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The Biology and Behaviour of the Woodwasp *Sirex noctilio* F. in New Zealand

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Abstract

THIS paper describes the biology of *Sirex noctilio* F. giving information about larval development, including the variable number of instars found relative to conditions in the wood. The behaviour of adult woodwasps is discussed, with particular reference to differences in the behaviour of the sexes. The way in which the moisture content of the wood influences larval development, adult oviposition and fungal inoculation as well as its effect on the length of the life cycle in various parts of the host tree, is described. In the introduction, reference is made to most of the research, completed to date, on *noctilio* and certain other siricids, while in the discussion the implications of our findings on forest practices are outlined.

INTRODUCTION

THE woodwasp *Sirex noctilio* F., was first found established in the introduced pines of New Zealand in 1922. It had been seen, but apparently not collected, in the Wairarapa District of Wellington Province as early as 1900 (Miller and Clark, 1935). By 1928 it was widespread in the North Island and was established in *Pinus radiata* D. Don. plantations in Nelson Province and also in the northern section of Canterbury Province. By 1931 Miller & Clark (1935) had established *Rhyssa persuasoria* L. (Ichneumonidae), an external larval parasite of woodwasps, in forests at Nelson, Hanmer and Rotorua. An unsuccessful attempt to establish *Ibalia leucospoides* L. (Ibaliidae), an egg parasite of siricids, had also been made. Clark (1933) had also established the fact that *S. noctilio* carried a fungal symbiont and, following Buchner (1928) and Cartwright (1929), had established the presence of morphological structures, in the adult female woodwasp, which were associated with fungal storage in a resting spore (oidial) form. Clark (1933) also reported that, on one occasion, he obtained a fungal culture from "glands" attached to the hind gut of a female larva. He believed this to be the same as the fungus he had obtained from the organs in the adult and from the larval burrows in the wood. There was no identification of the fungus from any of these locations, though Clark felt that the ones from the wood resembled cultures of *Stereum sanguinolentum* Fr. he had received from Cartwright.

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Parkin (1941) discovered the hypopleural organs on the postero-lateral area of the first abdominal segment of female larvae of *S. cyaneus* F. and showed that these organs carried the symbiotic fungal oidia in similar form to the organs in adult females. Rawlings (1951) reported hypopleural organs from *S. noctilio.*

In the period 1948–52 the widespread death of trees in plantations of *Pinus radiata* D. Don. in the Rotorua District was associated with an outbreak of *S. noctilio.* Ultimately a team under the direction of G. B. Rawlings commenced work on the biology and biological control of the insect (Rawlings, 1948). *Ibalia leucospoides* was established by Rawlings (1951) and extended by Zondag (1959) and fruiting bodies of the fungal symbiont were obtained by Orman (1958). A tentative identification by Cunningham placed the fungal symbiont near to *Peniophora* sp. nov. Rawlings (1953) found that *S. noctilio* was facultatively parthenogenetic, unfertilised females producing viable eggs that developed into male insects. He postulated that this had some bearing on the male/female ratio in adults which was almost always overwhelmingly in favour of males.

A native wasp, *Guiglia schauinslandi* (Ashm.) (Fam. Oryssidae) has been reared from larvae of *S. noctilio* and a further ichneumonid, *Rhyssa lineolata* (Kby.), apparently introduced naturally from North America, became established on *S. noctilio* in the Hawke's Bay Province where it was collected in 1958 by M. A. Stoodley (Zondag and Nuttall, 1961). Zondag (1962) reported a nematode parasitic in the reproductive organs of male and female *S. noctilio.* Earlier, in 1955, Jackson published an account of the relationship between *S. noctilio* and *Pinus radiata* at Rotoehu Forest. He concluded that the first trees killed by *Sirex* died four years from planting; subsequently, tree mortality increased until about the development of crown-closure and thereafter declined, in a forest where drought was not a serious factor.

Despite the bio-ecological work done, many factors which would permit a better understanding of *S. noctilio* and its long-term effects on forests and forest management were not examined. Some of these were a proper evaluation of the immature stages and their ecology, and a more intensive study of adult behaviour in the field. In the latter, some evaluation of the reasons for differential rates of oviposition in trees and an attempt to obtain some knowledge of the dispersal of *Sirex* to new areas and its subsequent establishment there were considered important. Other matters requiring further study were concerned with the relationship of the insect to its fungal symbiont, the correct taxonomy of the fungal symbiont and its relationship to the host tree of the woodwasp.

Our study was designed to gain evidence on some of these matters. The study was projected for 12 years but, because both authors left New Zealand, it ran for four years only. The present paper will be followed by others on the ecology of *S. noctilio* and its parasites.

Biology

Adult Emergence and Sex Ratio. The adult woodwasps emerge between October and May, though occasional emergences (usually males) have been recorded throughout the year. Over 90 per cent of the population emerges between 15 January and 31 March in most years and over 70 per cent in the four weeks mid-February to mid-March. In years having cool, wet springs and summers, emergence is more haphazard and often without obvious peaks. A few cool days in the peak emergence period has often virtually stopped emergence for up to a week in the study areas. Male woodwasps have outnumbered females by an average of 7 to 1 over the four years, during which many thousands of adults were reared. Logs, subjected to oviposition by mated females only, had ultimate emergences in which the male/female ratio approached 1:1. Log collections from forest areas where the woodwasp was in an endemic phase, have had emergences where males outnumbered females by over 20:1. Thus the male/female ratio tends to change according to whether forest conditions favour the insect or not. That is to say, when woodwasp numbers are increasing, the sex ratio is nearer 1. When woodwasp numbers are decreasing, the sex ratio is greatly in favour of the males. The position in the infested tree where the insect develops has also some relationship to the sex ratio found there. Females are relatively more numerous in the butts of infested trees to about 4 feet from the ground, while males increasingly outnumber females from this point upward. In some trees the males outnumber the females by more than 100:1 in the top 10–15 feet of the trunk. Observations on the behaviour of female woodwasps may indicate one of the probable causes of these differences in sex ratio along the tree. This will be discussed in the next section.

Emergence from the pupal chamber to the outside of the tree is accomplished by the adult, no preparatory tunnel being constructed by the larva.

The circular exits through which adults emerge vary in diameter from 3mm–6.6mm, the cutting of such round exits being greatly assisted by the flexibility of the neck of the insect. The body position is, however, changed at rather regular intervals by withdrawal of the insect into the mine and subsequent advance to the surface with the body suitably reoriented. When the exit is almost ready, the insect will often test it, then recut a little until it is completed. Adults will often remain just within the wood for varying lengths of time before emergence and sometimes die there.

During passage out some wood borings may occasionally be eaten by adults, though the gut appears as a relatively undifferentiated structure. Shortly after emergence faecal pellets are passed, though these appear to contain no wood and are probably excretory products resulting from metamorphosis. However, a little chewed wood has been found on occasions in the oesophagus of newly emerged adults, but it appears from the evidence that adult *S. noctilio* do not feed during or after emergence.

Following emergence, adults of *S. noctilio* usually rest on the bark close to the exit for more than 15 minutes. From this time the behaviour of the sexes may differ. Male insects usually rest much longer (30 minutes to several hours) than females, and when they become active tend to move into the upper branches of the tree from which they have emerged. Subsequently, periodic short flights may occur from about 10 a.m. to 5 p.m. on sunny, warm days. During these flights, which take place just above and around the tree tops, movement from tree to tree occurs. The flights often resemble small swarms when woodwasps are numerous. All activity is preceded by vibration of the wings, producing a loud buzzing noise.

Female woodwasps rest for 15 minutes or more after emergence, then fly off through the forest. This first flight is often more than 100 yards in length. It is preceded, as in the males, by short bursts of noisy wing vibration which continues as a low-pitched buzzing sound during flight. Following the first flight females may move up to the soft upper stem of the tree and begin inserting their ovipositors into the bark. It is during this time that mating takes place. The aggregation of oviposition in the upper trunk may be related to this early activity by newly emerged females. Mating appears to be initiated by a female woodwasp passing close to a male which is resting in the foliage. The male is attracted and follows the female along fluttering its wings and using its forelegs and antennae in a play on the body of the female. If receptive she stops, and copulation occurs.

It appears that mating is more likely to occur when numbers of males are in the same locality and they have been disturbed by constant contact with one another. A female entering such a locality attracts increased numbers of males. Temperatures over 70° F. and high light intensities seem to have an important role in stimulating mating.

About 3–5 days from mating, female woodwasps enter an oviposition phase, which dominates their behaviour until they die, often with their ovipositors partially inserted into a tree. During this period of intensive oviposition they may be caught easily and can be placed on any tree wherein they will commence to oviposit. Once this behavioural pattern has begun, female woodwasps seldom appear to move far from the tree in which they are ovipositing, and this may in part account for the grouping of attacked trees, which is common in many stands. Also, it would seem, that any large-scale dispersal must occur in the few days following emergence or before oviposition behaviour begins.

Oviposition behaviour varies somewhat between individuals and also by the same individual on different trees, especially trees having different moisture contents in their wood. Certain generalisations may, however, be made. Apart from insertions of the ovipositor in the upper trunk or leader soon after emergence, female woodwasps usually work up the trunks of trees from near ground level, moving in an anti-clockwise spiral and inserting their ovipositors every few inches. The distance between insertion points varies between 3 and 20 inches. A greater number of insertions per foot of trunk are usually made immediately below, and for several feet above, the first whorl of green branches. When the top of the tree is reached, the process is repeated by flying downward, landing at a different point and moving up again. Sometimes insertions are concentrated in the mid-crown area of the trunk by females which do not fly down the trunk very far.

The number of points of insertion of the ovipositor is not necessarily indicative of the numbers of eggs deposited. In the first place the number of insertions per point may vary from 1 to 5. This is accomplished by the female woodwasp partially withdrawing her ovipositor, re-aligning it and inserting it again. The first insertion is usually directly into the wood but slightly angled toward the anterior of the ovipositing insect. Later insertions at the same point may be made at about 20° angles from this in up to four directions. All have the common entrance and diverge from the common gallery at about the same point. In general single insertions outnumber the multiple ones. Twin insertions are commoner than 3, and 4 and 5 are rarely found. The number of eggs deposited (including all the multiple types) is about 1 egg per 5–10 actual insertions.

The depth to which the ovipositor is inserted into the wood has probably little bearing on the thickness of the bark of the tree since female woodwasps usually use the bark crevices in thick-barked areas of tree trunks. However, the width of the spring-wood in the two annual rings immediately below the bark seems to influence the depth of the oviposition puncture. If the spring-wood band is wide, the ovipositor is inserted deeper than if it is narrow. This could merely be a function of the softer nature of the former for if the annual rings are narrow, the wood is harder because of the greater proportion of summer-wood present.

The depth of the oviposition puncture may have a bearing on the number of eggs laid. In deep punctures 2 eggs may be deposited one above the other. In multiple punctures there is often 1 egg in twin punctures, 1 or 2 in 3 punctures, and 1–3 eggs in 4 or 5 punctures. Rarely are all punctures, in multiple insertions, found with eggs in them.

Sirex noctilio will oviposit in wood with a wide range of moisture content. These, based on the oven-dry weight, have been found as high as 200% and as low as 20%. However, the number of actual insertions of the ovipositor per square foot of bark surface varies somewhat with the moisture content of the wood, and the number of eggs deposited vary in a similar manner. From limited tests at Nelson in March 1957, it would appear that female woodwasps may show preferences for wood with a certain range of moisture present. This preferential moisture content can be determined by the ratio of eggs to oviposition punctures. It would appear that, where the moisture content of wood is high (over 90% of oven-dry weight), the female woodwasp inserts her ovipositor many times without laying eggs. During these insertions the symbiotic fungus is inoculated into the wood, and these inoculations greatly outnumber the number of eggs deposited, the ratio being as high as 12 to 1. In wood with a moisture content between 40 and 75 per cent, the number of eggs laid increases in relation to the number of inoculations of the fungus, the latter always being greater than the former, but the ratio being as low as 5:1 and the optimum moisture content for oviposition being about 60%, based on oven-dry weight. It would appear that few eggs are deposited in wood with 25 per cent moisture content or lower (Table I).

TABLE I

Log No.	Moisture Content % O.D. Wt.	No. Insertions of Ovipositor	No. Actual Punctures per Insertion Point	No. Eggs per Puncture
1A	157	22	1.1	0.11
1B	189	17	1.0	0.06
1C	105	41	1.3	0.12
2A	63	50	1.6	0.20
2B	64	54	1.6	0.15
2C	48	59	1.8	0.20
3A	25	12	1.1	0.00
3B	20	7	1.0	0.00
3C	23	9	1.0	0.00

Ovipositions by *Sirex noctilio* F. in *Pinus radiata* D. Don. related to moisture content of the wood (March 1957 at Nelson).

The number of eggs deposited by a female woodwasp varies according to her size, longevity and those conditions which affect oviposition activity, such as air temperature and moisture content of the wood. Examination of the ovaries of variously-sized *S. noctilio* have shown that the paired ovaries are compact, ball-like structures about 5mm in diameter, the common oviduct of each giving rise at one point to a number of ovarioles (often 8), each of which again divides into about 4. The total number of ovarioles varies between 24 and 36 depending on the size of the insect, the average number being about 32. Sometimes the number of ovarioles differs between one ovary and the other in the same insect.

TABLE II

The Number of Eggs in the Ovaries of a Newly Emerged *Sirex noctilio* F.

Number of Ovarioles		Frequency of Eggs per Ovariole							Total Eggs per Ovary
		1	2	3	4	5	6	7	
Right Ovary	32	—	1	2	5	10	12	2	164
Left Ovary	31	—	—	1	6	10	12	2	163
Total	63		1	3	11	20	24	4	327

Average number of eggs per ovariole = 5.2.

The number of eggs per ovariole averages 5, with a range from 2–7. There is always variability in the number of eggs per ovariole in any ovary, so that not all have high counts. A typical situation is shown in Table II.

From the examination of a range of sizes of female *S. noctilio* it is apparent that the smallest may produce less than 200 eggs and the largest slightly more than 400 eggs. Dissection of field-collected, dead females from the trunks of trees indicates that there is a small number of eggs not deposited. We also found that the smaller the insect, the fewer the eggs laid, and vice versa.

Attack On Trees By *S. noctilio*

As stated earlier, Jackson (1955) reported an association of *S. noctilio* and *Pinus radiata* and found deaths of trees, due to woodwasp attack, occurring at four years from planting. Subsequent increases in tree deaths up to about the age of 15 years was recorded. A similar trend was found at Rai and Golden Downs in this study.

Tree species in which development of *S. noctilio* has been completed fall into 3 genera in New Zealand: *Pinus, Larix* and *Pseudotsuga.* To these may be added *Picea* and *Abies* from European records. In New Zealand the species of *Pseudotsuga* and *Larix* are attacked successfully only when moribund, while most species of *Pinus,* grown in New Zealand, have been attacked successfully when in an apparently healthy condition. Pine species killed by the activity of *S. noctilio* and its fungal symbiont include *P. radiata, nigra calabrica, nigra austriaca, ponderosa, elliottii, patula, contorta, caribaea, pinaster, attenuata, muricata* and *strobus.*

In early colonisation of an area, *S. noctilio* may utilise the branches of trees, particularly those damaged by wind or overtopped by other branches and therefore less vigorous or moribund. The insect may maintain a low population in such material for many years. Increases in its population seem to depend on increasing supplies of suitable material in which to breed, for, while its numbers are low, the woodwasp apparently cannot concentrate an attack of sufficient magnitude to kill relatively vigorous trees. When the woodwasp enters a plantation of pines, several factors appear to assist its numerical increase. Some of these are purely fortuitous, such as fire, and windthrow, the trees so damaged being wholly susceptible to attack and unimpeded woodwasp development. Others are concerned with normal stand development and the attainment of dominancy such as intra-specific competition, which reaches a peak at or about crown-closure. In these instances trees apparently present a range of physiological conditions from highly susceptible to resistant. Drought, though falling into the former category, usually has a differential effect on individual trees. It often affects trees along dried-up watercourses, or the larger, faster-grown trees in a stand, more than the sub-dominant, less vigorous specimens. All these conditions permit *S. noctilio* to flourish, and when its numbers are high, it appears to be able, through successive attacks over several months, to cause the decline of a vigorous tree.

Successful breeding by the woodwasp may occur in trees which survive attack. In these cases strips up the trunk or patches on the trunk are killed, but the remainder of the tree is unharmed. In all instances adults emerge through dead wood. Successful breeding of *S. noctilio* has been recorded from logs and timber from infested logs. Completion of woodwasp development and subsequent emergence occurs where the diameter of infested logs is greater than 3 inches. In standing trees, however, successful emergence of adult woodwasps from branches one inch thick and from small trees down to about 1 inch in diameter has been recorded. In the latter, emergence is always close to the ground, while in the former it is close to the main trunk of the tree. Emergence from timber having a moisture content of 15 per cent (based on the oven-dry weight) has also been recorded. Few insects complete development and emerge from small-diameter material and dry wood. Over 90 per cent of emergences have been recorded from breast height to a top diameter of 3 inches.

(N.B.—The average number of woodwasps obtained per cubic foot of wood in this study was 270. Trees sampled had an average volume of about 2 cubic feet.)

THE IMMATURE STAGES

EGG. The egg is enclosed in a loose membrane which apparently allows it to pass through the ovipositor somewhat compressed. It is sausage-shaped, creamy white, and 1.35–1.56mm x 0.30–0.35mm. The incubation period varies from about 16–28 days. It is probable that longer incubation periods could be recorded for eggs deposited in late autumn as the incubation period appears to be shorter in early February than it is in late March. Temperature could be the significant factor in this. The eggs are laid about 8mm in the wood and usually within the second annual ring from the cambium.

LARVA. Larvae do not differ in shape throughout their development. The first stage larva is, however, paler and somewhat transparent compared with later stages. It is also about the same size as the egg from which it hatched. It commences to penetrate upward or downward from the egg gallery along the line of the tracheids and about 8–12mm in from the bark. Where two larvae hatch in the same gallery, each constructs a different point of entry into surrounding wood. In some cases the first instar is spent within the egg gallery.

By the end of the third stage, the larva has usually progressed about 15–20mm through the wood and has a body length of about 6–8mm. In the fourth stage it turns inward towards the centre of the tree and during the following two stages may penetrate about 60mm in a somewhat meandering mine which then turns upward again and outward toward the surface. The pupal chamber is constructed within 50mm of the surface and is often slightly angled upward (more infrequently downward) from the horizontal plane. In trees with diameters of less than 10cm, larvae reach the centre of the tree or pith in the 5th or 6th stage.

The number of larval instars in the development of *Sirex noctilio* is still in doubt. Some evidence that the number varies according to conditions in the wood, as well as between sexes, has been obtained. Fourth instar larvae removed from the wood and held in tubes underwent ecdyses and pupated. In general those that became pupae from 5th instar were males, while females had an additional larval instar. Larval mortality in these few experiments was high, and a few larvae did not conform to the above pattern. There appears to be no likelihood of larval development being completely understood without extensive experiments involving rearing in artificial media under standard conditions of moisture and temperature in the microclimate. Measurements of head capsules do not appear to assist an evaluation from natural populations, but should be useful where many rearings can be made under similar environmental conditions.

In nature, full grown larvae from the top of a tree can be mistaken for 4th instar larvae from the lower trunk. The only way they can be distinguished is on the relative length of their mines and number of exuviae found there. The larval mine up to the end of the 4th stage is less than 50mm long, while the completed mine is 120–150mm long. Some evidence for the number of instars can be obtained by examination of the larval tunnels and detecting the points at which they enlarge. Search of the frass in this region may result in a collection of exuviae which can then be counted. From such evidence it would appear that *S. noctilio* has usually 7 instars. It would appear that the number of instars is variable because of the evidence from rearings in tubes. Further support for this contention was obtained by finding as many as 9 exuviae in some larval mines. Stillwell (personal communication) working on *Sirex* sp. in New Brunswick, has found as many as 11 exuviae, but the usual condition is 5 or 6. Much more work of this kind is necessary. The sexes may be distinguished in larvae by the presence of hypopleural organs in females. These organs are situated in the postero-lateral region of the first abdominal segment below and behind the spiracle (Parkin, 1941; Rawlings, 1951). Two small sclerites on the terminal abdominal sternite of female larvae is an additional reliable character. Male larvae have no hypopleural organs and 3 ventral sclerites on the terminal sternite.

Pupa. Following a prepupal period which is variable in length but usually completed in less than 4 weeks, the pupal period occupies 20–28 days. The moult from the prepupa is characterised by the retention of the exuviae as a cap over the terminal third of the abdomen. After the next ecdysis the terminal cap, now including the pupal exuviae, is retained by the teneral adult. This cap is lost at the time the adult commences to emerge. The period over which it is retained by the adult, however, is about 15 days on the average. It has been shown Francke-Grossmann, 1939; Rawlings, 1951) that this terminal cap is important to the satisfactory inoculation of female siricids with the symbiotic fungus *Amylostereum chailletii* (see also Stillwell, 1960; Talbot, 1964).

Summary

In examining the life history of *Sirex noctilio* we have made additions to the knowledge of its biology and of the post-emergence behaviour of the adult insect. Preliminary tests have indicated that the moisture content of the wood influences oviposition. The optimal range for oviposition appears to be between 40 and 75 per cent of the over-dry weight of the wood, and it seems probable that this is concerned with both the development of the fungal symbiont and the growth of the immature stages. The effect of moisture on the larval stages will be discussed in a subsequent paper. The number of larval instars is apparently variable, but averages 7. Variability in the number of instars may be related to moisture content of the wood, fewer stages of development being present where the wood is of low moisture content (below about 50% oven-dry weight). Female larvae may have more instars than male larvae under some circumstances.

Woodwasp attack on host trees has been recorded over a wide range of both localities and age classes of the hosts. These indicate that aggregations of the host-plant, large enough to induce severe competition for available resources at some time in the growth of the stands, are important to significant increases in the number of woodwasps. Such aggregations are not vital to the establishment of siricids as they are apparently capable of maintaining small numbers in moribund and broken branches, in and around damaged parts of the trunk as well as in wind-thrown trees and trees dying from other causes such as root rots, water-logging of roots and drought.

Dispersal of woodwasps probably occurs in the first few days after emergence of individual females. Male insects do not appear to move far from the area of emergence by their own efforts, the main ways in which long distances are covered are probably by transfer of infested material by man or floods and by transfer of adults by wind. Female *S. noctilio* show a marked tendency to fly away from the area of emergence in the first 5 days of life outside of the wood. The main factor which might retain females in the area of emergence is the availability of highly attractive host material.

Discussion

We have attempted to point out important aspects in the behaviour of *S. noctilio* which would permit a better understanding of factors necessary for the establishment and maintenance of the insect as well as the build-up of its numbers. We have also included observations and experimental evidence on the effect of the moisture content of the wood on oviposition by *S. noctilio.* We have put forward what evidence we have obtained on the dispersal habits of the woodwasp. All of these matters are, in our opinion, vital to any attempt to develop methods for controlling woodwasp damage to forests of susceptible species. Much more work is necessary on certain of these subjects. For instance, in examining dispersal we felt that females which emerge in late autumn appear to fly longer distances than those which emerge early in the flight period. This could be related to both the greater number of woodwasps and the greater utilisation of available host material per unit area. Both of these factors would tend to increase the likelihood of dispersal of females searching for satisfactory sites for oviposition. This does not mean that large numbers of females will not aggregate even on the same tree, however. Many ovipositing females may be attracted to the same locality and to the same tree at times. What must eventually happen, however, is that, in time, such attractive localities become less attractive because of the degree of utilisation of them. The resources there are diminished.

Movement of adult *S. noctilio* from place to place has been observed on logging trucks, ovipositing females often continuing to "work" the logs in transit. There is little doubt that carriage of woodwasps in this and in similar ways, is an important factor in the dispersal of siricids. There is little doubt, in our minds, that man has played an important part in the relatively rapid spread of *S. noctilio* throughout New Zealand. The importance of unthrifty plantations to the build-up of woodwasp numbers also indicates that man has greatly assisted the insect by planting large areas of pine plantations which could not be properly tended silviculturally. It would seem that, without the relatively large acreages of unthrifty pines, *S. noctilio* could not have developed outbreak numbers over such an area as it did in the late 1940's in New Zealand. The severity of the droughts preceding this outbreak must have had a significant effect, but the large numbers of susceptible trees available in stands, which were in need of, and, indeed, well overdue for, thinning, was more important. This is supported by evidence of larger numbers of trees being killed as young stands approach crown-closure, particularly in areas where no droughts were recorded, such as Rai Forest. The intraspecific competition present at crown-closure and prior to it is apparently the factor here which makes the trees susceptible. We do not in any way want to create the impression that severe drought cannot make trees susceptible, but we do believe that, under such conditions, a forest, which has been given adequate silvicultural treatment, will not present as favourable an environment for unimpeded increase of the woodwasp as an untended stand of similar age and growing on a similar site.

The ability to establish and maintain a small population in moribund branches on old pine trees, such as are found in windbreaks on farms, indicates that the woodwasp would be difficult to eradicate. The successful utilisation of such a resource also emphasises the importance of root-rot fungi which contribute to the decline of many *P. radiata* used for windbreaks throughout Australasia. Thus in any attempt to minimise the effects of *S. noctilio* in pine plantations, we believe that regular, appropriately-timed thinnings, combined with good forest hygiene, should be among the first considerations of forest owners.

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