gross area | No. per sq. ft. in Crevices |
| 1 | 27·0 | 4·0 | 10 | Crevices only | 84 | 840 |
| 10 | 7·5 | 2·5 | 20 | Crevices only | 240 | 1,200 |
| 20 | 5·5 | 2·3 | 25 | ¾ in crevices | 317 | 952 |
| 30 | 5·0 | 2·0 | 35 | ⅔ in crevices | 531 | 1,020 |
| 40 | Bark missing from Sample | | | ...... | 552 | .. |
| 50 | 2·0 | 2·0 | .. | ...... | 505 | .. |
| 60 | .. | 1·5 | .. | ...... | 285 | .. |
| 70 | .. | 1·0 | .. | ...... | 100 | .. |

Sirex, particularly large ones, show a preference for rough bark, quite apart from the condition of the wood and soft bark underneath (see Section 2 (iv) ).

The number of oviposition sites per square foot does not follow quite the same trend on the graph as the line for the number of oviposition tunnels because of the varying number of multiple tunnels.

Oviposition sites having one, two or three tunnels occur in different proportions at different heights up the tree. The proportion of double tunnels is highest in the middle of the tree, but there is no great variation with height. The percentage of triple tunnels is at a maximum at 10 feet (66 per cent.) and generally decreases with height to a minimum at 70 feet (5 per cent.). The proportion of single tunnels behaves in the reverse way to triple tunnels, reaching a maximum at the top of the tree, and also being high at the very base of the tree.

In the experiments with logs, it was found that at very high and very low moisture contents the largest proportion of the single tunnels are made, and the smallest proportion of the triple tunnels. As the type of oviposition is connected with the number of eggs laid, it was concluded that the type of oviposition shows how favourable the log is to the Sirex. Judging by the pattern of oviposition, this dominant tree appears to have been most favourable at ten feet and least favourable at the top and right at the bottom. Fielding (1952) found that trees often have a minimum moisture content at ten feet. It is certainly very much higher in the tops of the trees at Pittwater than in the lower parts of their stems.

As in the experiments on logs, triple-tunnel ovipositions generally had more eggs than the double tunnel type, and the single tunnels had fewer still. There was a sudden drop in the numbers of eggs in double tunnels at the bottom of the tree.

The survival from eggs to adults for the whole tree was only 20 per cent. The greatest percentage of eggs which produced adult insects is in the lower part of the tree, well below the part with the heaviest attack. The lower part of the tree may have been attacked later than the upper part, when the tree's vigour was reduced, or it could even have been attacked the year after the tree was killed. The complete failure of eggs and larvae right at the butt is a feature common to many trees.

Most of the deaths among larvae occurred in the first and second instars, before they had tunnelled beyond the edges of the cores taken for sampling and dead larvae could not be found by splitting up the sample logs. They were all too small to see. Mortality is slight among larvae which have passed beyond the second instar.

Some adult insects were found which had died before emerging.

The numbers of oviposition tunnels made, eggs laid and flight holes are shown for the whole tree in Table XIV.

TABLE XIV

Data on Sirex Attack and Emergence from a Dominant Tree Killed when it was Thirty Years Old

| Section of Stem (Feet) | Mean Dia. (ins.) | Surface area (square feet) | Oviposition Tunnels | | Eggs Laid | | Flight Holes | |
|---|---|---|---|---|---|---|---|---|
| | | | No. per sq. foot | No. per Section | No. per sq. foot | No. per Section | No. per sq. foot | No. per Section |
| 0—10 | 12·1 | 30 | 162 | 4,860 | 65 | 1,950 | 15 | 450 |
| 10—20 | 11·3 | 28 | 278 | 7,784 | 111 | 3,109 | 30 | 840 |
| 20—30 | 10·5 | 26 | 424 | 11,030 | 169 | 4,394 | 41 | 1,066 |
| 30—40 | 9·4 | 23 | 541 | 12,450 | 233 | 5,359 | 44 | 1,012 |
| 40—50 | 8·1 | 20 | 528 | 10,560 | 218 | 4,360 | 34 | 680 |
| 50—60 | 6·3 | 15 | 395 | 5,926 | 125 | 1,875 | 12 | 180 |
| 60—70 | 3·9 | 10 | 192 | 1,920 | 31 | 310 | 0·5 | 5 |
| 70—75 | 2·0 | 2 | 50 | 100 | 3 | 6 | 0 | 0 |
| | | 154 | .... | 54,630 | .. | 21,363 | .. | 4,233 |

The number of Sirex required to lay the twenty-one thousand or more eggs, would depend on their size—the number of eggs per female varies from less than fifty to about five hundred (Rawlings, 1953).

The oviposition tunnels rarely penetrated beyond the outer annual ring, which was 3 mm. wide up to about thirty feet; at forty feet it averaged 3·5 mm. and from fifty to seventy feet it was 4 mm.

### (ii) A CO-DOMINANT KILLED WHEN IT WAS ABOUT THIRTY YEARS OLD

The tree was 68 feet tall, with a diameter of 8·4 inches under bark at breast height.

This tree was not dissected for eggs. The pattern of oviposition (Figure 15) is like that of the dominant, but the percentage of triple tunnels reaches a maximum higher up the tree than on the dominant and the number of tunnels per square foot reaches a maximum at 40 feet and shows a very sudden fall at 50 feet. There was least emergence in the part of the tree most heavily attacked. The wood was very resinous.

### (iii) A SUPPRESSED TREE, KILLED WHEN IT WAS THIRTY YEARS OLD

The tree was 36 feet tall and had a diameter at breast height of 3.3 inches under bark. From Figure 16, it will be seen that the number of oviposition tunnels per square foot is much lower than in the dominant of the same age, with a maximum of 140 compared with 550 for the dominant.

The number of eggs per tunnel is higher than in the dominant. There are few empty tunnels. (The large number of empty tunnels in the dominant probably contain fungus which would reduce the vigour of the tree.) Even the single tunnels had one egg to every five tunnels. Mortality was very much lower, and the line for the number of eggs laid is only just above the line for flight holes (Fig. 16).

The pattern of oviposition has some similarity to the pattern for the dominant and co-dominant. The triple tunnels increase from zero at one foot to a maximum half way up the tree, and then decrease again and the single tunnels behave in a reverse way to the triple ones. The proportion of triple tunnels is generally much lower than in the dominant and co-dominant.

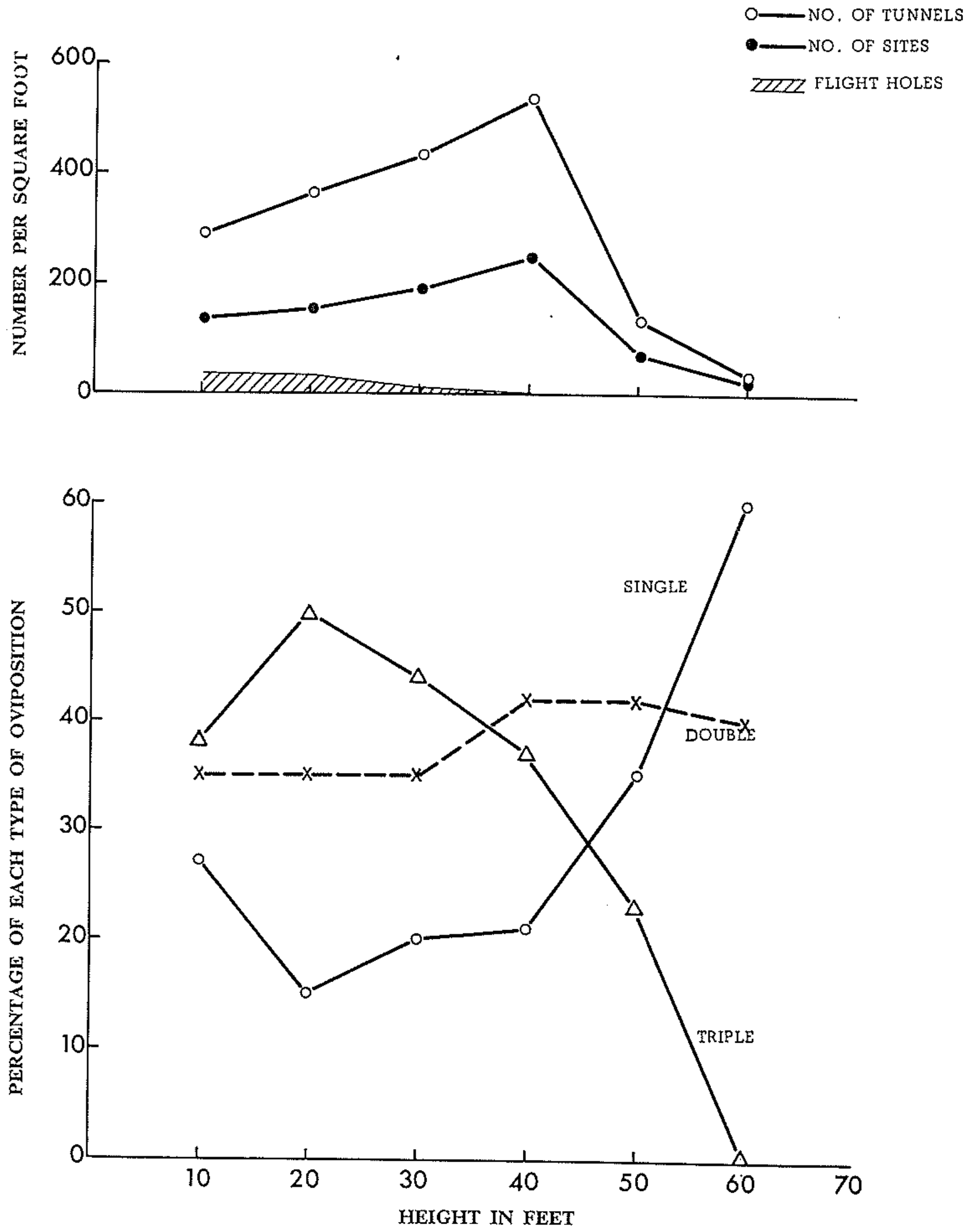

**Figure 15.—Observations from a co-dominant tree killed by Sirex when it was thirty years old.**

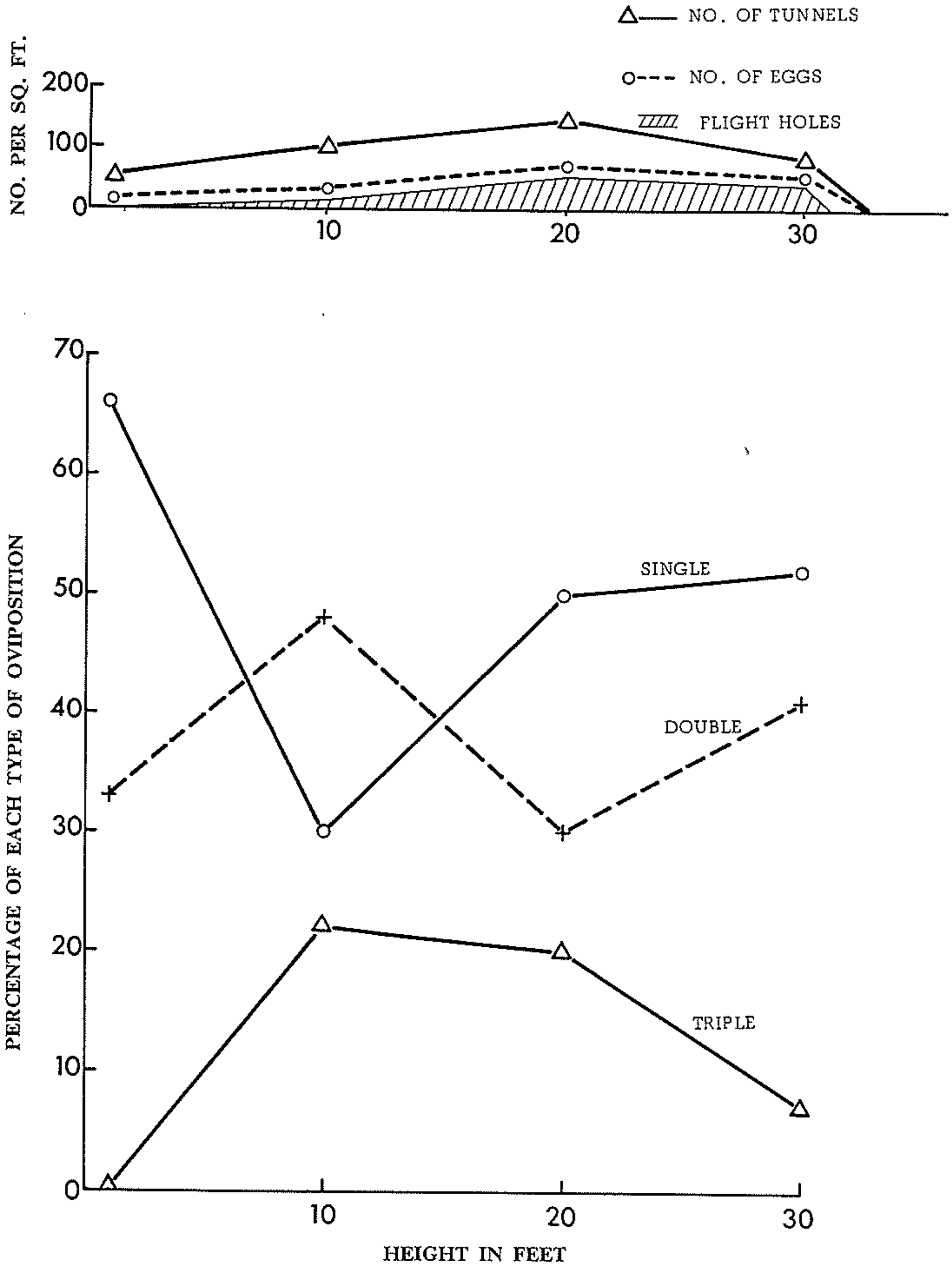

Figure 16.—Observations from a suppressed tree killed by Sirex when it was thirty years old.

Fifty-four of the oviposition tunnels dissected were measured in the wood :—

| *Length in mm.* | *No.* | *Percentage* |
|---|---|---|
| 1 | 1 | 2 |
| 2 | 10 | 18 |
| 3 | 20 | 37 |
| 4 | 16 | 30 |
| 5 | 4 | 7 |
| 6 | 2 | 4 |
| 7 | .. | .. |
| 8 | 1 | 2 |

The mean length of the tunnels in which eggs were laid was almost the same as the mean for tunnels without eggs (3·3 mm. compared with 3·4 mm.).

The annual rings were very close together at the outside of the tree, there being five in the outer 3 mm. near the base and at 20 to 30 feet the outer ring was only 1 mm. wide.

| *No. of Growth Rings Penetrated by Ovipositor* | *Percentage of Oviposition Tunnels* |
|---|---|
| 1 | 8 |
| 2 | 49 |
| 3 | 37 |
| 4 | 6 |

The bark was creviced from the base to 15 feet. The hard bark in the crevices varied from ½ mm. thick near the top of the tree to 2 or 3 mm. at the bottom.

The bark was not creviced much above ten feet.

TABLE XV

30 YEAR OLD SUPPRESSED TREE

| Ht. of Sample (feet) | Bark Thickness in mm. | | Percentage of Area of Stem occupied by Crevices | Oviposition | | |
|---|---|---|---|---|---|---|
| | Thick Bark | In Crevices | | % in Crevices | No. per sq. ft. of gross area | No. per sq. ft. in Crevices |
| 0 | 6·0 | 2·5 | 13 | 100 | 56 | 430 |
| 10 | 2·5 | 1·5 | 20 | 20 | 102 | 510 |
| 20 | .. | 0·7 | 0 | .. | 143 | .. |
| 30 | .. | 0·5 | 0 | .. | 104 | .. |

The total numbers of eggs and emergence holes are shown in Table XVI.

TABLE XVI

DATA ON SIREX ATTACK AND EMERGENCE FROM A SUPPRESSED TREE KILLED WHEN IT WAS THIRTY YEARS OLD

| Section of Tree | Length (feet) | Mean Diam. (in.) | Surface Area (sq. ft.) | No. of Eggs Laid | | No. of Flight Holes | | Oviposition Tunnels | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | per sq. ft. | Section | per sq. ft. | Section | per sq. ft. | Section |
| 0—10 | 10 | 3·8 | 9·6 | 21 | 202 | 13 | 125 | 79 | 758 |
| 10—20 | 10 | 3·0 | 7·5 | 54 | 405 | 40 | 300 | 122 | 915 |
| 20—30 | 10 | 1·9 | 4·7 | 64 | 301 | 49 | 230 | 123 | 578 |
| Total for the Tree | .. | .. | 21·8 | 908 | | 655 | | 2,251 | |

The survival for the whole tree was 72 per cent., but nothing survived at the foot of the tree. This was not because the larvae tunnelled upwards and no flight holes were found at the butt; the eggs failed to hatch.

## (iv) A SEVEN-YEAR OLD DOMINANT

Height 27 feet. Diameter at breast height 3·4 inches under bark.

This tree was attacked twice, once when it was five years old and again when it was seven. The growth rings were as follows:—

| | | *Outer Ring* | *Second Ring* | *Third Ring* |
|---|---|---|---|---|
| Ring width in mm. at 5 feet | .. | 4 | 8 | 9 |
| Ring width in mm. at 15 feet | .. | 3 | 7 | 13 |

The first attack seems to have slowed up the tree's growth and the narrowness of the outer ring was due to the second attack having killed the tree early in the season. The number of tunnels per square foot was less than 100 and most of the ovipositions were of the single tunnel type, with a few double ones and no triple ones.

TABLE XVII

THE FIRST SIREX ATTACK WHICH FAILED ON A DOMINANT TREE WHEN IT WAS FIVE YEARS OLD

| Height of sample (in feet) | Diameter in inches | No. of oviposition tunnels per sq. ft. | Percentage of oviposition sites with— | |
|---|---|---|---|---|
| | | | 1 tunnel | 2 tunnels |
| 1 | 3·1 | 24 | 75 | 25 |
| 5 | 2·2 | 79 | 89 | 11 |
| 10 | 1·6 | 45 | 100 | 0 |

The growth ring which was attacked was completely separated from the next (sixth) year ring by traumatic resin ducts when the stem was cut open; the outer two rings could be broken cleanly away from the ring which was attacked. No Sirex emerged.

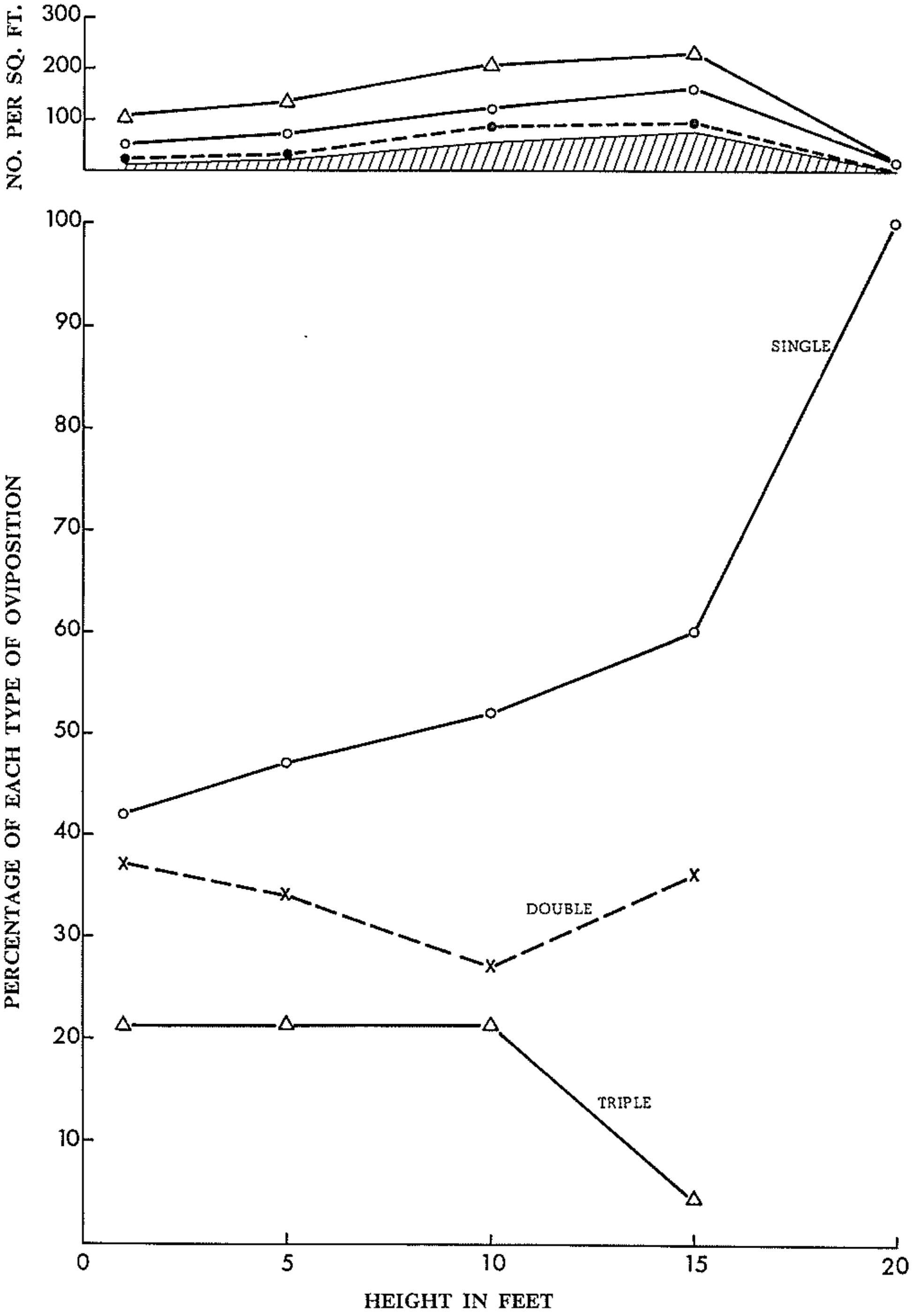

Figure 17.—Observations from a dominant tree killed by Sirex when it was seven years old. (Height 27 feet.)

The attack at seven years (Fig. 17) killed the tree. The number of tunnels per square foot was higher than on the 30-year-old suppressed tree. The oviposition pattern shows the usual increase in single tunnels and decrease in triple tunnels towards the top of the tree, but there is no corresponding change at the bottom of the tree. The actual number of triple tunnels is low and is comparable to the 30-year-old suppressed tree.

A possible explanation of the pattern of attack is as follows :—

The tree was lightly attacked when it was fairly healthy. The high moisture content made it rather unsuitable for oviposition, so most of the tunnels were single ones. The tree reacted by producing a layer of resin ducts. The cambium was not killed. The next year the tree was not attacked (or not enough to be noticed) and grew well. In the seventh year it may have suffered from drought. Young trees are wet all the way through and use the reserves of water from the inner growth rings when they need it. But the inner part of this tree was sealed off by a layer of resin, which hardened in the ducts and medullary rays, so it dried out and was successfuly attacked. The drying of the tree could help to explain the difference in the pattern of oviposition in the two attacks, but the diameter also changed and this too affects the pattern.

Perhaps the influence of diameter on the oviposition pattern (see 3 (iv) ) can be further separated with the figures for this tree. The diameter/height graph for the tree when it was seven years old is almost a straight line. The diameters of the samples taken at 3·1 and 2·2 inches from the inside of the tree for the first attack cut this line at points corresponding to heights of 5 ft. 9 ins. and 12 ft. 9 ins.

The proportion of each type of oviposition taken from Figure 17 at these heights are presented against diameter, along with those for the first attack, in Table XVIII.

TABLE XVIII

THE OVIPOSITION PATTERN OF THE FIRST AND SECOND ATTACKS AT THE SAME DIAMETERS ON THE YOUNG DOMINANT TREE

| Diameter in Inches | Percentage of Oviposition Sites with— | | | | | |
|---|---|---|---|---|---|---|
| | 1 tunnel | 2 tunnels | 3 tunnels | 1 tunnel | 2 tunnels | 3 tunnels |
| | First Attack | | | Second Attack | | |
| 3·1 | 75 | 25 | 0 | 48 | 33 | 21 |
| 2·2 | 89 | 11 | 0 | 56 | 32 | 12 |

At 3·1 ins. diameter the first attack has 1·56 times the proportion of single tunnels and at 2·2 ins., 1·59 times as many as in the second attack. This could be due to a change in moisture content.

The pattern on small trees like this one is very much like that on the tops of big trees. (Compare Fig. 17 with Figs. 14 and 15).

### *Tunnel Length and Egg Laying*

Ovipositions from the attack at seven years were sampled and had a relatively high number of eggs per tunnel (Fig. 17). The average width of the outer annual ring was 4 mm. at five feet and 3 mm. at fifteen feet, but at fifteen feet there was scarcely any lignification of the late wood of the previous year and the tunnels went through two rings. The effect of this on the lengths of the tunnels is shown in Table XIX.

## TABLE XIX

### THE LENGTH OF OVIPOSITION TUNNELS ON THE SEVEN YEAR OLD DOMINANT (SECOND ATTACK)

| Length of Oviposition tunnel in mm | Number of Tunnels Measured— | | | | | |
|---|---|---|---|---|---|---|
| | At Five Feet | | | At Fifteen Feet | | |
| | Triple | Double | Total | Triple | Double | Total |
| 3 | 5 | 2 | 7 | .. | .. | .. |
| 4 | 4 | 4 | 8 | 1 | 2 | 3 |
| 5 | 6 | 2 | 8 | 3 | 3 | 6 |
| 6 | .. | 1 | 1 | 1 | 3 | 4 |
| 7 | .. | .. | .. | 1 | 2 | 3 |
| 8 | .. | 1 | 1 | .. | .. | .. |
| Total No. .. .. | 15 | 10 | 25 | 6 | 10 | 16 |
| Mean Length .. | 4·1 | 4·6 | 4·3 | 5·3 | 5·5 | 5·4 |

If the outer annual ring of a tree is 4 or 5 mm. wide, the oviposition tunnels rarely penetrate through the hard late wood of the next ring.

At five feet, only single eggs were found in the tunnels, but at fifteen feet a third of the tunnels containing eggs had two eggs. Tunnels with two eggs were all more than 6 mm. long.

The concentration of oviposition in the upper part of this tree (Fig. 17) might have something to do with the easier conditions for boring in the wide outer ring.

Most of the larvae from the second attack tunnelled in the two outer rings—they did not eat through the resinous layer towards the inside of the tree. Survival was almost as high as in the thirty year old suppressed tree.

## TABLE XX·

### THE SECOND SIREX ATTACK AND EMERGENCE FROM THE SEVEN YEAR OLD DOMINANT TREE

| Section of Stem (Feet) | Mean Diam. (ins.) | Surface Area in sq. ft. | Oviposition Tunnels | | Eggs Laid | | Flight Holes | |
|---|---|---|---|---|---|---|---|---|
| | | | per sq. ft. | Section | per sq. ft. | Section | per sq. ft. | Section |
| 0— 5 | 3·5 | 4·7 | 121 | 569 | 29 | 136 | 16 | 75 |
| 5—10 | 2·9 | 3·9 | 172 | 671 | 59 | 230 | 38 | 148 |
| 10—15 | 2·2 | 2·9 | 219 | 635 | 97 | 281 | 67 | 194 |
| 15—20 | 1·4 | 1·9 | 124 | 236 | 45 | 85 | 39 | 74 |
| Total for the Tree | .. | 13·4 | .. | 2,111 | .. | 732 | .. | 491 |

## (v) A SUPPRESSED TREE, SIX YEARS OLD

The number of tunnels per square foot was very low on this small tree. The pattern is shown in Fig. 18. There were few ovipositions with triple tunnels and those which were found were all at the bottom of the tree.

The single tunnels contained no eggs. The average number of eggs per tunnel was 0·5 in the double tunnels. Many of the tunnels went through two growth rings and some of the longer tunnels had two eggs. There was some emergence from where the tree was less than one inch in diameter, but most emergence came from the lower part. There was no oviposition on the stem below 0·7 ins. diameter. One very small female would be capable of laying all the eggs in this small tree.

TABLE XXI

Sirex Attack and Emergence—Suppressed Tree, Six Years Old

| Section (Feet) | Mean Diam. (ins.) | Surface Area (sq. ft.) | No. of Oviposition Tunnels | | No. of Eggs | | No. of Flight Holes | |
|---|---|---|---|---|---|---|---|---|
| | | | per sq. ft. | Section | per sq. ft. | Section | per sq. ft. | Section |
| 0—1 | 1·2 | 0·3 | 106 | 32 | 51 | 15 | 40 | 12 |
| 1—2 | 1·1 | 0·3 | 72 | 22 | 25 | 7 | 17 | 5 |
| 2—3 | 1·0 | 0·3 | 83 | 25 | 26 | 8 | 13 | 4 |
| 3—4 | 0·9 | 0·2 | 27 | 5 | 4 | 1 | 0 | 0 |
| 4—5 | 0·8 | 0·2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total for the Tree | . . | 1·3 | . . | 84 | . . | 31 | . . | 21 |

Over the tree as a whole, 68 per cent. of the eggs survived. The oviposition pattern is not so definite as it is in bigger trees; the samples were much too small—the surface area of the tree to five feet was only 1·3 square feet.

The larvae make very complicated tunnels in such small trees, crossing and recrossing the pith from one side of the tree to the other.

## (vi) SOME RESULTS OF ARTIFICIAL ATTACK ON YOUNG TREES

Sirex with glued wings were put on the stem of a tree at the beginning of February, 1964. The tree was five years old, with a diameter of 3·5 inches at breast height and showed no signs of previous attack. For Pittwater, it was a fairly vigorous tree. During the following two and a half weeks, several other Sirex were put on until the number of oviposition holes on the bark of the middle part of the tree was 130 per square foot. (This would be equivalent to about 260 tunnels per square foot.) Some of the oviposition was made by wild Sirex which were seen on the tree ten days after the first artificial attack was tried. At different heights, oviposition sites made at different times were marked with different colours so that they can be recognised when the tree is dissected. It is possible that many of the eggs laid during the first wave of attack are overcome by resin, the early ovipositions serving to change conditions in the tree making it suitable for subsequent attack.

Four weeks after the first attack, the crown of the tree turned a yellowish green. The yellowing appeared first in the stem needles and spread outwards along the branches. By five weeks the whole tree was yellow except for the leading shoot and a few branch tips. It may have died so quickly because it was quite small. Rawlings (1948) has observed that trees which succumb to Sirex usually die in from two to six months.

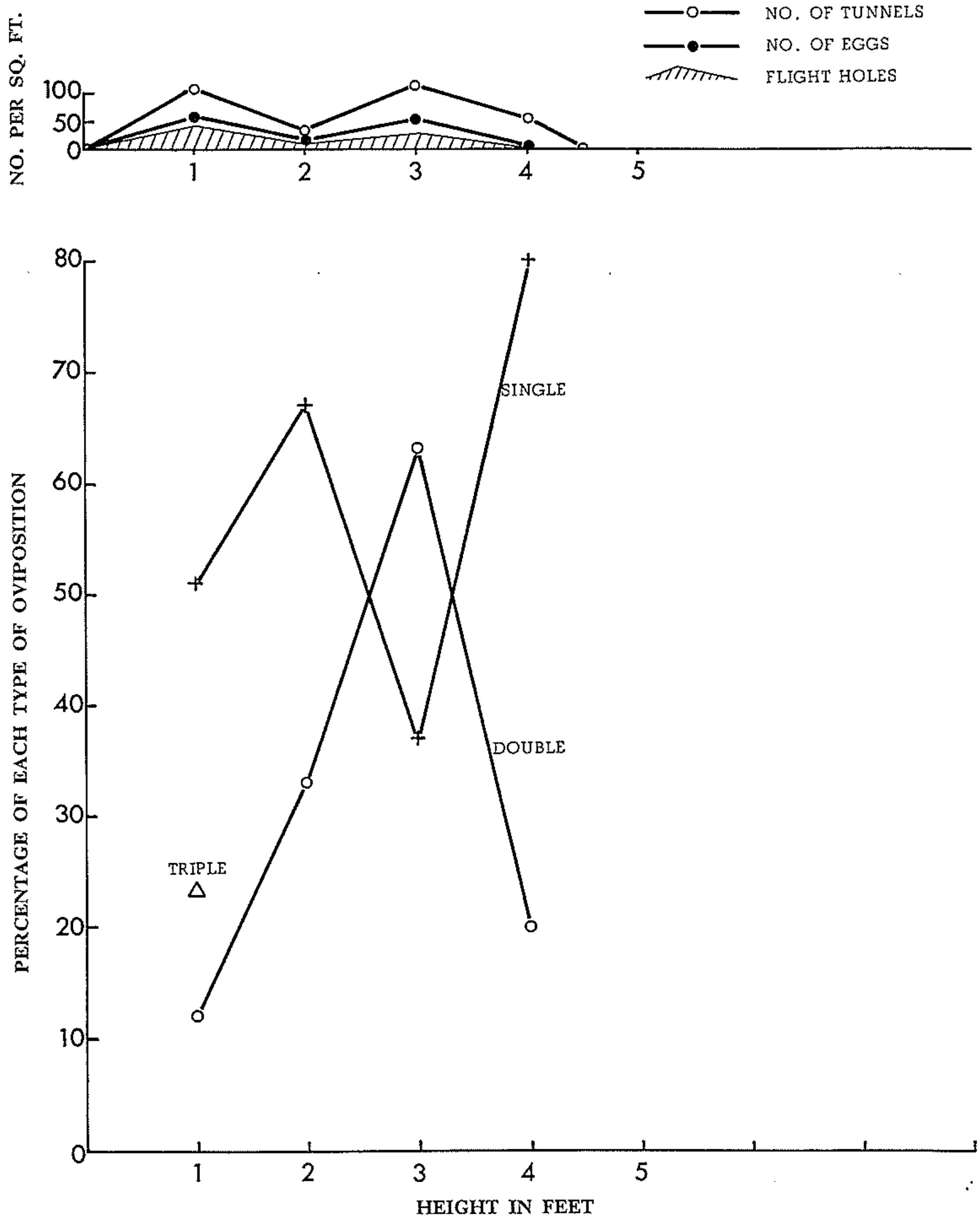

Figure 18.—Observations from a suppressed tree killed by Sirex when it was six years old. (Height 9 feet.)

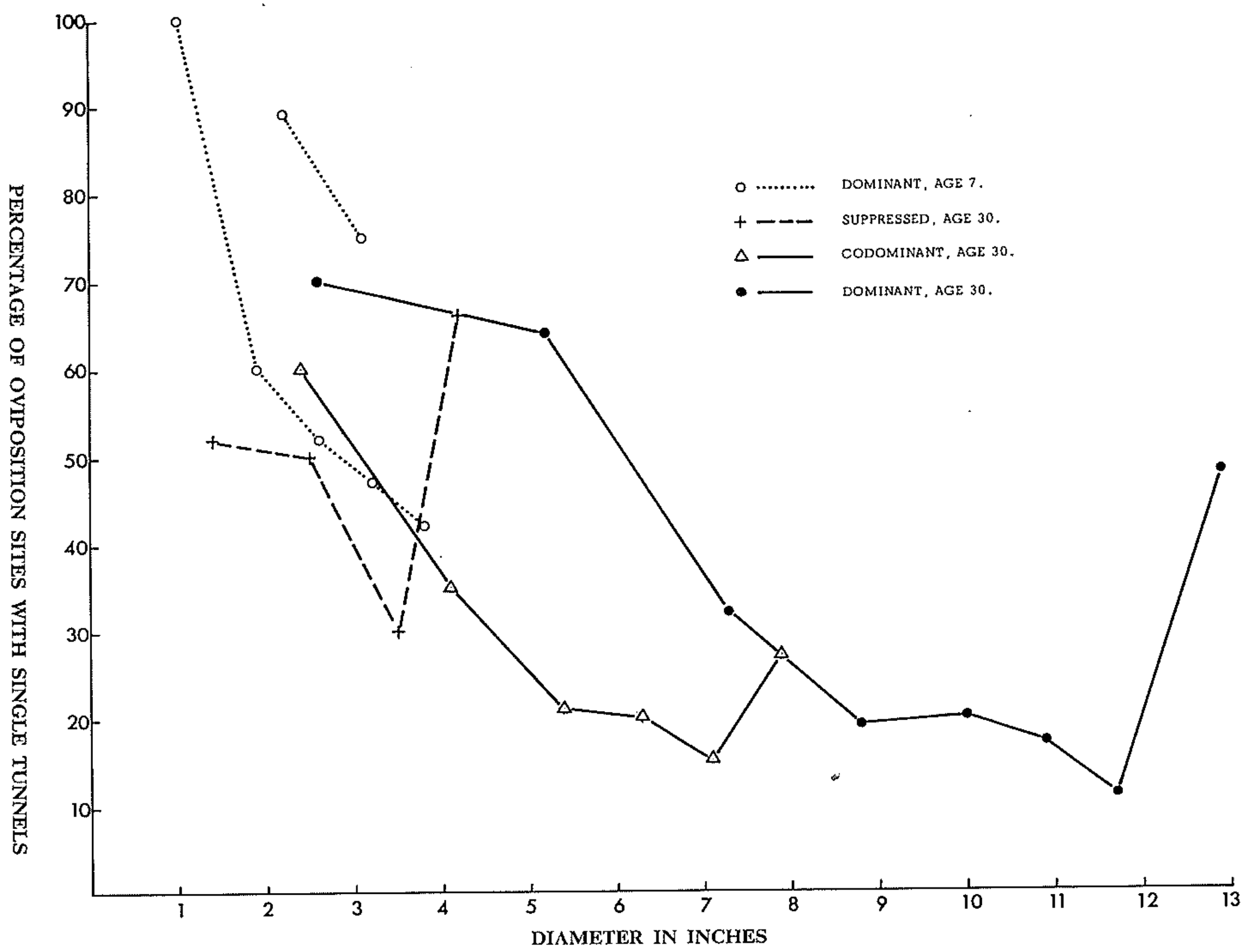

Figure 19.—The variation with diameter of the proportion of oviposition sites having single tunnels in four trees.

The tree was attacked again by wild Sirex very slightly just after the crown had gone yellow. Sirex were seen on the tree on three occasions six weeks after the first attack, but very few extra oviposition holes were made. The tree had probably passed beyond the suitable condition. This may explain why small trees and tops generally have a lower number of ovipositions per square foot, than old trees killed by Sirex.

Another regrowth tree, a vigorous dominant, five inches in diameter, with the previous year's growth rings half an inch wide and a high resin pressure and no signs of previous attack, had a few female Sirex put on it in February. The insects had been used in other experiments and were more or less worn out, but a few oviposition tunnels were made, from which flowed long streams of resin. Attack from wild Sirex followed within two weeks and was repeated again and again in March. By mid-March, the crown started to turn yellow in the same way as the first tree described.

Small squares of bark were cut from the stem when the crown started to go yellow. The outside of the wood felt dry, and the phloem had lost its normal juicy character. Small beads of resin eventually came from the radial resin ducts. This treatment normally produces much stronger resin flow from healthy trees. The resin pressure was measured. Before attack, it was comparable to that of two other trees nearby. Three weeks after the tree had been fairly heavily attacked, the resin pressures were as follows :—

| | *Midnight* | *Noon* |
|---|---|---|
| Two control trees | 9·4 atmospheres | 3·6 atmospheres |
| | 10·0 atmospheres | 3·2 atmospheres |
| Attacked tree | 4·7 atmospheres | 2·5 atmospheres |

Sirex attack had halved the maximum pressure reached. At midday, when the weather was hot and windy, the pressure was lower than that of the control trees, but not so much lower.

One Sirex with its wings glued walked onto an adjoining suppressed tree and drilled some tunnels in it. The tree soon started to go yellow. This behaviour may contribute to the group dying of trees, common in the dense regrowth at Pittwater. Even wild Sirex, after they have done a lot of drilling, become loath to fly and wander groggily around. On logs in cages, after making many ovipositions, they become so concentrated on their work that they will even attempt to drill in rubber or metal.

Sirex were put on three other trees which had no sign of previous attack. Two of them were vigorous trees with healthy green crowns. One was a very small suppressed tree about one inch in diameter. The vigorous trees bled quite a lot of resin from the oviposition tunnels. After less than three weeks the stem needles of one of them started to turn yellow and both trees were attacked by wild Sirex.

If a tree is attacked, other Sirex are certainly attracted to it. The most obvious cause of attraction is resin, but dying trees and tops without fresh resin on them also seem to be attractive. Six trees were ringed with an axe to a depth of one inch into the sapwood at the beginning of February. Two of them were then attacked by wild Sirex which stayed just above and below the cuts for a few days. On one tree, the resin pressure was measured and a foot above and below the cut, no pressure was recorded. Ten feet above the cut, the resin pressure was 2·5 atmospheres, compared with 8·0 atmospheres on the control trees. The resin soon hardened and although Sirex were very active during the next month, no further attack was recorded until four of the trees were broken by the wind in March, at the places where they had been ringed. Three of them were attacked soon afterwards. There was little resin flow from the breakages. Until the trees were broken their crowns appeared quite healthy. This and the continued attack on the tops makes it appear as though dying foliage is attractive. The ringed trees looked quite healthy until they blew over—there was no yellowing of their crowns.

# 6. THE EFFECT OF THINNING, MANURING AND PRUNING ON SIREX ATTACK

## (i) THINNING AND MANURING

Any treatments which will increase the vigour of the forest stand are likely to increase its resistance to Sirex attack. To test the effect of thinning and manuring, twelve $\frac{1}{10}$th acre plots were laid out in the regrowth, each one chain square with a quarter chain buffer around it. Eight of the plots were thinned in June, 1962, four of them to leave 600 per acre and four to leave 300 per acre. Four were left unthinned. On the four unthinned plots, the trees which would be left if the plots were thinned to 600 or 300 trees per acre were marked.

Before thinning, an assessment was made of the stand by examining trees on two $\frac{1}{100}$th acre strips on each plot. The results summarized for all plots, are shown in Table XXII.

TABLE XXII

Mean of Two 1/100th Acre Samples on each of 12 Plots

(Figures per Acre)

| Dia. Class (ins.) Breast Height | No. of Trees in Class | % of Total | Dead Trees | % of trees in class | Dead Trees with Flight Holes | % of trees in class | Total dead and dying | % of Class Total |
|---|---|---|---|---|---|---|---|---|
| 0—0·99 | 6,641 | 70·2 | 280 | 4·2 | 23 | 0·35 | 320 | 4·8 |
| 1—1·99 | 2,295 | 24·3 | 183 | 8·0 | 31 | 1·4 | 229 | 10·0 |
| 2—2·99 | 442 | 4·6 | 25 | 5·7 | 4 | 0·9 | 34 | 7·7 |
| 3—3·99 | 43 | 0·4 | 1 | 2·3 | . . | . . | 1·3 | 3·0 |
| 4—4·99 | 13 | 0·1 | 0·3 | 2·3 | . . | . . | 0·3 | 2·3 |
| 5—5·99 | 0 | . . | . . | . . | . . | . . | . . | . . |
| 6—6·99 | 4 | 0·4 | 0 | . . | . . | . . | 0 | . . |
| Total . . | 9,438 | . . | 489 | 5·2 | 58 | 0·6 | 584 | 6·2 |

Trees which had not reached a height of four feet three inches were not assessed. The trees in the 0 to 0·99 class were rather small for Sirex to attack. The percentage of trees with flight holes in the 1—1·99 inch class was four times larger than in the 0—0·99 inch class. Dead trees of three to five inches in diameter did occur but they were uncommon and were not encountered in the rather small samples taken.

In November, 1962, half of the plots were manured with 7·4 cwt. of John Innes Base Fertilizer per acre.

The effect of thinning on growth and Sirex attack is shown in Table XXIII. The fertilizer appears to have had no effect so far. Thinning has more than doubled the mean diameter increment, and has reduced Sirex attack on selected trees. There have been few deaths since the experiment was started.

## (ii) PRUNING

It is well known to New Zealand foresters that Sirex attack and kill trees which are pruned in the summer months. To study this further an experiment has been started at Pittwater. Four hundred trees were selected in the area of dense nine year old regrowth at Pittwater plantation. They were all dominants with a minimum distance apart of eight feet. The area was divided into five

# TABLE XXIII

1/10TH ACRE THINNING AND MANURING PLOTS. SUMMARY OF INCREMENT (SEPTEMBER, 1962, TO SEPTEMBER, 1963) AND SIREX ATTACK IN SUMMER, 1962-63.

| Plot No. | Treatment | Mean inc. per tree | | B.A. Inc. per acre (cu. ft.) | Dead Trees No B.A. Acre | | Sirex Attack (Trees per Acre) | | | | % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Dia. (ins.) | B.A. (cu. ft.) | | | | Little | Some | Much | Total | |
| A1 Control 600 .. | Fertiliser .. .. | 0·24 | ·0003 | 4·287 | 10 | ·197 | 50 | 40 | 20 | 110 | 18·6 |
| B3 .. .. .. | Fertiliser .. .. | 0·28 | ·0004 | 3·361 | 50 | 2·379 | 50 | 110 | 90 | 250 | 41·0 |
| A2 .. .. .. | No fertiliser .. | 0·21 | ·00025 | 4·483 | .. | .. | 50 | 50 | 10 | 110 | 19·6 |
| B5 .. .. .. | No fertiliser .. | 0·36 | ·0007 | 6·848 | 20 | ·908 | 90 | 90 | 50 | 230 | 40·4 |
| Mean .. .. .. | | 0·27 | ·00041 | 4·754 | 20 | ·871 | 60 | 72·5 | 42·5 | 175 | 30·0 |
| A3 thinned to 600 .. | Fertiliser .. .. | 0·54 | ·0016 | 11·637 | .. | .. | 10 | 10 | .. | 20 | 3·3 |
| B1 .. .. .. | Fertiliser .. .. | 0·74 | ·0030 | 14·671 | .. | .. | 50 | 50 | .. | 100 | 16·1 |
| A5 .. .. .. | No fertiliser .. | 0·53 | ·00155 | 27·622 | .. | .. | 10 | 20 | .. | 30 | 5·0 |
| B4 .. .. .. | No fertiliser .. | 0·63 | ·00215 | 13·129 | .. | .. | 80 | 30 | .. | 110 | 18·0 |
| Mean .. .. .. | | 0·61 | ·00207 | 16·763 | .. | .. | 37·5 | 27·5 | .. | 65·0 | 10·7 |
| A1 Control 300 .. | Fertiliser .. .. | 0·24 | ·0003 | 2·707 | .. | .. | 40 | 10 | .. | 50 | 16·7 |
| B3 .. .. .. | Fertiliser .. .. | 0·33 | ·0006 | 3·614 | 10 | ·668 | 20 | 60 | 20 | 100 | 13·2 |
| A2 .. .. .. | No fertiliser .. | 0·26 | ·0004 | 2·707 | .. | .. | 30 | 10 | 10 | 50 | 17·9 |
| B5 .. .. .. | No fertiliser .. | 0·43 | ·00105 | 5·111 | .. | .. | 20 | 30 | 50 | 100 | 35·7 |
| Mean .. .. .. | | 0·315 | ·00059 | 3·535 | 2·5 | ·167 | 27·5 | 27·5 | 20·0 | 75·0 | 25·4 |
| A4 thinned to 300 .. | Fertiliser .. .. | 0·78 | ·0033 | 8·544 | .. | .. | 10 | .. | .. | 10 | 3·3 |
| B6 .. .. .. | Fertiliser .. .. | 1·02 | ·0057 | 16·072 | .. | .. | 40 | 10 | .. | 50 | 15·6 |
| A6 .. .. .. | No fertiliser .. | 0·70 | ·0027 | 8·056 | .. | .. | .. | .. | .. | .. | .. |
| B2 .. .. .. | No fertiliser .. | 0·85 | ·0039 | 9·564 | 10 | ·264 | 20 | 10 | .. | 30 | 9·7 |
| Mean .. .. .. | | 0·837 | ·0039 | 10·559 | 2·5 | ·066 | 17·5 | 5·0 | .. | 22·5 | 7·3 |

blocks with eighty of the selected trees in each. In each block, the selected trees were allotted to eight treatments at random. The treatments were pruning to eight feet in the months August, 1962 to February, 1963, and no pruning.

Before pruning all trees were examined and 21 per cent. of them showed signs of Sirex attack from previous years. Probably many more had been attacked, but the trees had grown and showed no signs of it.

The trees were examined again after pruning, in June, 1963. The result is shown in Figure 20. Evidently pruning, especially when it is done in summer, increases Sirex attack. There were more deaths also among trees pruned in December and January.

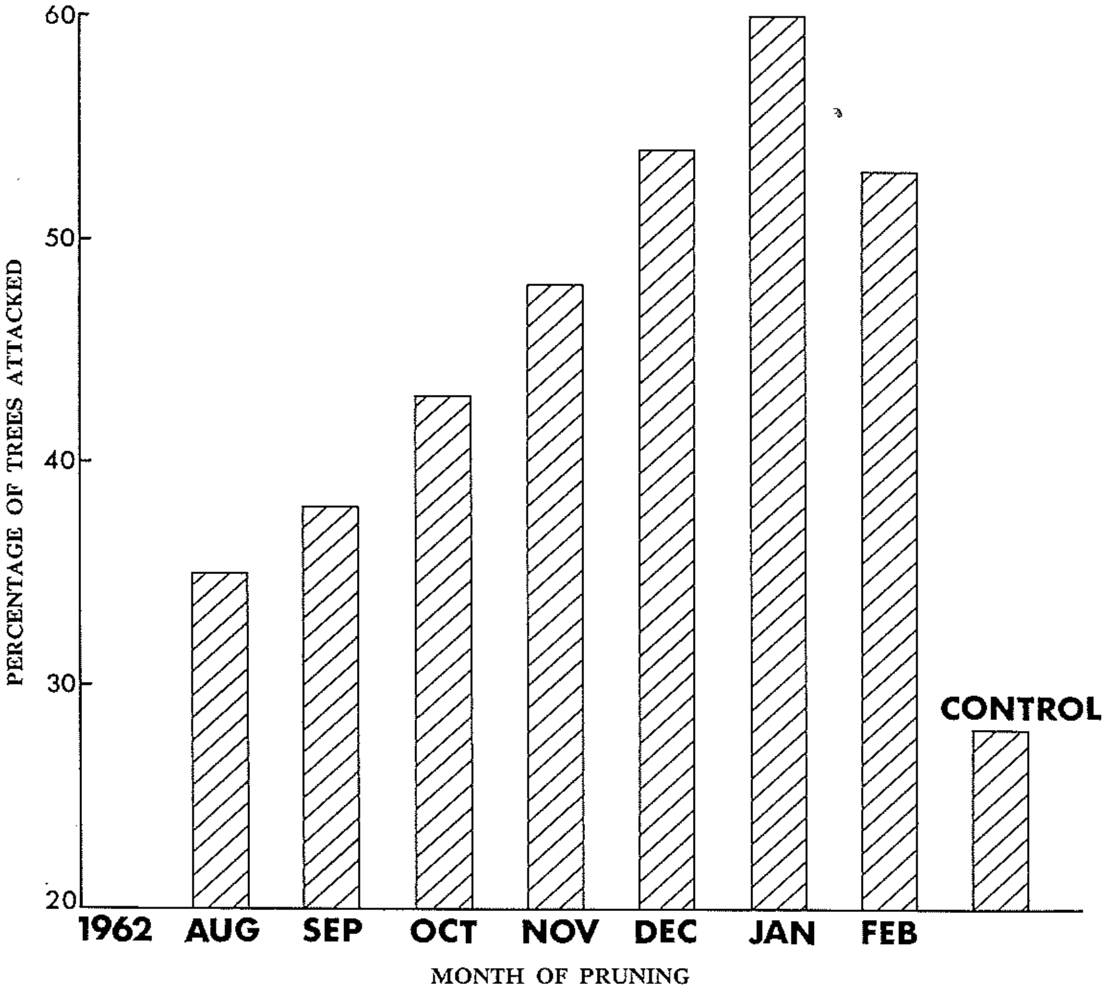

**Figure 20.—The effect of month of pruning on Sirex attack in the summer of 1962-63**

TABLE XXIV

DEATHS AMONG PRUNED TREES. (THERE WERE 50 TREES IN EACH TREATMENT)

| Time of Pruning | No. of Dead Trees in June, 1963 | New Deaths in March, 1964 | Total |
|---|---|---|---|
| August, 1962 | 1 | 0 | 1 |
| September, 1962 | 0 | 0 | 0 |
| October, 1962 | 2 | 0 | 2 |
| November, 1962 | 0 | 0 | 0 |
| December, 1962 | 4 | 1 | 5 |
| January, 1963 | 7 | 1 | 8 |
| February, 1963 | 2 | 0 | 2 |
| Unpruned control | 1 | 0 | 1 |

The diameters of selected trees ranged from two to seven inches.

Sirex attack showed no correlation with diameter (presumably because all the selected trees were dominants). Fewer of the selected trees were attacked where the regrowth was densest perhaps because of the greater number of suppressed trees available to Sirex. Also, trees in dense stands have fewer living branches below eight feet. They may have been less affected by pruning.

Although the summer pruned trees were attacked (they would have had fresh resin on them from pruning wounds), trees from the earlier months of pruning were also attacked more than the unpruned trees. The pruning was not severe enough to have had much effect on the trees' vigour. It is not yet known whether pruning reduces a tree's resin pressure. Dead and dying branches on the ground might be attractive. It is unlikely that resin would be attractive for long after it had hardened.

The trees will be pruned again in later years.

## 7. DISCUSSION

The results of experiments and observations have shown that the nature of the tree has a great influence on the behaviour of the insect. Whether Sirex is actually attracted to trees suitable for oviposition or suitable for the fungus and eggs and larvae to develop is still uncertain.

Person's (1931) theory of attack by *Dendroctonus brevicomis* on Western Yellow Pine might be relevant to Sirex attack, although later workers (Wood and Vite, 1961) have cast doubt on some of his explanations as applied to bark beetles. Like Sirex, the beetles attack suppressed trees in preference to dominants. (They also leave the *very* suppressed trees as Sirex does.) Person thought that the inner bark, fermented by fungi associated with the beetle, was very attractive to other beetles, but an initial weak attraction would be due to by-products of respiratory fermentation resulting from abnormal enzyme activity in sub-normal trees. The concentration of reducing sugars (levulose) is higher, and the concentration of sucrose lower in suppressed trees than in vigorous trees. When a tree is felled or severely injured there is an increase in levulose and a decrease in sucrose, indicating a sucrose hydrolysis such as would probably be associated with fermentation. When a tree has been attacked by beetles which were nearby, the fermentation caused by their associated fungi would attract other beetles from far and wide.

However, any explanation of Sirex attack must account for the large number of trees, including dominants, which are attacked unsuccessfully and often very lightly.

The most obvious source of attraction is resin. This would lead Sirex to pine trees. It seems then to visit trees at random, rejecting those with a high moisture content and perhaps with some other unfavourable characteristic. At least twenty-one per cent. of the 400 dominant trees selected for the pruning experiment had been attacked before the experiment was started, but not heavily enough to do them much harm. It may sometimes need to drill into the tree to find whether it is suitable. If a tree is wounded, as by pruning, Sirex females are attracted more strongly to it by the resin. When a suitable tree is found, they will stay on it, boring oviposition tunnels. The subsequent resin flow attracts other insects to the tree and waves of attack follow. Moisture content and resin pressure are reduced and the dying foliage may become a second source of attraction. If the Sirex population is high enough, trees which are unsuitable might receive so many exploratory attacks that they pass into a suitable condition for oviposition or into a condition which attracts mass attack because of resin flow.

The timber fallers have described how, as soon as trees are felled, Sirex females pounce on the tops, but they may be attracted by the smell of resin, and then reject the tops in favour of others felled a day or two before. Very little attack has been recorded on tops until a few days after felling. There are reports of how, when Sirex were very numerous at Pittwater, they would even attack the tyres of timber lorries which were smeared with resin.

Trees resist Sirex mainly by being unsuitable for attack in the first place, and it is probable that any tree can be killed if it is attacked heavily enough in the summer, even a vigorous dominant tree. Trees which, once attacked, appear to resist Sirex best are those which produce a lot of resin.

The Sirex cannot develop unless the tree, or part of it, is killed. If a tree receives a moderate attack, its survival depends on many things. It may have a high or low resin pressure, depending not only on conditions of climate and site, but also on its inheritance. Other facts concerned with resin, such as the number and size of ducts, and viscosity, are also partly under genetic control. Apart from making it unsuitable for attack, the tree's vigour can help it by increasing the production of oleoresin, and probably of compounds which limit the spread of the fungus and by hastening the formation of callous tissue with traumatic resin ducts. Trees with a high moisture content in their outer layers, by maintaining the turgidity of their medullary ray cells and the cells lining their resin ducts, may be expected to resist the Sirex fungus more strongly than drier trees. The unwillingness of Sirex to attack vigorous trees of high moisture content may be an adaptation for avoiding unsuitable conditions for development. The actual size of the tree also has a bearing on its survival. A very large number of Sirex are needed to give a heavy attack on a big tree and if one side of the tree escapes heavy oviposition, the tree will survive. A wide band of sapwood will leave the tree a pipeline to its crown for longer than a narrow band, once the drying starts to spread inwards, giving it more time to prepare its defences. Trees growing on dry sites or under conditions of permanent physiological drought, have a greater proportion of sapwood than those with an abundant water supply (Harris, 1954). Weather affects a whole host of factors, including the state of the tree, the development of Sirex eggs and probably the fungus also, besides the mating and flight habits of the insect.

Future work will include the study of the tree's mechanism of resistance, and will involve artificial attacks on trees of different physiological characteristics. The temperature will be controlled by keeping various parts of the trees warm and cool after attack. Some trees will have their health gradually reduced, and when wild Sirex attack them and stay on them, the trees' condition will be assessed.

The full role of the fungus is still unknown and it may play a part in nourishing the larva, but the reduction of resin flow following the drying of the wood must be essential for the larva's survival. If it started tunnelling in healthy sapwood it would be completely swamped by resin.

Sound silviculture designed to maintain the tree's vigour is probably the best method of control and for inherited resistance one must look to the tree's resin condition.

# ACKNOWLEDGMENTS

The writer wishes to acknowledge the cooperation of the Forestry Pulp and Paper Company of Australia Ltd. in permitting entry to the Pittwater plantation, for allowing the establishment of sample plots and for preserving any marked trees on the felling areas required for experimental purposes. The company has also provided a number of millable trees, free of charge, and Mr. B. Crosby, the Plantation Manager, is especially thanked for his ready cooperation. Dr. J. M. Gilbert of the Tasmanian Forestry Commission is Consultant Director of the Tasmanian Regional Station, and his continued help and advice is greatly appreciated. Many of the observations reported were made by W. J. Fraser and J. I. Dolezal, and their capable technical assistance is gratefully acknowledged. In particular, W. J. Fraser has helped by ingeniously solving many practical problems, and J. I. Dolezal by his skilful dissecting work. It is desired also to thank Mr. K. Taylor, Officer in Charge of the C.S.I.R.O. research team working on the biological control of Sirex, for assistance with the experiment on the drying of tops.

# REFERENCES

Allen, P. J. (1959). Physiology and biochemistry of defence, Plant Pathology, Vol. I, pp. 435-467. Edited by Horsfall, J. G. and Dimmond, A. E. New York, Academic Pr., 1959.

Berkel, A. and Hus, S. (1952). The resin content of the stem wood from the Turkish Pines, *P. sylvestris* and *P. pinea.* Istanbul Univ. Orm. Fak. Derg. 2*A* (2), 3-18. For. Abstr. 15 No. 697, 1954.

Bethge, Per Olof, and Lindgreen Bengt, O., (1962). Composition of Spruce fat and its change during wood storage. Svensk Papp Tidn. 65 (17), 640-646.

Bordeaux, P. F. and Schopmeyer, C. S. (1957). Oleoresin exudation pressure in Slash Pine. The Physiology of Forest Trees. Harvest Forest Symposium. K. V. Thimann (Ed.) New York, Ronald Pr., pps. 313-319.

Buchner, P. (1928). Holznahrung und Symbiose. Berlin. J. Springer.

Buckland, N. J., Dalley, O. T., and Mathieson, C. J. (1953). The distribution and nature of resinous material in *Pinus radiata.* 165-82. Proc. Aust. Pulp Pap. Ind. Tech. Ass. 7 165-182.

Chrystal, R. N. (1928). Natural enemies of Sirex Cyaneus Bull. Ent. Res. 19 Pt. 1 67-77.

Chrystal, R. N. (1928). The Sirex woodwasps and their importance in Forestry. Bull. Ent. Res. 19 Pt. 2. 219-247.

Chrystal, R. N. (1930). Studies of the Sirex parasites. Oxf. For. Mem. 11.

Clark, A. F. (1933). The horntail borer and its fungal association. New Zealand J. Sci. Tech. 15, 188-190.

Dimmond, A. E. (1955). Pathogenesis in the wilt diseases. A. Rev. Pl. Physiol. 6, 329-350.

Da Costa, E. W. B. (1959). Control of Blue Stain. C.S.I.R.O. (Aust.) For. Prod. Newslett. 258.

Fielding, J. M. (1952). The moisture content of the trunks of Monterey pine trees. Aus. For. 16 (1), 3-21.

Franke-Grosmann, H. (1957). Bericht uber die 8 wandersammlung Deutscher Entomologen Tagungsbericht Nr. 11. (R. Zondag's translation).

Franke-Grosmann, H. (1939). Uber das Zusammenleben von Holzwespen (Siricinae) mit Pilzen. Z. Angew Ent. 25, (4) 647-680. (E. A. Parkin's translation).

Gibbs, R. D. (1957). The physiology of forest trees. Harvard Forest Symposium. K. V. Thimann (Ed.) New York, Academic Pr.

Gilbert, J. M. and Miller, L. W. (1952). An outbreak of *Sirex noctilio* in Tasmania. Aus. For. 16 (2). 63-69.

Gordeev, A. N. (1954). Nature and dynamics of resin flow in *Pinus nigra*, var., caramanica. Derev. Lesohim. Prom. 3 (10), 9-11. For. Abstr. 16, No. 1786, 1955.

Harm, H. (1953). New findings on better resin yields. Allg. Forstztg. 64 (19/20), 243-9. For. Abstr. 17, No. 3988, 1956.

Harris, J. Maddern (1954). Heartwood formation in Pinus radiata. Tech. Pap. No. 1, N.Z. For. Serv.

Harris, J. Maddern (1961). The resinification of knots in Radiata pine. For. Res. Notes. N.Z. For. Serv. No. 28, p. 11.

Harris, J. Maddern (1961). Water conduction in the stems of certain conifers. Nature *189* (4765), 678-9.

Harris, J. Maddern (1964). Personal communication.

Hepting, G. H. (1954). Gum flow and pitch-soak in Virginia pine following Fusarium innoculation. Sta. Pap. Sth. east For. Exp. Sta., No. 40. p. 9.

Huckenpahler, B. J. (1936). A comparison of several methods of making moisture content determinations of standing trees and logs. J. of For. *34* (2), 165-168.

Hughes, R. V. and Mackney, A. W. (1949). Density and moisture content of New Zealand Pinus radiata. D. Don. Proc. Aust. Pulp Pap. Ind. Tech. Ass. *3*, 387-407.

Jackson, D. S. (1955). Pinus radiata/Sirex noctilio relationship at Rotoehu Forest. N.Z. J. For. *7* (2), 26-41.

Kanak, K. (1956). Resin content of Pinus sylvestris stems under different site conditions in Bohemia. Sborn. Csl. Akad. Zemed. (Lesn.) *29* (9), 645-56. For. Abstr. *18*, No. 3332, 1957.

Mergen and Echols, R. M. (1955). Number and size of radial resin ducts in Slash pine. Science *121* (3139), 306-7.

Mergen, F., Hoekstra, P. E. and Echols, R. M. (1955). Genetic control of Oleoresin yield and viscosity in slash pine. F. Sci. *1* (1), 19-30.

Messeri, A. and Saya, I. (1960). The anatomical and physiological mechanisms of resin tapping. III Mechanism of the immobilisation and draining of the resin after wounding. Ann. Acad. Ital. Sci. For. *9*, 153-66. Forestry Abstracts *23*, No. 616, 1962.

Mirov, N. T. (1945). Effect of the crown on the composition of oleoresin in pines. J. For. *43* (5), 345.

Mirov, N. T. (1957). Distribution of turpentine components among species of the genus Pinus. The physiology of forest trees. Harvard Forest Symposium, K. V. Thimann (Ed.) New York, Ronald Pr., pps. 251-268.

New Zealand Forest Service (1949). Annual Report 1948-49.

Parkin, E. A. (1942). Symbiosis and Siricid woodwasps. Ann. Appl. Biol. *29*, 268-274.

Person, H. L. (1928). Tree selection by the Western pine beetle. J. For. *26*, 564-578.

Person, H. L. (1931). Theory of explanation of the selection of certain trees by the Western Pine beetle. J. For. *29*, 696-699.

Rawlings, G. B. (1948). Recent observations on the Sirex noctilio population in Pinus radiata forests in New Zealand. N.Z. J. For. *5* (5), 411-21.

Rawlings, G. B. (1951). The establishment of Ibalia leucospoides in New Zealand. For. Res. Notes. N.Z. For. Serv. *1* (3), 1-4.

Rawlings, G. B. (1953). Rearing of Sirex noctilio and its parasite Ibalia leucospoides in New Zealand. For. Res. Notes. N.Z. For. Serv. *1* (8), 21-34.

Rawlings, G. B. (1957). The pathology of Pinus radiata as an exotic. Brit. Com. For. Conf. Australia and New Zealand.

Rawlings, G. B. and Wilson, N. M. (1949). Sirex noctilio as a beneficial and destructive insect to Pinus radiata in New Zealand. N.Z. J. For. *6* (1), 20-29.

Schwerdtfeger, J. (1948). The causes of bark beetle epidemics in spruce forests. Z. Weltforstw. *12* (4/6), 57-61.
For. Abstr. *12*, No. 762, 1950.

Schopmeyer, C. S. and Larsen, P. R. (1954). Predicting yields of gum from measurements of trees. Naval Stores Rev. *64* (7), 19.

Smith, R. H. (1961). The fumigant toxicity of three pine resins to Dendroctonus brevicomis and D. jeffreyi. J. Econ. Ent. *54* (2), 365-9.

Stillwell, M. A. (1960). Decay associated with woodwasp in Balsam fir weakened by insect attack. For. Sci. *6* (3), 225-31.

Valentini, G. (1958). Anatomical observations on resin tapped pines. Ann. Acad. Ital. Sci. For. *6*, 283-91. For. Abstr. *19*, No. 4224, 1958.

Vasiljevic, S. (1959). Distribution and number of resin ducts in some conifers. Sumarstvo *12* (5/6), 259-67. For. Abstr. *21*, No. 2292, 1960.

Vite, J. P. (1961). The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in Pinus ponderosa. Contr. Boyce Thompson Inst. *21* (2), Pt. 1, 37-66.

Vite, J. P. and Wood, D. L. (1961). A study on the applicability of the measurements of oleoresin exudation pressure in determining susceptability of second growth ponderosa pine to bark beetle infestation. Contr. Boyce Thompson Inst. *21* (2), Pt. 1, 67-68.

Warcup, J. H. and Morgan, F. D. (Editors) (1963). Report on Sirex Fungus Conference. Waite Agricultural Res. Inst.

Wettstein, W. von (1952). Tests of the progeny of good resin yielders. Abstr. in. Z Forstgenet. *2* (1), 22. For. Abstr. *14*, No. 992, 1953.

Wood, D. L. and Vite, J. P. (1961). Studies on the host selection behaviour of Ips confusus (Le Conte) (Coleoptera : Scolytidae) attacking Pinus ponderosa. Contr. Boyce Thompson Inst. *21* (2), Pt. 1, 79-95.

Yarwood, C. E. (1947). Water loss from fungus cultures. Am. J. Bot. 34, 515-520.

Yelft, J. T. (1962). The development of a power increment borer. For. Chron. *38* (3), p. 313.

Zondag, R. (1959). Progress report on the establishment in New Zealand of Ibalia leucospoides, a parasite of Sirex noctilio. For. Res. Notes. N.Z. For. Serv. No. 20.