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# An analysis of an outbreak of the woodwasp, *Sirex noctilio* F. (Hymenoptera, Siricidae), in *Pinus radiata*

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**Abstract**

The development of an outbreak of the woodwasp, *Sirex noctilio* F., in a 30-year-old population of *Pinus radiata* in Tasmania was traced by growth ring analysis of killed trees. The outbreak probably developed from small foci; it reached its peak when the trees were 18–19 years old and then declined rapidly. Attack per tree was directly related to the density of emergents from trees killed in the previous season and the intensity of oviposition drilling was modified by the rainfall during the emergence season; the frequency of treble oviposition drills was directly related to summer rainfall. Survival of insects within trees declined with the years; this was related to the greater vigour and resistance of the surviving trees, but was apparently modified by spring rainfall. Resinosis and polyphenols associated with growth rings in stems living in 1964 indicated an increase in the proportion of trees resisting attack during the outbreak. The growth patterns of attacked and unattacked trees, and the obvious susceptibility of the weaker understorey trees, are discussed and due attention to site quality and plantation management are recommended to reduce *Sirex* attack in future.

## Introduction

The woodwasp, *Sirex noctilio* F., was first discovered in Australian softwood plantations in a 1092-ha plantation of *Pinus radiata* at Pittwater, Tasmania, in February 1952 (Gilbert & Miller, 1952). During emergency quarantine measures, the pest became established and was subsequently discovered in the mainland state of Victoria in 1960–61 (Irvine, 1962).

The Pittwater plantation was established during 1929–35 on a peninsula of dune sands with a water table at approximately 2·4 m. The plantation was clear felled during 1952–67, and the *Sirex* population is at present confined to areas of natural regeneration. *Sirex* caused considerable losses before the felling programme was completed.

Trees are attacked by *Sirex* females during the summer and autumn. These trees may be recognised superficially by the appearance of small beads of resin on the trunk although detailed inspection of the bark is required to confirm the presence of oviposition drills. The arthrospores of the symbiotic fungus, *Amylostereum areolatum*, and a muco-secretion are inoculated into the tree during drilling, and the combined effect of these two materials results in the death of susceptible trees (Coutts, 1969*a,b*). The phytotoxic effect of *Sirex* attack is indicated by the development of leaf chlorosis a short time after attack.

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The life-cycle of the insect at Pittwater takes 12 months with some carry-over into the second and third years. Feeding activity by the larvae results in extensive galleries filled with compacted frass throughout the entire stem and, following pupation, the adults chew through the remaining wood and bark to emerge through circular exit holes.

The objectives of the study were: (1) to determine the course of the Pittwater outbreak by estimating the ages of a sample of dead trees; and (2) to analyse the progress of the outbreak in terms of class of tree attacked, the intensity of attack, insect survival and the effects of weather.

## Methods

The area chosen for extensive sampling was Compartment 4 at Pittwater; this area had been planted in 1929–30 and its location is shown in Fig. 1*A*. The compartment comprised 121·5 ha and the trees were spaced at 2·5 × 2·5 m. There were 324 rows each of 100 trees. In 1946–47 every ninth row was removed to facilitate the removal of the largest trees for saw logs and these operations undoubtedly damaged the remaining, smaller trees. The two outermost rows and the first and final two trees of each row were excluded from the study area which was subdivided in plan to give 30 equal areas in 10 columns and three rows, each consisting of 16 sample plots. Each sample plot measured 0·04 ha and contained 64 trees (8 × 8) (Fig. 1*B*).

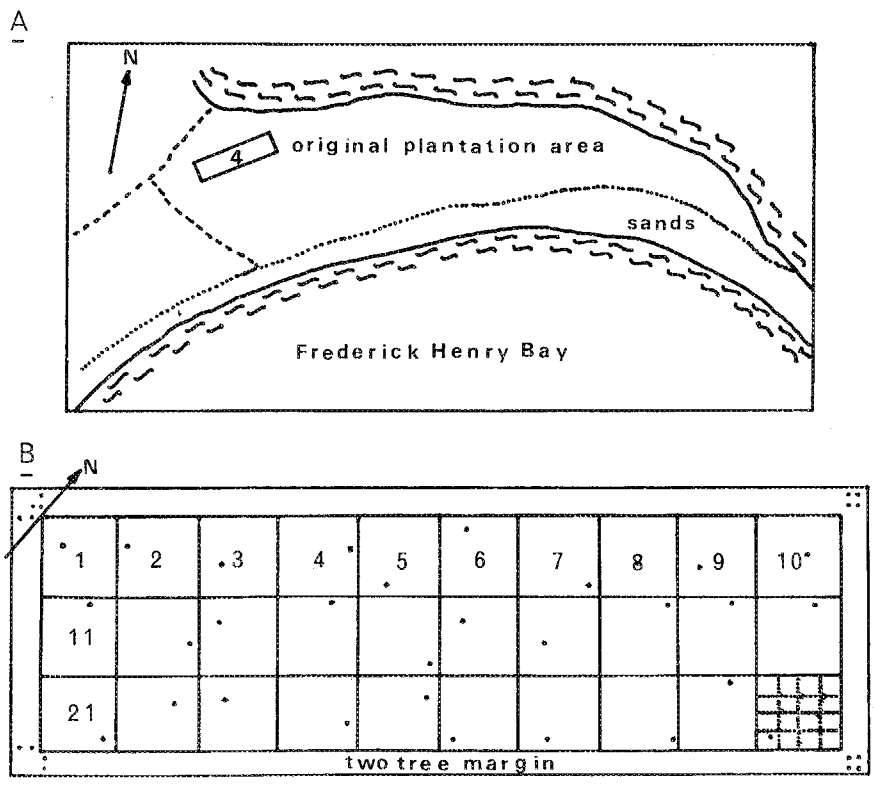


Fig. 1.—*A*, *P. radiata* plantation area at Pittwater, Tasmania, showing location of study site, Compartment 4 (scale 1 cm ≡ 340 m); *B*, Compartment 4 showing location of 64-tree study plots (scale 1 cm ≡ 50 m).

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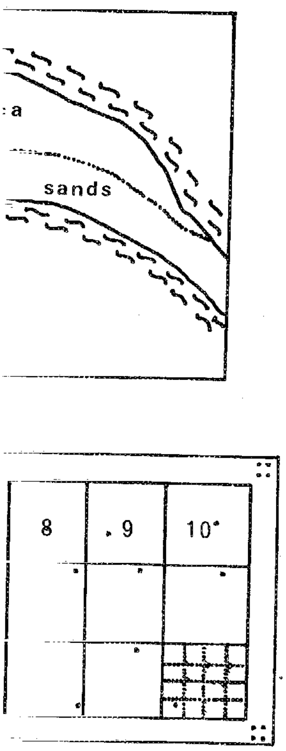


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= 50 m).



Sampling commenced in June 1964. Two sample plots were chosen at random from each of the 30 primary subdivisions. The number and position of living and dead trees, trees which failed to establish and those which had been felled were recorded for each sample plot. The procedure for sampling *Sirex*-killed trees was dependent upon their frequency within the plot. All five dead trees were sampled if only five trees were killed; six dead trees were selected at random if 6–10 trees were killed; seven dead trees for 11–15 trees, and so on. Selected trees were felled; their age, diameter and height were recorded and the density of oviposition drills and emergence per unit area were assessed.

Meteorological information on average monthly rainfall and temperature for the period 1946–64 was obtained from Cambridge Airport located 3·2 km west of the plantation.

In the absence of live stages, trees killed by *Sirex* were recognised by (i) the presence of oviposition drills, (ii) exit holes, (iii) larval galleries and frass in which exuviae could be recognised, and (iv) dead insects. Trees in which the presence of *Sirex* was detected by any of these criteria were assumed to have been killed solely by the wasp.

Wood degradation proceeds slowly at Pittwater and, as the time of planting was known (1929–30), the age of killed trees was estimated by counting growth rings on a face cut close to ground level. The accuracy of the method was assessed by comparison with currently felled material; the error was ± one year. Two estimates of age were made independently by two operators and, if they disagreed, closer examination of sections was made in the laboratory. As the work proceeded it was found that the 1947 growth ring was immediately preceded and followed by a wide band of early wood. This characteristic feature made it possible to establish the exact age of the majority of the trees sampled.

The size of killed trees was measured in terms of diameter and height. Diameter was recorded under bark at breast height (1·27 m). Many trees had broken off at different heights and two additional diameter measures were made at known heights above ground level on all trees. From these measurements the parabolic height was assessed by the 'taper' line method (Gray, 1944) and this value was used to express the height and volume of individual trees.

Oviposition and emergence was estimated on five 7·5 × 7·5-cm sample areas located at the midpoint of the stem, and at two sites on each side of the midpoint.

The *Sirex* female may drill 1–4 holes into the sapwood through a single hole in the bark. The frequency of eggs within these types of oviposition drills was found in a separate study to be 0·04, 0·7, 1·5 and 2·2, for 1, 2, 3 and 4 drills respectively (Madden, 1974). Using these estimates, the numbers of the different types of drills in the 56·3-$cm^2$ sample areas were converted to give a measure of the number of eggs laid per unit area of stem.

*Sirex* attack may or may not kill a tree. Trees which had resisted attack in one or more previous years were recognised by distinctive longitudinal bands of resinosis and polyphenol staining arising from the majority of the original drill lesions. These expressions of resistance, which were fully described by Coutts & Dolezal (1966), underlie the growth ring of the year of attack in cross sections of resistant trees. The frequency of unsuccessful attacks during the outbreak was estimated in 1964–65 by recording the presence or absence of these symptoms in cross sections made every 3·6 m along the lengths of 200 living but currently felled trees.

Ten trees which showed no evidence of attack were measured to provide control data on diameter, height and annual radial increment.

A correction was made for felling operations by assuming that in a given year a tree of average diameter was marketable and that marketable volume could be determined from the parabolic height. Records of the annual volumes of timber removed from the compartment were obtained and these were divided by the calculated average volume per stem for that year to give an estimate of the number of stems removed. When the

TABLE I. *Annual reduction in the number of* P. radiata *trees per hectare in a compartment planted out in 1929–30 at Pittwater, Tasmania: figures indicate the number of trees killed and attacked by* S. noctilio *or removed by other agencies*

| Year | Age | Live trees | Trees failing to establish | Trees felled | Trees killed by *Sirex* | Trees killed by *Sirex* (%) (i) | Trees attacked and survived | Trees attacked and survived (%) (ii) | Total trees attacked (%) (i) & (ii) |
|---|---|---|---|---|---|---|---|---|---|
| 1929–30 | 1 | 1580·8 | 45·4 | | | | | | |
| 1946–47 | 17 | 1535·4 | | 395·2* | | | | | |
| 1947–48 | 18 | 1140·2 | | | 7·7 | 0·68 | | | 0·68 |
| 1948–49 | 19 | 1132·5 | | | 7·7 | 0·68 | | | 0·68 |
| 1949–50 | 20 | 1124·8 | | | 15·3 | 1·37 | | | 1·37 |
| 1950–51 | 21 | 1109·5 | | | 19·0 | 1·72 | | | 1·72 |
| 1951–52 | 22 | 1090·5 | | 104·7† | 26·7 | 2·45 | | | 2·45 |
| 1952–53 | 23 | 959·1 | | 32·1† | 36·8 | 3·83 | | | 3·83 |
| 1953–54 | 24 | 890·2 | | | 57·1 | 6·41 | | | 6·41 |
| 1954–55 | 25 | 832·9 | | 24·7† | 50·9 | 6·16 | | | 6·16 |
| 1955–56 | 26 | 757·5 | | 12·4† | 83·7 | 11·08 | 13·1 | 1·73 | 12·81 |
| 1956–57 | 27 | 661·5 | | 10·9 | 83·7 | 12·68 | 11·1 | 1·67 | 14·35 |
| 1957–58 | 28 | 566·9 | | | 76·3 | 13·46 | 36·1 | 6·36 | 19·82 |
| 1958–59 | 29 | 490·5 | | 1·2 | 95·3 | 19·44 | 20·0 | 4·06 | 23·50 |
| 1959–60 | 30 | 394·0 | | | 44·5 | 11·28 | 7·7 | 1·94 | 13·22 |
| 1960–61 | 31 | 349·5 | | 27·7 | 19·0 | 5·45 | 6·7 | 1·91 | 7·36 |
| 1961–62 | 32 | 302·8 | | | 11·4 | 3·76 | | | 3·76 |
| 1962–63 | 33 | 291·5 | | 95·3 | | | | | |
| 1963–64 | 34 | 196·1 | | | | | | | |

*1st thinnings.
†Estimates weighted by 1·5, 1·2, 0·8 and 0·3 trees for years 1952, 1953, 1955 and 1956 respectively as estimate of number of trees felled, computed from felling data, was 3·8 trees less than the 7·9 trees remaining in the plots.

results were computed it was found necessary to adjust these estimates slightly (see Table I, footnote).

## Results

### *The progress of the Pittwater outbreak*

*The distribution of attack in time.*—The estimates of tree mortality and survival and the degree of unsuccessful attack are summarised in Table I, and the progress of the outbreak is depicted in Fig. 2. Although the presence of *Sirex* was not discovered until 1952 the small number of trees killed when they were less than 20 years old indicate that it was present at Pittwater in low numbers as early as 1947–48. The infestation developed into outbreak proportions in the period 1954–59. An examination of the 200 stems of trees living and felled in 1964 indicated that, coincident with this period, there was an increase in the frequency of unsuccessful attack. Maximum percent tree mortality which occurred in 1958–59 was followed by a rapid decline in the percentage of trees killed.

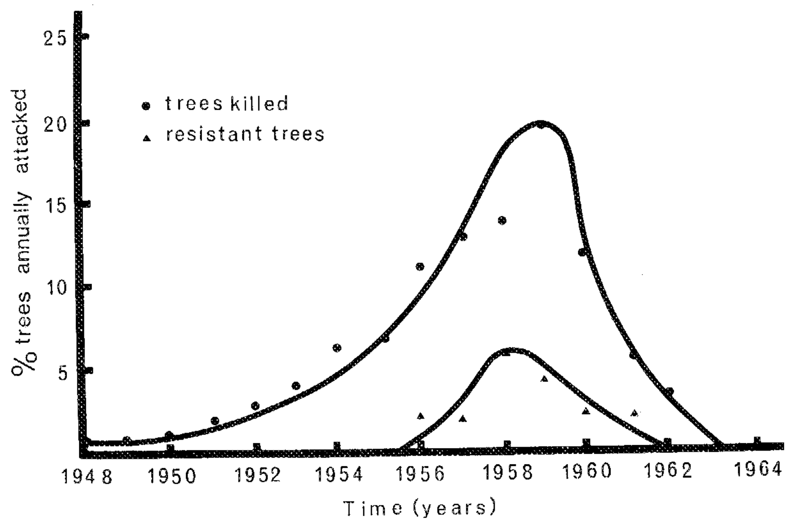


Fig. 2.—Annual incidence of *Sirex* attack, Pittwater, Tasmania, 1948–64, resulting in killed and resistant trees.

*The distribution of attack within the compartment.*—The analysis of variance on the average age of *Sirex*-killed trees within the row and column subdivisions indicated that there were differences betwen the mean ages of trees within the 10 columns ($P<0{\cdot}05$). There was no difference between the mean age of killed trees within the three rows. The LSD value for comparing the difference between the column means was 1·410 years (at $P = 0{\cdot}05$) and a summary of the differences is shown in Table II.

The results indicate that attack within the compartment was not uniform but that trees in certain areas were attacked, in general, at different times. Although these spatial events were undoubtedly affected by the patterns of attacks in adjacent compartments it is suggested that the outbreak developed from initially small infestation foci within the compartment.

TABLE II. *The difference between column mean ages (years)*

| Column no. (ranked) | 5 | 2 | 1 | 8 | 7 | 3 | 6 | 10 | 4 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| Mean age (years) | 25·7 | 25·8 | 25·9 | 26·1 | 26·3 | 26·4 | 27·0 | 27·4 | 27·6 | 28·0 |
| Means not significantly different are underlined. | | ——— | ——— | ——— | ——— | ——— | ——— | | | |
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## *Analysis of attack*

*Survival of insect.*—The ratio of emergence per unit area to eggs per unit area was used as an index of generation survival within each tree. The survival index declined during the course of the outbreak and the regression of survival against time was significant ($P<0{\cdot}001$) (Fig. 3).

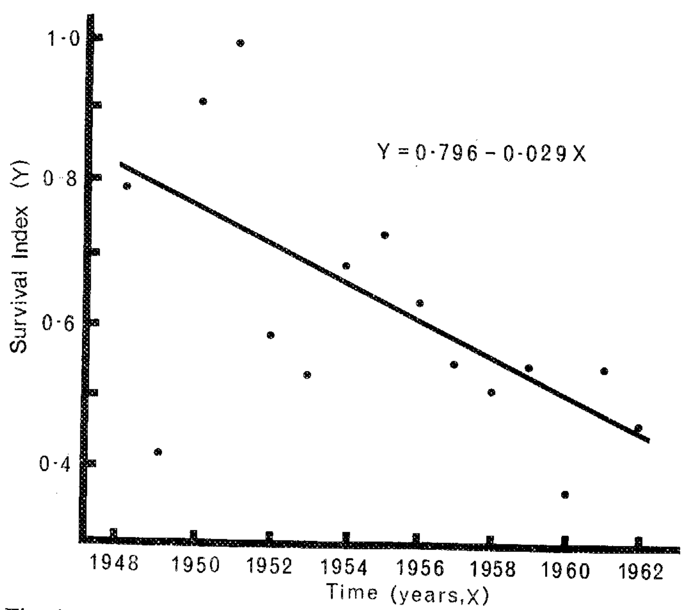


Fig. 3.—The relationship between average *Sirex* survival within trees and time from commencement of Pittwater outbreak (1948 = Year 1).

The decline in the index of survival from 1948 to 1962 was, in view of the increase in the proportion of trees resisting attack (*cf.* Table I, Fig. 2), undoubtedly related to the greater average vigour and resistance of the remaining trees resulting from the progressive elimination of the more susceptible trees. Although the survival index was not significantly affected by seasonal rainfall, in time a comparison of the deviations from regression of the annual average survival values and precipitation suggested that survival within trees could be modified by the August–November (spring) rainfall preceding the attack. An inverse relationship between insect survival and spring rainfall is detected in the comparison shown in Fig. 4; thus, higher-than-average spring rains tended to suppress insect survival within trees and *vice versa*.

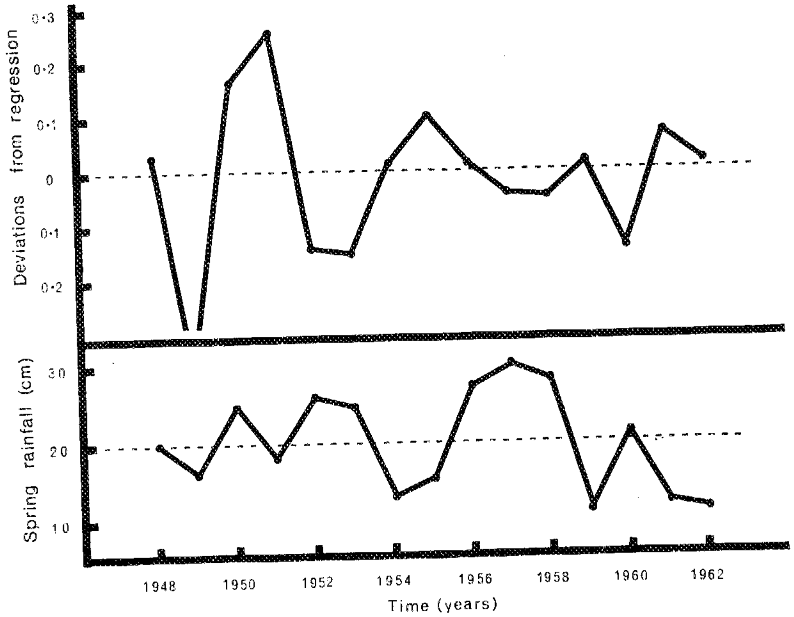


Fig. 4.—The relationship between annual spring rainfall and deviations from average insect survival within trees for the period 1948–62 (average values depicted by broken line).

An examination was made of the relationship between the density of oviposition drills per unit area of stem surface on trees killed in year $x$, the rainfall during the period of attack (December through March) and adult emergence per unit area of stem surface on trees killed in the previous season, *i.e.*, in year $x-1$. These emergents constituted the attacking population.

The following relationship was found:

$$y = 26{\cdot}41 + 3{\cdot}66X_1 + 1{\cdot}07X_2$$

where $y$ = drills/dm$^2$ in trees killed in year $x$; $X_1$ = emergents/dm$^2$ from trees killed in year $x-1$ and $X_2$ = average summer rainfall (December–March) in millimetres.

The intensity of attack was directly proportional to the estimated numbers of emergents from year $x-1$ trees and the analysis of attack intensity on the attacking population and summer rainfall was highly significant ($P<0{\cdot}001$ and $P<0{\cdot}05$, respectively). A higher number of oviposition drills per unit area was found in trees attacked in years with above average rainfall, *i.e.*, $>17{\cdot}0$ cm for the December–March period.

The analysis was extended to consider the density of single, double and treble drills per unit area with respect to the December–March rainfall and the attacking population. The density of each type of drill on year $x$ trees was related directly to the density of emergents from the trees killed in year $x-1$ ($P<0{\cdot}001$) but only the incidence of treble drills was affected significantly by summer rainfall ($P<0{\cdot}05$), and a higher proportion of treble (and quadruple) drills occurred in years of increased precipitation.

*Class of tree attacked.*—The average annual diameters of *Sirex*-killed trees were significantly less than the progressive annual diameters assessed on the unattacked control trees (Fig. 5). However, in the latter years of the outbreak many large trees were killed. Examination of cross sections of these large trees revealed that the majority had been unsuccessfully attacked in one or more years prior to ultimate successful attack.

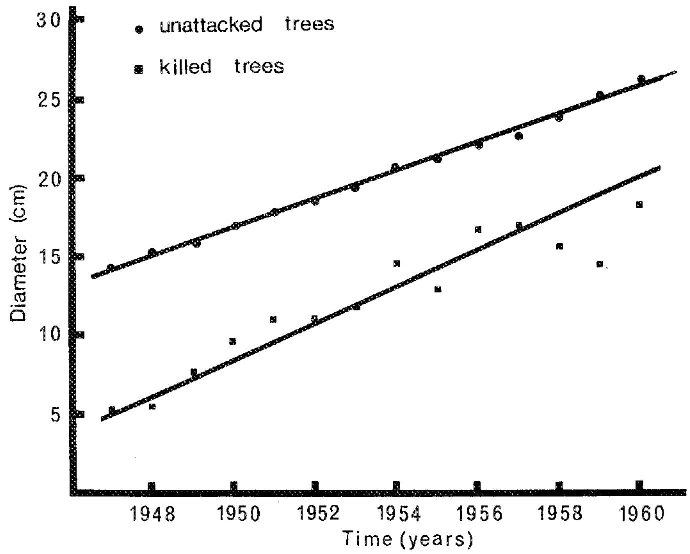


Fig. 5.—The average annual diameter recorded at 1·27 m above ground of unattacked (control) trees and trees killed by *Sirex*.

Unattacked trees showed, in general, a regular and uninterrupted pattern in their annual growth increments (*cf.* Fig. 5) as did some of the trees attacked late in the outbreak. Trees, unsuccessfully attacked in one or more years before the year of death, were checked in growth following attack while the majority of killed trees had grown very slowly from 1939–41, *i.e.*, from the time of probable crown closure. Trees attacked in the early stages of the infestation were on the other hand characterised by poor increment from the time of their establishment.

## Discussion

The Pittwater plantation area has a poor site index and it is apparent that there was a high proportion of potentially susceptible trees within this stand in 1947. Surveys in 1964 indicated that the mortality of trees due to *Sirex* attack ranged from 80% in some western compartments to as low as 30% in the east. It is very likely that delayed thinning and logging damage were the chief factors affecting tree susceptibility to *Sirex* attack. Trees harvested in 1946–47 were taken for lumber and involved the preferential removal of the dominant, least susceptible trees. The accompanying damage to the understory and the accumulation of slash and tops also provided abundant host material for *Sirex*. The following excerpts of a letter, dated 16 April 1953, from the late Mr E. J. Kirwan, Forest Manager to his Company, emphasise this point: 'Since we commenced systematically searching for *Sirex*-killed trees, we had felled and burned about 3000 trees, many small ones and a large number could be classed as worthless and would not have made timber trees . . . this work [continued] until we found that tops left on the ground after thinning . . . during the summer of 1952 had been heavily attacked. . . . It was impossible to detect the presence of *Sirex* in these tops as they would die off in any case . . .'.

The numbers of *Sirex* increased rapidly after establishment and resulted in an increased annual tree mortality. However, a consequence of the thinning effect of *Sirex* in killing susceptible trees was an increase in vigour of the remaining trees accompanied by an increase in the proportion of trees possessing natural resistance as reflected in an increased number of unsuccessful attacks and a decreasing survival of the insect within the tree. The chief factors affecting establishment of the fungus and insect survival were resinosis and polyphenol formation. The survival of individual trees or of insects within trees were not significantly related to seasonal rains, but the data do suggest that insect survival within trees in a given year could be modified by spring rains.

Transpiration rate is directly affected by soil moisture content (in Kramer & Kozlowski, 1960); thus the rapid concentration of the muco-secretion in the apical regions of trees with high transpiration rates at the time of attack would, through its effect on translocation and tissue hydration, inhibit the resistance mechanisms and thereby enhance the survival of eggs and early instars. Conversely, trees would take longer to succumb if transpiration rates were low and this slower effect would allow the processes of resistance to operate and enhance insect mortality. Greatest mortality of *Sirex* within trees, excluding that due to natural enemies, occurs in the egg and first-instar stages (author's unpubl. data). Observations by Coutts & Dolezal (pers. comm.), that irrigated pines were more susceptible to the effects of *Sirex* attack than were droughted trees, supports the explanation of the apparent effects of spring rains, and resulting soil moisture contents, on the survival of the insect within the tree.

The role of biological control agents in the decline in tree mortality was insignificant as the parasites, *Rhyssa persuasoria* (L.) and *Ibalia leucospoides* (Hochenw.), were not introduced into Pittwater until 1957 and 1959, respectively (Taylor, 1967). Avian predation of the *Sirex* population does occur; however, under the conditions of the outbreak its effect would have been slight. Furthermore, the bird population density at Pittwater in subsequent years has been enhanced by the presence of secondary insects in the killed trees.

The data indicate that the proportions of treble drills were directly related to rainfall. The type of drill made by the *Sirex* female is related to the osmotic pressure of phloem and cambial sap at the drilling site (Madden, 1974). An increase in ground moisture content leads to a decrease in the osmotic pressure of a tree system (Harris *et al.*, 1921) and the variation in the number of treble and quadruple drills could result from this effect.

The class of tree initially preferred and killed by *Sirex* was of the smaller diameter and suppressed type, although in later years dominant trees were also attacked and killed. The data infer that, as the outbreak advanced to epidemic status, the over-abundance of insects obscured inter-tree discrimination with subsequent attack on normally healthy trees. This attack so severely affected the tree's metabolism that growth was retarded. This effect has been achieved experimentally by Coutts (1968) and Spradbery (1973).

The highly susceptible condition of the Pittwater plantation in 1952, when *Sirex* was discovered, was such that the introduction of biological control agents or changes in management would have had little effect on the increase of *Sirex* and the accompanying loss of trees, for tree damage and felling provides suitably attractive material for the wasp (Madden, 1971).

The study suggests that timber losses caused by *Sirex* can be minimised in the first instance by growing *P. radiata* only in high site index areas in combination with rigorous management practice to maintain health and vigour of individual trees.

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**The dispersion of bro
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**Abstract**

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**Introduction**

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