RECENT OBSERVATIONS ON THE SIREX NOCTILIO POPULATION IN PINUS RADIATA FORESTS IN NEW ZEALAND*

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Introduction.

The last 100 years has seen the destruction of much of New Zealand's indigenous forests and their replacement by forests of exotic species. In these exotic forests *Pinus radiata* is the dominant species. From the time of their establishment the forests have been protected from fire but have received practically no silvicultural treatment.

As a result of lack of attention the forests have become overcrowded and, during periods of unfavourable climatic conditions, have suffered mortality due to attack by *Armillaria mellea*, *Diplodia pinea* and other factors consequent upon the congested and stagnant condition of the stands.

The mortality in most cases took the form of dying trees distributed throughout the stand and was regarded as normal suppression. *Sirex* was usually present but was regarded as secondary. Recently, however, the dying of all trees over areas of more than an acre has caused some concern and an investigation is now being made of the factors involved in the mortality.

During the course of this investigation some interesting details have been studied which point to *Sirex noctilio* and its associated fungus as the chief biological factors involved.

Most of the points investigated have already been discussed by various writers. *Sirex* has been dealt with by Chrystal and Hanson in England, and by Clark and Miller in New Zealand. Buckner, Cartwright, Muller, Francke-Grosman and Parkin have dealt with the question of symbiosis and the forestry principles involved have been given in numerous papers and text books.

There are certain economic, climatic and forest conditions peculiar to New Zealand which render these observations particularly pertinent at the present time and, at the risk of repetition, some account of the relationship between *Pinus radiata*, *Sirex noctilio* with its associated fungus, and possible control measures, will be given. In Europe, and particularly in England, *Sirex* species are not regarded as a serious menace to the forest, and it was largely in response to requests from New Zealand that a study of the ecology of the species of *Sirex* and their parasites was undertaken.

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The life history of *Sirex noctilio* in New Zealand differs in several details from that of species described in England by Chrystal and Hanson, many of these details may prove to be of considerable economic importance.

It has been recorded frequently that trees have been attacked and killed by *Sirex*, but the belief has been generally held that the attack was secondary to injury from other causes. It now appears evident that *Sirex* attack must be considered as the primary cause of death in many instances and that death is caused by the fungus inoculated into the tree during oviposition. In the past those who considered that death was caused by *Sirex* attack, attributed the killing to the bleeding of resin and to the tunnelling of the larvae, neither of which could bring about the death of an otherwise healthy tree.

The discovery of a symbiotic fungus associated with the *Sirex* permitted a new interpretation of the observed symptoms. The mechanism by which the trees are killed does not appear to have been mentioned previously nor has the role of the fungus as an active parasite been discussed. These points are at present under investigation and tentative conclusions are outlined in this paper.

**The Exotic Forests.**

The early colonists who settled in the almost treeless Canterbury Plains were the first to realise their need of trees for timber, fuel and shelter. To provide for their requirements they established plantations of exotic trees, utilising for this purpose the species with which they were familiar in Europe, besides eucalypts from Australia and conifers from North America.

In the forested areas the exploitation and destruction of the native bush which accompanied the spread of agriculture, caused the more prudent members of the Colony to see the need for the establishment of new forests throughout the country. *Pinus radiata* was found to be the ideal tree for the purpose and it quickly became the favourite species.

At the present time there are roughly 800,000 acres of exotic forests made up of 540,000 acres of *P. radiata*, 160,000 acres of other pines and 100,000 acres of various species other than pines.

If we assume a rotation of under 40 years for *P. radiata* and about 80 years for all other species, the annual area cut should be in the neighbourhood of 13,000 acres of *P. radiata* and 3,000 acres for other species. The labour required for the felling of 16,000 acres is considerable, and, if we assume two or three thinnings in a rotation, the area thinned annually would be between thirty and fifty thousand acres; a task which, obviously, is economically impossible at present.

*P. radiata* timber provides one quarter of the total annual cut and is second only to rimu in volume.

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With the possible exception of some areas of Nothofagus, all but an insignificant amount of the volume of timber from managed forests must, for at least the next 40 years, be of P. radiata and the species must be regarded as of the utmost importance to forestry in this country.

In its native habitat, where it occupies a restricted area, P. radiata is attacked by mistletoe and numerous species of insects and fungi. When introduced into this country with none of the biological factors which inhibited its optimum growth in California, it showed promise of remarkable possibilities by its ease of establishment, rapidity of growth and freedom from disease. In consequence it was planted in all parts of the country, in every variety of climate and type of soil. Some areas failed, particularly those subject to severe frosts, and from time to time fresh insects and fungi were introduced from abroad; most of these were harmless but some attacked the plantations causing minor damage.

When we consider the risks attached to the predominance of a single species, and particularly an exotic species prone to disease in its own country; and that this species has been widely planted to the very margin of its climatic and edaphic boundaries; that the plantations suffer from stagnation and suppression due to inadequate silvicultural treatment; that they are mostly of one age so that large areas must eventually become overmature, and that, as may be seen from past records, there is a very real danger of the introduction of fresh destructive forest insects, it is obvious that there is cause for concern as to what the future may have in store with regard to the pathology of this species.

**Exotic Insects—Sirex noctilio F.**

Of the large number of forest insects which have been introduced, two, Hylastes ater and Sirex noctilio, have become important as destructive factors in the pine forests.

Sirex noctilio was probably imported with timber from Europe and was established before 1900; it has probably been reintroduced repeatedly since then. Other species of Sirex, such as S. gigas are captured quite frequently but do not appear to have become established. Records of Sirex noctilio in Europe are very incomplete and most of the available information concerns S. gigas, S. juvencus, S. spectrum and S. cyaneus. The study of Sirex noctilio in New Zealand has been, to a large extent, based on records concerning these species.

In this country S. noctilio is recorded as ovipositing in pine, larch, Douglas fir, rimu, miro and kauri; it has also been observed trying to oviposit in creosoted P. radiata timber and has been reported ovipositing in Eucalyptus globulus. It has not, however, been recorded as emerging from any species other than pine, so that it appears
probable that it cannot complete its development in species of other genera.

In the Rotorua district Sirex begins to emerge about the middle of December; the males appear first and the females a few days later. The main emergence takes place in February, at which time they collect like swarms of bees in the treetops where copulation takes place. The mature female is governed by an intense urge to bore. This instinct is in excess of her capacity to lay eggs and in consequence more oviposition punctures are made than there are eggs laid. European species are recorded as laying several eggs in each puncture but more than one has not yet been recorded in this country.

The female selects a suitable site, usually the trunk of a living tree, and proceeds to bore oviposition punctures at the rate of one every 5 or 10 minutes. She usually proceeds from low down on the trunk and works upwards, boring into the stem every few inches; on reaching a certain height up the tree she flies down and the process is repeated. The length of trunk worked over varies considerably and there is a tendency to concentrate on the more exposed portions below the lowest green branches, particularly if exposed to the sun. The number of eggs deposited may be as low as one to every ten holes. The cambium surrounding the punctures discolors very quickly suggesting the action of some chemical which may also stimulate the flow of resin. From each puncture a stream of resin flows down the trunk, often for a distance of several feet, and globules of resin form at the end as the resin hardens. The smell of this resin appears to attract other Sirex and these combine in a mass attack on the tree. In each puncture, whether an egg is laid or not, spores are deposited and a fungus develops which damages or kills the tree. Females continue boring until they are exhausted and many die with their ovipositors fixed into the trunk. This may have given rise to the theory that they have been caught by the wood fibres of fast growing trees. It is recorded that the ovaries contain 400 eggs. Following mass attack, exit holes, which tend to be more frequent on the southern side of the tree, may number more than 200 to a square foot of bark. Counts made of Sirex larvae show that there may be over 700 per cubic foot of wood. This concentration of larvae means an even greater concentration of initial fungus infection and explains the extremely rapid dying of the trees.

The eggs are recorded as taking some little time to hatch, which gives the hyphae of the fungus time to get well established in the wood.

On hatching, the larvae bore longitudinally in the wood and later turn inwards towards the pith. When nearly full grown they turn again towards the exterior and, after a resting stage, pupate.
The life cycle occupies ten to thirteen months, but those which fail to emerge after the completion of the first year may emerge in the second year. Other species of Sirex in England are recorded as having a life cycle of three years. If this applies also to *S. noctilio* then the life cycle under New Zealand conditions has become considerably shortened. This is of importance, as *Rhyssa*, the parasite of *Sirex*, is recorded as ovipositing on *Sirex* larvae only during the second and third year, or, if first year larvae are parasitised, then the *Rhyssa* are unable to complete their development. If this applies in New Zealand, with the majority of *Sirex* emerging in one year, then the effectiveness of the control established by *Rhyssa* would be negligible.

Life history records are as yet incomplete but there is evidence to show that *Sirex* adults are active over a longer period in the north than in the south. In North Auckland they are recorded on the wing from September to May, in Rotorua from December to April and in South Island from January to March. The majority probably emerge in February and odd specimens may occur in any month except July and August.

The factors predisposing a tree to initial attack are not yet known, but the most important single factor appears to be that the tree should have a light, open crown of less than one quarter the height of the tree. This is correlated with exposure to full sunlight, high temperature and the smell of resin resulting from silvicultural operations between January and March. Once a tree is attacked the attraction for *Sirex* is increased by the smell of resin exuding from the punctures. Successful attack is associated with mass oviposition, high temperatures favouring rapid fungus growth, and probably by the moisture conditions within the tree.

It follows that drought conditions are present in the years most favourable to *Sirex* and drought may have a direct bearing in rendering the trees more susceptible to attack.

**The Symbiotic Fungus.**

In the female *Sirex* there is a pair of glands, situated at the base of the ovipositor, containing spores (oidia) of a fungus.

These oidia are deposited within the oviposition puncture made by the female and give rise to hyphae. The hyphae attack the living tissue and wood of the tree, and the infection extends upwards and downwards from the puncture and also inwards to the pith or heart wood. The cambium surrounding the puncture is also attacked and killed.

With mass attack the wedges of infection unite and the portion of the tree above is killed through the action of the fungus in stopping the flow of water to the crown. When the concentrated attack occurs below the lowest green branches the death of the whole tree follows rapidly. In some cases trees appear capable of resisting the attack,
no Sirex larvae develop and the fungus infections become isolated by resin formation. In other cases the trunk may be killed on one side or else the cambium may be killed in strips which causes a fluting of the trunk when growth takes place the following season.

Commonly, attack in February and March prevents the formation of the last layers of the summerwood and so injures the cambium that the next year’s wood may be separated with ease from that of the previous year.

The fungus causes a white rot of the wood and decay is extremely rapid.

In some 9-year-old regeneration which had been thinned and pruned in February, Sirex immediately attacked many of the standing trees with the result that they were dead and severely rotted in from two to three months. In contrast, the thinnings left on the ground were not attacked and remained green and living for up to six months after felling.

The fungus associated with S. gigas has been identified from cultures as resembling Stereum sanguinolentum. The fungus found with S. noctilio could, from its cultural characteristics, be a species of Stereum but is not S. sanguinolentum. Pinus and Sirex are both ancient genera and it is probable that the ancestors of both genera were associated in the forest and that the origin of the symbiont is equally ancient. Considering the probable antiquity of the association it would appear quite likely that the fungi associated with species of Sirex are specific and not identical with any free-living forms.

No sporophore has been found attached to trees attacked by S. noctilio which gives a culture similar to that invariably obtained from near Sirex oviposition punctures. Attempts to secure sporophores in flask cultures have, so far, failed, and it appears probable that the fungus is propagated only through Sirex.

Symptoms of Sirex Attack.

The symptoms accompanying Sirex attack are sufficiently distinct from damage by other agencies for the cause to be recognised. The damage grades from the sudden death of the trees within two months of the attack, through conditions in which the trees die after six months to the stage where there is partial or complete recovery. Trees which do not die within six months usually recover but are liable to breakage by wind and to heart rot. Trees in which the attack fails from the start may show little external evidence, but an examination of the wood shows characteristic resin formation between the summer wood and the new season’s growth and radial wedges of fungus infection.

The first symptom observed is the exudation of resin which streams down the trunk from the oviposition punctures and solidifies in globules. About a month later the cambium is found to be killed
in a strip above and below each puncture. This symptom is sometimes absent and is not of great importance in determining whether the tree will live or die.

The crown of the tree usually dies before the lower trunk and there may be no other sign except the yellowing of the foliage to indicate that the tree is in an unhealthy condition, in which case it is only by the microscopic examination of the wood that the cause of death can be determined. In a cleanly cut cross section of the trunk, at some point between the dead foliage and the butt, radial streaks of light and dark coloured wood show where the fungus has penetrated, and in section, the rays and tracheids are seen to be corroded and stuffed with hyphae.

Once the water supply to the crown is cut off, fungus penetration is rapid, and as the infection spreads the bark becomes loose and the wood rotten. The crown stays green for some time after death and frequently the leaves display a characteristic mottling before turning red. The foliage tends to droop and this gives the tree the general appearance of *Pinus patula*. This symptom is particularly evident where death is delayed until after spring growth has commenced.

In the wood the *Sirex* larvae may be found in various stages of development.

The symptoms observed are due to two causes; those due to the *Sirex*, such as punctures and resin flow, the larval tunnels in the wood and later the exit holes of the adults; and those due to the fungus, such as killing and discoloration of the cambium, staining and rot of the wood, the killing of the crown and ultimately of the whole tree.

The position may be complicated by the attack of *Armillaria mellea* from the roots and *Diplodia pinea* on the foliage.

Confirmation of the diagnosis can be obtained by the comparison of cultures taken from the wood.

**Control Measures.**

Control measures which might be adopted fall into three groups.

1. Chemical control.
2. Silvicultural control.
3. Biological control.

At present the extent of the damage is insufficient to warrant the expenditure of large sums of money and chemical control is out of the question.

It cannot be expected that any one measure will be successful and it is by the adoption of silvicultural measures coupled with biological control that control may be achieved.

By attacking areas in which silvicultural operations have been carried out, *Sirex* has dealt a hard blow to the practice of forestry at what is, in New Zealand, its weakest point. There are many
thousands of acres of P. radiata in urgent need of silvicultural treat-
ment and by attacking areas which have received more or less experi-
mental treatment, Sirex has provided some confirmation for the
ideas of those who consider these operations to be unnecessary. The
fault lies with the planning and execution of the work rather than with
the silvicultural principles involved, and although the results could
hardly have been predicted beforehand, it is possible to adjust the
silvicultural methods to prevent further damage.

On the other hand Sirex has demonstrated that there are limits
beyond which it is unsafe to go in the treatment and maltreatment
of P. radiata, and has shown clearly that correct silvicultural methods
must be determined and adopted.

One unknown quantity is the influence of climatic factors, but
it may be noted that the three months, December, January and
February for 1945-46 were the driest ever recorded at Kaingaroa,
where records have been kept since 1914. Over the same period for
both 1946-47 and 1947-48 rainfall was below average. Strong sun-
light appears favourable to Sirex for oviposition and high temperatures
favour the rapid growth of the fungus.

In the case of the area of P. radiata, consisting of 9-year-old regen-
eration at Waiotapu, which was heavily thinned and pruned in
1945-46 and examined in January, 1947, the portion treated between
January and March 1946 suffered severe mortality and some acres
were completely killed. In speculating as to the cause of this pheno-
menon it was noted :—

1. That the trees had been very dense and had poor crown
development.
2. That the thin bark had been suddenly exposed to strong
sunlight.
3. That the site conditions were poor with a northerly aspect.
4. That many trees which had not died had the trunk either
killed on one side or badly fluted with strips of dead cambium
between the last year’s growth.
5. That many of the trees on the edges of adjoining stands
exposed by the felling, had died and provided breeding
grounds for Sirex.
6. That there was considerable exudation of resin on the young
trees due to Sirex oviposition, and there were Sirex exit
holes.

In addition workmen stated that they had watched Sirex ovi-
positing on trees immediately after they had been pruned.

In view of the supposedly secondary nature of Sirex attack, the
damage to the cambium was at first thought to be due to exposure
to the sun, but after a similar area treated in 1947-48 at Whakarewa-
rewa State Forest had been studied, the killing was attributed to mass *Sirex* attack due to attraction by fresh resin on the pruned trees.

In the case of an area of twenty-year-old *P. radiata* at Kaingaroa in which considerable mortality followed a heavy first thinning, it was noted:

1. That the trees had extremely light and small crowns.
2. That the dead trees had been severely attacked by *Sirex* immediately below the lowest green branches.
3. That there was abundant material containing *Sirex* already present.

This case was complicated by the presence of *Armillaria mellea* as a contributory cause of death in many cases, and root damage by tractors during extraction.

The disturbing point was that the mortality in the thinned area was greater than in the surrounding unthinned portions of the forest. The conclusion arrived at was that the strong sunlight and conditions associated with the light crowns had brought about a concentration of *Sirex* from surrounding infested trees. Damage to the upperbole during felling operations may have served to attract the *Sirex*.

In the third case, at Rotoehu State Forest, spacing trials in which *P. radiata* was planted 3 ft. x 3 ft. and 4 ft. x 4 ft. suffered severely, the trees being killed over considerable areas. Mortality decreased with wider spacing. The explanation in this case is difficult but there must have been a build up in *Sirex* population over a number of years.

Similar cases have been reported from many districts throughout the country and the predisposing factors have been in most cases those leading to light and small crowns, exposure to isolation, and frequently, silvicultural operations.

*Sirex* does not appear to breed to much extent in slash but prefers live standing trees. Ideal conditions are provided by felling operations where unmerchantable trees are left standing in a narrow strip between felling areas. Logging roads and the newly exposed edges of areas not cut provide additional breeding grounds.

From these observations the following silvicultural measures are suggested:

1. Provide for clean logging and the salvage of dying trees.
2. Refrain from thinning and pruning operations between December and March.
3. Prescribe frequent light thinnings rather than thinnings too heavy and too late.
4. Do not expose stands of pine by making fellings on the northern face.
5. By thinnings maintain good crowns of more than one third of the total height of the trees.

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Biological control has already been attempted by the introduction of one of the two European parasites. Owing to the concern over the increase of *Sirex*, an attempt was made to introduce the two parasites *Rhyssa persuasoria* and *Ibalia leucospoides* from England. No success was achieved with *Ibalia* but *Rhyssa* was successfully reared in 1929 and 1931. Liberations were then made in various parts of the country and the parasite is now well established.

*Rhyssa* females display a highly developed instinct to bore, in the same way as *Sirex*, and move eagerly over the surface of tree trunks containing *Sirex* larvae. They have, however, no sixth sense for locating the larvae and bore more or less at random. The wood at this stage is well rotted, and in small diameter stems the rotted leaf traces leave open holes to the pith, and these points are frequently selected by the female for boring.

The ovipositor is very flexible and it appears probable that it can turn at a fair angle along *Sirex* burrows to find the larvae.

In two cases noted the *Rhyssa* bored between several larvae in heavily infested wood and failed to pierce any burrows. From this it would appear that, in spite of the great industry of *Rhyssa*, the ratio of host to parasite must remain high.

The natural spread of *Rhyssa* is very slow as it tends to remain near the tree from which it emerges. It is common in Whakarewa Forest but does not appear to have crossed the few miles separating it from Waiotapu Forest, even though there are numerous pine trees scattered over the area between.

The first males emerge early in October and the females somewhat later. Oviposition commences almost immediately and the larvae become fully grown in about six weeks. After the exhaustion of the food supply the larvae construct cocoons and rest throughout the remainder of the summer and winter, pupating shortly before the time of emergence.

In England, *Rhyssa* is recorded as parasitising only *Sirex* larvae of a year or more, that is to say during the second and third years. As in Rotorua the majority of *Sirex* emerge in one year, it was thought that the parasite might be ineffectual. This however, has proved not to be the case, as *Rhyssa* oviposits readily in larvae eight or nine months old, and as these larvae are almost full grown at this stage it is probable that *Rhyssa* will complete development.

Thus *Sirex* is exposed to *Rhyssa* attack from October until February. Those *Sirex* which fail to emerge during the first year are again exposed to attack from October onwards in the second year.

The effectiveness of *Rhyssa* may be estimated as its capacity for keeping *Sirex* below epidemic proportions, the important point being the number of females which are destroyed, and since *Sirex* males are recorded as being more numerous near the surface, a higher proportion of males than females may be destroyed.
On the whole it does not appear that Rhyssa has made much difference to the Sirex population in New Zealand, and more effective control might be achieved by introducing *Italia leucospoidea*, which parasitises the eggs and young larvae. There are also other species of *Rhyssa* and *Italia* which could be studied with a view to their introduction.

**Conclusions.**

It is as yet too early in the investigation to arrive at any definite conclusions and the results given in this paper must be regarded as tentative only.

Much research is required before definite proof can be obtained of the accuracy or otherwise of the implications drawn from the observations made. It appears positive, however, that under certain climatic conditions *Sirex* can cause appreciable damage, and its impact on regeneration, such as follows clear felling or fire, can be serious. The apparent effect of silvicultural operations in increasing the incidence of *Sirex* damage indicates the need for more care in the tending of the forests. Trees with less than one quarter of their height in crown are more liable to attack, while those in which the crown exceeds one third of the total height are not attacked, or, if attacked, are more likely to survive.

**Summary.**

*Pinus radiata* is the most important exotic forest tree in New Zealand, and, owing to its disproportionate use, the effects of any factor causing significant mortality would be serious.

Tentative results of an investigation into mortality in forests of this species indicate that *Sirex noctilio* and its associated fungus are the direct cause of death. The importance of predisposing factors in reducing the vitality of the tree, or in increasing the activities of the insect and the virulence of the fungus are being investigated. Silvicultural control measures afford the best means of reducing the damage but, owing to the large area involved, these measures are difficult to apply. Biological control may afford some measure of protection by reducing the *Sirex* population below that necessary for mass attack on the forest.

**References.**