SIREX NOCTILIO AS A BENEFICIAL AND DESTRUCTIVE INSECT TO PINUS RADIATA IN NEW ZEALAND

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Introduction

In a previous paper (7) an account was given of the roles played by *Sirex noctilio* and its fungus symbiont in causing mortality in *Pinus radiata* stands. It is now proposed to deal more fully with the predisposing factors which render the trees more susceptible to attack, and to give additional notes on *Sirex* and measures for its control.

At the beginning of the investigation into the causes of mortality in *Pinus radiata* two questions were raised. How were the trees being killed, and why ? To answer the first question all factors had to be considered, and, by a process of elimination, *Sirex* attack remained as the most probable cause. It was then necessary to consider whether or not the new symptoms were caused by the *Sirex* and symbiont already known or by a new race or strain of either or both. However, on account of the apparently spontaneous appearance of the trouble in widely separated districts it appears improbable that any new biotic factor is involved.

The question that then arose was why *Sirex* was capable of causing the death of trees in certain instances while not in others, and what predisposing causes were operating to render them susceptible to attack. Lack of fundamental information on the physiology of *Pinus radiata* and on the physical properties of pumice soils made it difficult to draw any definite conclusions, but it has been possible to form a reasonable and logical hypothesis to account for the observed phenomena.

The Cause of the Sirex Epidemic

Plants suffer from drought when the supply of water obtained through the roots is less than the demand for water made by the foliage. Drought is purely relative to normal local conditions and plants adapted to conditions of high rainfall and plentiful water supply will be affected by drought although an equal rainfall would be ample for plants growing in areas of low average rainfall.

If we examine the variation in summer rainfall for the months of December, January and February, as recorded by the Kaingaroa Forest Headquarters rain gauge, we find that the average monthly rainfall for the period since 1914 is 4.40 inches. Except for 1938-39, when the figure was 3.50 inches, every summer from 1933 to 1945 was well above average and for eight years over six inches a month were recorded. In 1945-46 there was a prolonged drought period from November, 1945, to March, 1946, the figures being as follows :—

November, 1945	1.09 inches
December, 1945	2.02 ,,
January, 1946	1.60 ,,
February, 1946	0.07 ,,
March, 1946	3.59 ,,
Total	8.37 ,,
Average per month	1.67 ,,

This was the most severe drought ever recorded at this station and, coming after thirteen years of high summer rainfall, it was to be expected that there would be considerable mortality of suppressed trees, but no abnormal number of deaths was observed except in planted areas with very close spacing, and in areas of dense regeneration which had been heavily thinned in February and which adjoined areas with high *Sirex* infestation.

It might be thought that by thinning, and thus reducing the number of trees per acre, that the effects of drought conditions would be lessened, but when the thinning is made in summer the remaining trees cannot send roots into soil formerly occupied by those of the felled trees and so cannot obtain an increased supply of water. To what extent lateral movement of water will take place in pumice soils under dry conditions is not known.

It is probable that if any advantages are derived from such thinnings they do not compensate for disadvantages of increased exposure to sun, wind and heat reflected from the ground. Possibly also, there may be direct heat injury to the cambium of the stem. Green pruning in the summer is one of the main contributing causes of injury and mortality following *Sirex* attack. Food materials which pass down the branches feed the cambium of the stem immediately below and when a branch is cut off the strip of cambium beneath suffers from starvation, causing sunken areas to appear beneath the branch stubs as growth proceeds. Frequently these areas are attacked by *Sirex* and appear particularly suitable for the rapid development of the fungus, so that the strips or the whole of the tree may be killed.

With thinning and pruning carried out between March and September it is probable that the roots would be able to spread and tap a greater volume of soil, and that the conducting tissues around the branch stubs would become adapted for the conduction of food to the areas of cambium formerly fed by the pruned branches. Crown growth would take place before the trees were exposed to summer conditions and the trees would have the benefit of the increased shade. Crown height or, more particularly, crown density appears to be a very important factor affecting resistance to attack. Possibly a dense crown is capable of exerting more suction, and so extracting more water from the soil or, more probably, a dense crown indicates a larger, healthier and better fed root system. It would appear probable that the foliage cannot have any effect on transporting water not already absorbed by the roots, but, on the other hand, in pines root pressure is said to be of far less importance than leaf suction. The whole question of the ascent and circulation of sap is so controversial that no definite statements can be made.

The drought of 1946 had little apparent effect on the trees unless we assume that many of the more superficial roots may have been killed. The soil moisture was replenished by the winter rainfall, so that there should have been little or no carry-over of the drought effects to the following year. However, the average summer rainfall for December, 1946, and January and February, 1947, was again low, being 2.20 inches per month, and there was a definite increase in the *Sirex* population. During the winter and early spring of 1947 considerable mortality was observed in the plantations. For the same period in the summer 1947-48 the monthly average rainfall was 3.60 inches and in the following winter there was a definite, although not serious, increase in mortality. For the summer of 1948-49 the monthly average was 3.00 inches but, on account of the cool and cloudy weather it was expected that there would be a decrease in the number of winter deaths. However, there was severe and widespread mortality throughout most stands, 25-30% of the trees died over many thousands of acres and in places losses were far heavier. The summer rainfall for 1949-50 was nearly average (4.34 inches) and the *Sirex* population, to the end of February at least, appeared to be normal.

It is possible to explain the course of the epidemic if we assume that, in periods of drought, free water is lost from the wood tracheids and is not replaced. Those with low water content are suitable for the *Sirex* fungus and *Sirex* larvae to develop, and although it follows that in 1946 the trees were rendered susceptible to attack the *Sirex* population was normal and, therefore, no unusual mortality resulted. In the following years the trees remained susceptible and moderately severe drought conditions were experienced which enabled the *Sirex* population to increase until it reached epidemic proportions by 1948.

Owing to mass attack in February, 1949, heavy mortality was experienced the following winter, but as the conditions within the trees were no longer favourable to the *Sirex* larvae few developed, and the population reverted to normal.

At the time of writing, the final outcome of the 1950 summer is still in doubt and it will be of interest to observe whether the prediction of only slight mortality this winter proves correct.

Rainfall figures are not very reliable data upon which to base evidence of drought severity. Other factors such as cloud, dew or cool winds may lessen the severity of the conditions, while high temperatures, bright sunlight and dry winds will have the opposite effect. Another factor is the prevalence of summer thunderstorms with heavy local rain. It is conceivable that a heavy shower, coming at a critical period, might soak one half of a compartment and leave the other untouched. Six months later mortality might show up in the part which had had no rain but not in the other. Without knowing the exact rainfall of each portion of the compartment it would be difficult to explain this difference. Depth of soil, aspect, slope and other local factors naturally have a considerable bearing upon local drought severity.

Sirex and its Symbiont.

The oviposition puncture made by the female *Sirex* penetrates through the cortex and into the wood making a hole up to an inch deep and 300 μ wide. The width is equal to about twelve tracheids so that with mass attack there is considerable disruption of the conducting elements of both the phloem and the xylem. In addition, in some way not yet explained, the cambium is killed above and below the puncture. This is done, possibly, by a chemical injected by the female or by a toxin produced by the fungus. Injury is visible so soon after oviposition that the chemical theory would appear more probable, but on the other hand, since the injury continues to spread for several weeks the idea that the fungus is responsible tends to be supported. It is possible that a toxin is produced by the fungus within the female *Sirex* and injected with egg, and that later the same toxin is produced by the fungus in the tree.

The ooidia of the symbiotic fungus, which are injected into the oviposition puncture with the egg, germinate and hyphae invade the ruptured tracheids. From this point further development probably depends upon the relative amounts of free water and air in the tracheids. When air is absent and there is a copious supply of water the fungus cannot develop, but under drought conditions it can spread upwards, downwards and inwards, rotting the wood and providing the conditions necessary for the development of the *Sirex* larvae.

On emerging from the egg, the larva makes a tunnel, 400 μ in diameter, into the springwood, where it is faced with the torn walls of about 150 tracheids. Thus it does not bore through "solid" wood but along thin walled tracheids containing fungal hyphae. After boring for about 1mm. the first ecdysis takes place and the cast skin is pushed back into the oviposition puncture. The larva tunnels in the summerwood until after the fourth ecdysis when it turns towards the centre of the tree. After the seventh ecdysis the larva is usually beyond the reach of *Rhyssa*.

The following table shows the normal length of the tunnel to each cast skin and the depth of the larva in the wood, exclusive of the bark.

Exuviae	Distance from Oviposition Puncture	Depth in Wood
1st	0 mm.	5 mm.
2nd	1 mm.	5.5 mm.
3rd	3 mm.	5.5 mm.
4th	7 mm.	6 mm.
5th	13 mm.	10 mm.
6th	23 mm.	18 mm.

After the 6th instar progress depends upon the changing moisture content of the wood.

It has been shown in flask cultures that the fungus will not grow in very wet wood taken from fast growing trees, and it appears also, that humidity has more effect than temperature upon the duration of larval and pupal stages. These points may help to explain the relationship between drought and insect abundance, and are being further investigated.

During the past year *Sirex* have been bred out of spruce (*Picea sitchensis*) and larch (*Larix decidua*), in both cases from trees which had recently died. The *Sirex* proved to be the same species and cultures from the wood yielded the same fungus.

Silvicultural Considerations

Had it been possible to carry out light thinnings at frequent intervals and so maintain the stands in a healthy condition, free from too much competition, then there can be little doubt that no *Sirex* epidemic could have developed. Under the conditions which existed in 1946 all fully stocked stands, planted 6 by 6 ft. or 8 by 8 ft. and over 15 years old, were in great need of thinning. Over many thousands of acres mortality from *Sirex* attack has reduced the stocking by 30% or more and the trees killed were, in an overwhelming majority of cases, just those which should have been removed by thinning, that is, suppressed trees and those with double leaders or other malformations.

The larger proportion of the trees killed could not have been utilized profitably except as pulpwood, so that no monetary loss has been incurred. On the contrary, *Sirex* has conferred an inestimable benefit on the stands and in a few years the apparent loss of volume will be recouped by the dominant trees.

The *Sirex* fungus is very efficient in rotting the wood of the trees killed so that these disappear much more rapidly than thinnings lying on the round or standing fire-killed trees. Extraction difficulties have been increased temporarily because of the dead standing trees, but in about five years logging will be facilitated through the elimination of so much unmerchantable material.

Trees which are attacked but not killed may be severely damaged by rot or discolouration of the wood, heavy resin impregnation, resin pockets, ring shakes or by the killing of portions of the cambium of the bole. This type of damage is not as serious with large dominants as was at one stage feared, but in small trees and dense natural regeneration it may seriously detract from the future value of the trees for timber or pulp wood.

Mortality of up to 30% represents only a light thinning and should prove of great benefit to the stands. A noticeable feature is the appearance of "recovery tufts," dense, dark green tufts of foliage which appeared this last winter and spring. These occur at the ends of leaders and branches in stands where mortality had occurred the previous winter. They have not yet been found in stands where mortality occurred only in the winter of 1949. Recovery tufts are considered to be the response of the trees to the improved conditions due to rainfall and root room and in some cases to recovery from direct damage by *Sirex*.

With temporary freedom from root competition, improved crowns and ample rainfall, the surviving trees should be able to resist *Sirex* attack this year and no further deaths should occur in stands which have already suffered mortality. Practically no stands in State forests have suffered mortality beyond the beneficial stage. In some private areas, where heavy mortality occurred last winter, it is possible that the pines may not have recovered sufficiently to resist mass attack and should large numbers of *Sirex* emerge further mortality may occur.

Root grafting is extremely common in all plantations and may have a considerable bearing upon natural suppression and *Sirex* attack, and upon the spread of diseases, such as *Armillaria*, following thinning.

Natural regeneration provides a new set of conditions and, under the intense competition in many areas, considerable mortality may occur together with serious damage to the surviving trees. Even trees under five feet in height have been found killed by *Sirex* attack.

The treatment of natural regeneration presents many difficult silvicultural and administrative problems, and much experimental work is required before solutions can be found. It has been shown that thinning, pruning or other operations done in the summer months may have serious results when carried out under conditions favourable to *Sirex* attack. It is not desirable to make restrictive rules based upon the experience of a few dry summers because in years with ample summer rainfall it may be possible to carry out any operation without risk to the trees. No rules can replace common sense or an understanding of sound silvicultural principles.

Biological Control

Assuming the correctness of the statements already made about the relationship between stocking, drought and *Sirex* attack and the ultimate benefit to the forest, it might be thought that biological control of *Sirex* would be unnecessary.

It is obvious, however, that while the summers since 1946 have been exceptionally dry and yet mortality has been excessive over only relatively small areas, the drought conditions and consequent *Sirex* epidemic have approached perilously near the point where, had they been a little more severe or prolonged, mortality would have amounted to a national calamity.

Biological control aims at checking the increase of *Sirex* in order to prevent or lessen the severity of an epidemic in times of adverse climatic conditions. Where *Rhyssa persuasoria* is well established it has perhaps helped to check the epidemic, but there appears to be some factor which hinders its natural increase in large areas of forest. It is intended to import *Ibalia leucospoides* from England and this should prove useful particularly in the South Island, while in the North Island *Ibalia ensiger* from California would probably be more suitable.

The possibility has been noted that *Rhyssa* may have two generations in one year in the Rotorua district. The larva reaches its full development in about three weeks (2) and there is a possibility that the resting stage need not necessarily last 10 or 11 months. In order to test this possibility *Sirex*-infested logs from trees which were known to have died in the winter of 1949 were brought from an area where *Rhyssa* was thought not to occur. These logs were exposed to *Rhyssa* for periods of about one week at the end of October and were then removed to a separate cage. On January 13th, 1950, three male *Rhyssa* were found in the cage with the test logs and from that date to the end of January, 15 very small male *Rhyssa* emerged from these logs. This evidence is not in any way conclusive as there is a chance that *Rhyssa* were already present in the logs before they were brought in. Strictly controlled experiments must be made before it can be definitely established whether two generations can occur. However, there appear to be two main periods of *Rhyssa* emergence, one in early October and the other early in February.

It is possible for *Rhyssa* to parasitize *Sirex* larvae in the seventh instar. This has been demonstrated by tracing the cast larval skins back from a resting stage *Rhyssa* larva to the oviposition puncture of the *Sirex*. The *Rhyssa* developed into a small male. The *Sirex* larva at the seventh instar would be about 15 mm. long and about two months old so that the logs collected could have contained *Rhyssa* if they had been present in the area.

Chemical Control

The mortality which occurred in the winter of 1949 could have been prevented had it been possible to apply an insecticide from the air to kill the *Sirex* at the peak period of emergence in February, 1949. The requirements for such an insecticide are that it shall be :

1. A contact insecticide lethal in minute quantities.
2. Suitable for use in aerial spraying, preferably with an oil carrier.

3. Effective for at least one month after application.

It would also be necessary for the insecticide to be available in sufficient quantity and at a sufficiently low price to make this spraying economically possible. As no information from other countries was available as to any effective insecticide against *Sirex* it was first necessary to determine whether any of the available insecticides would be suitable and, if so, how they could be applied to the forest. Towards the end of February, *Sirex* congregate in great numbers for copulation at the tops of trees, selecting for this purpose the tallest leading shoots. An aerial application of an insecticide about the middle of February might be effective in killing the females during this period.

Sirex were reared in incubators to procure specimens for testing but they were found to be very resistant to such insecticides as D.D.T., Gammexane, Toxaphene and Rothane, even when there were applied in concentrations far in excess of that which would have been possible in the field. The control of such a mobile insect as *Sirex* presents a problem of extreme difficulty. It was considered that to be suitable an insecticide would require to be effective in killing the insect after one quarter hour's contact with foliage treated two or three weeks previously. It was noted that the females were far more resistant than the males, which may be explained by the fact that the males drag the abdomen and hind legs over the surface when moving, whereas the females hold their bodies away from the surface. Also, the females naturally live longer after copulation than the males. As the ratio of males to females is very high it is the females at which control must be aimed, and as yet no insecticide has been found which will do this effectively.

Chemical control of a well established and widespread insect species is of doubtful value, as an epidemic of such a species indicates that climatic, silvicultural or site factors are primarily responsible. However, it is possible that spraying of selected stands at the peak period of the epidemic and just before its natural decline might be worth-while, although with *Sirex* there would be a considerable risk of invasion from untreated stands unless the treatment was carried out over large areas.

Chemical control, like biological control, can assist but not replace sound silviculture.

Relationship to World Conditions

Reports are now appearing from many parts of the world of epidemics of forest insects following drought periods from 1946 onwards. These indicate that the *Sirex* epidemic in *Pinus radiata* forests in New Zealand has its counterparts in many regions of the world in so far as insects, normally of secondary importance, have reached epidemic proportions under certain climatic conditions. *Sirex* has come into prominence only on account of the absence of more aggressive species and, had *Sirex* not been introduced into this country, it is probable that *Hylastes ater* or some other insect would have become capable of killing the trees. The predisposing factors are in all cases very similar. For example, Roth (8) reports an alarming increase in the numbers of bark beetles in Swiss and German forests; this he attributes to a combination of warm dry summers and other factors. Hadorn (4) reports epidemics of bark beetles in spruce forests in Switzerland as a sequel to postwar neglect and the drought of 1947, while Pfeffer and others (6) report similar damage. Kalandra (5) reports damage to Norway spruce in Bohemia. Vlad (9) reports that as a result of the 1945-46 drought there is a serious die-back of trees in the Baragan steppe. Boomsma (1) reports deaths of *Pinus radiata* in South Australia which he attributes to drought. In this case the deaths are not surprising as the mean annual rainfall is only 26.85 inches as compared with 55.76 inches at Kaingaroa Forest Headquarters. Unfortunately the rainfall during the drought period is not given.

One of the most severe droughts on record was experienced in 1946-47 in Queensland, while parts of South Africa have had drought conditions for five years.

Most of the cases reported of damage to forests, indicate the same conditions; lack of rain with high temperatures followed by epidemics of insects normally of secondary importance.

Frequently lack of normal silvicultural and extraction practices, due to war conditions, have contributed to the epidemics. These reports lend support to the conclusions already reached that the 1946 drought and the following dry summers have predisposed the trees to *Sirex* attack and so enabled the population of this insect to build up to epidemic proportions, while lack of silvicultural treatment and bad logging practices have combined to increase the severity of the attack.

A paper has just come to hand by Chrystal (3) who gives an account of bark beetle epidemics in North America and Europe placing the emphasis on war and drought conditions as the prime causal agencies. He reiterates that there is a definite need for control measures to be based on silviculture.

Summary

This article is intended as a supplement to a previous paper on *Sirex noctilio*. Drought is postulated as the main cause of the *Sirex* epidemic and details of the summer rainfall are given. The effects of silvicultural operations and the relation between over-stocking, drought and *Sirex* attack are discussed.

Various aspects of *Sirex* and its symbiont are briefly dealt with. An account is given of the benefits derived from the natural thinning due to *Sirex* attack, the damage to trees attacked but not killed, and the signs of recovery by the trees from the effects of adverse conditions.

The possibility of biological and chemical control measures are discussed and the epidemic is compared with similar occurrences in other parts of the world.

The main purpose of the paper is to record the progress of the *Sirex* epidemic and to place the emphasis on the general principles of climate, silviculture and site rather than on the insect itself.

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