

## BIONOMICS OF SIRICIDAE<sup>1,2</sup>

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The Siricidae, with three subfamilies and about 100 species and subspecies (47), is one of the larger families in the Siricoidea. Commonly called woodwasps or horntails, these insects develop in the wood of various trees and occur mainly in countries of the Palearctic (3, 7, 8, 61), Nearctic (9, 49, 56) and Oriental (47) regions of the world.

The subfamily Megapteritinae contains two monotypic genera of fossils, the Siricinae comprises one extinct and six extant genera, and the Tremicinae includes three modern genera (47). The recorded hosts of Siricinae are mainly conifers (softwoods) (7, 9, 16, 27, 56, 61, 74) while the Tremicinae develop within woody angiosperms (hardwoods) (7, 9, 27, 45, 47, 49, 75). Apart from records of host plants, there is a paucity of biological information for most species, general biologies being available for less than 20 species within the genera *Xeris*, *Sirex*, *Urocerus*, and *Tremex*.

The literature contains more than 500 references but those selected indicate the scope of research upon this insect group.

### DISTRIBUTION OF SPECIES

Most woodwasps are relatively rare indigenes of certain regions, few species occurring in more than one region of the world. In the Siricinae, *Urocerus gigas* and *Xeris spectrum* have subspecies in North America, Europe and Asia and occasionally reach Australasia in timber. *Sirex cyaneus* and *S. areolatus*, both Nearctic species, have become established in Europe (7, 9, 47), and the Eurasian species *S. juvencus* and *S. noctilio* are established in Canada (47).

*Sirex juvencus* is reported to be of widespread occurrence in North America (42) but Bradley (9), Essig (27) and Schaffner & Middleton (68) indicate that the species concerned is *S. cyaneus*. Muesebeck et al. (56) do not list *S. juvencus* among North American Siricidae.

*Sirex noctilio* became established in New Zealand about 70 years ago (20, 50), and in the Australian states of Tasmania (2, 31) and Victoria (34, 40) less than 20 years ago. It was identified from South Africa in 1962 (Mr. E. M. Callan, personal communication) but its establishment there has not been confirmed.

*Urocerus gigas*, *U. augur*, *X. spectrum*, *S. juvencus*, *S. noctilio* and *S.*

<sup>1</sup>The literature pertaining to this review was concluded in February 1967.

<sup>2</sup>Helpful criticism of the draft by a number of colleagues is gratefully acknowledged.

*cyaneus* are collected from timber imported into Australia and New Zealand. *Urocerus augur* and *X. spectrum* occasionally reach Great Britain from Europe, while *U. albicornis* and *U. californicus* are occasionally introduced from North America into Great Britain, none of the four species having become established there (8).

The subfamily Tremicinae includes few species which occur in more than one region of the world. *Tremex fuscicornis* is Palearctic and Oriental in distribution, while *Eriotremex smithi* and *E. insignis* are Oriental and Australasian, being indigenous to Malaysia, Indonesia and New Guinea. Three subspecies of *T. columba* are recognised in the Nearctic region (27) and the species has been collected from elm timber imported into New Zealand.

*Teredon cubensis*, indigenous to Cuba, is the only woodwasp reported from the Neotropical region, and a species of doubtful status but included tentatively in *Eriotremex*, occurs in the Congolese Republic (7, 47).

#### BIOLOGY AND BEHAVIOUR

The biologies of several species of *Sirex* (16, 22, 27, 32, 49, 50, 53, 63, 69, 74), *Xeris* (9, 27, 49) and *Urocerus* (7, 9, 26, 27, 45, 49, 69) are broadly similar, greater differences being apparent between these and the biologies reported for *Tremex* spp. (7, 47, 49, 75). The following life history is based upon *S. noctilio* in New Zealand with differences reported for other species included in appropriate places.

*Adult behaviour.*—Most adults emerge in late summer and early autumn, about 80 per cent emerging within three to four weeks, though some emergences may occur over about seven months from spring to early winter. Males begin to emerge about a week before females and tend to outnumber the latter in natural populations (53, 63). Few males of *Tremex fuscicornis* or *T. longicollis* appear early in the period of emergence, limited rearings indicating a final male to female ratio of four to three for *T. fuscicornis* (47). This compares with an average of about ten to one for *S. noctilio* (53, 63–65).

Mating takes place in the upper branches of trees, males periodically "swarming" above the trees on suitable days (16, 53, 63). Females are facultatively parthenogenetic (64, 65, 74, 75), many ovipositing before they have mated. *Tremex columba* deposits about half of its eggs in the frass of its gallery during emergence (75). Unfertilised eggs develop into males. Mated females have male and female progeny (64, 65). Peacock and Gresson, quoted by Rawlings (65), report that the males of *S. cyaneus* are haploid and the females diploid. Male haploidy may therefore be usual for Sircidae.

The habits of woodwasps vary when they are ovipositing, individuals sometimes drilling a number of galleries radiating out from the initial one at each site (16). *Sirex noctilio* constructs up to five galleries at each site

of oviposition, laying one or two eggs in some of them (22, 53). In Canada, *S. cyaneus* drills single galleries, laying two eggs in each, and *T. columba* also constructs single galleries but lays two to five eggs in each. Most species lay their eggs after drilling two to fifteen mm into the xylem (22, 53, 74, 75), but *S. areolatus* may deposit eggs in wood and bark (27). The number of eggs varies with the size of the insect, larger females containing between 300 and 500 (16, 53, 63) and laying most of them over a period of about 10 days. Smaller females have fewer eggs, and the smaller the insect the lower is the proportion of eggs it deposits (53).

*Larval behaviour.*—The eggs of all species studied are elongate-oval, 1.0–1.5 mm × 0.2–0.3 mm, and while those of *T. columba* are black (75), those of other species are white. They are always deposited with oidea of a symbiotic fungus (14, 20, 22, 53, 63, 74, 75) and secretions from insect glands (55), and usually hatch in 14 to 28 days (22, 53, 74). Some of those laid by *T. columba* do not hatch until the following summer (75).

Siricid larvae are whitish in colour and cylindrical, each having three pairs of vestigial thoracic legs, strongly pigmented and toothed mandibles, and a pigmented supra-anal spine (62, 65, 75) which is retained throughout all stages. Female larvae have hypopleural organs on the posterior latero-ventral aspects of the pleura of the first abdominal segment (31, 32, 59, 60, 65). In *S. noctilio* the presence of two small, pigmented sclerites on the terminal abdominal sternite also separates females from males which have three, two distal and one proximal (53). The mandibles are flattened dorso-ventrally on their inner median margins in *S. noctilio* and these flattened sections fit together, the left over the right. In some larvae of this species, the flattened margin of the right mandible fits into a cleft in the base of the left. This mandibular structure may play an important role in feeding (52).

The symbiotic fungus is utilised as food by larvae (12, 14, 28, 52). The larvae do not ingest wood, apparently extracting available nutrients from the fungal mycelium which is destroyed by secreted saliva. The salivary secretions and dissolved nutrients are subsequently ingested by larvae which then pass the fragments of wood along the outside of their bodies to join the accumulation of frass behind them.

Following eclosion, larvae enter the surrounding wood and initially mine parallel to the longitudinal axis of the tree or log. Later, the larvae may change direction, constructing a mine which may pass radially, tangentially or longitudinally through the wood (62). Often the larvae penetrate toward the centre of the tree or log until just prior to pupation when they turn toward the bark again (16, 22, 45, 52, 63, 74) before constructing their pupal chambers. The mines of *Sirex* spp. and *Urocerus* spp. are five to twenty centimetres long (16, 45, 53, 74) but those of *T. columba* are one to three metres in length (75).

Like many other wood borers, siricids within the same tree or log may

complete development in one or more years. In New Zealand (63) and Australia (22, 78), *S. noctilio* completes development in one or two years, about 75 per cent of the population within a tree emerging in one year. Most of the remaining 25 per cent mature and emerge in the second year but a few remain into the third year but apparently do not survive (54). In Canada, most individuals of both *S. juvencus* (74) and *T. columba* (75) complete development in two years. Life cycles up to three years have been reported from Great Britain (16). Larvae of *S. noctilio*, which complete their development in one year, have five to eleven instars with an average of seven, while those taking two years have an average of eight instars (52). In Canada, *S. juvencus* and *T. columba* have five to eleven larval instars (74, 75).

The length of the prepupal period varies but it is usually less than 30 days, and pupation occupies from three to five weeks (16, 53, 74).

*Factors affecting the behaviour of adults.*—It has been shown (51) that the behaviour of adults of *S. noctilio* is affected by variations in the weather. The air temperature at which activity commences is about 14° C and activity is not impaired at 30° C. In New Zealand, the mean air temperature during the main period of emergence varies between about 14° C and 21° C and all variations in weather may occur on days having the same mean temperature. In such a climate, variations in the percentage of emergence are not positively correlated with variations in the mean ambient temperature. More insects emerge on bright, sunny days with intermediate to low relative humidities; fewer insects emerge on cloudy, humid days, and on overcast, rainy days, few or no adults emerge.

A change from low to higher atmospheric pressure appears to stimulate increase in emergence, the major effect being apparent on the day after commencement of the change. Increases and decreases in emergence occur when changes from high to lower atmospheric pressures are recorded. Static low pressure systems increasingly inhibit activity while, during stable high pressure systems, woodwasps are markedly and consistently active in the field.

Variations in behaviour have been observed between the sexes of both *S. noctilio* and *T. columba*. As stated previously, males begin emerging earlier and remain near the site of emergence longer than females and tend to fly directly to the tops of the trees. This is probably the reason why males are seldom seen in the forest except when they are emerging. Females usually fly away from the site of emergence toward areas of high light intensity before entering the crowns of trees. The "swarming" of males at times above the tops of the trees may be a premating behaviour stimulated by contact with other males and the presence of females which periodically move up into the treetops, ovipositing in the upper trunk and branches of trees where males are located.

Females may oviposit up and down the trunks of trees, usually

depositing more eggs in the mid- than in the upper or the lower trunk (53, 63) but oviposition may vary with the species, and patterns of attack on trees also vary according to the vigour of the tree, the presence of damaged or moribund parts, and the moisture content of the wood (22, 52, 63). In large, vigorous trees insects may oviposit in the lower branches or in broken branches, while in small trees three or four centimetres in diameter most of the eggs may be laid in the lower trunk (53). *Sirex noctilio* prefers to deposit its eggs deeper into the wood of *Pinus radiata* with wide annual rings, than in wood with narrow annual rings, the latter containing a higher proportion of harder summer wood (22, 53). In trees "topped" below the lowest green branches, eggs are initially laid within the top section of the standing stem, oviposition commencing about 10 days following the damage to the tree (48).

Though activity is greater on sunny days with intermediate to low relative humidities, adults will fly and oviposit into the evening hours several days after they have emerged. It is possible that females will oviposit throughout the night when the temperature is satisfactory. They sometimes remain overnight with their ovipositors inserted into wood.

It has been shown (53) that, relative to the number of galleries drilled by females, more eggs are laid in wood with an intermediate moisture content (M.C.) than in wood with a high M.C. The ratio of multiple insertions to single insertions of ovipositors increases with decreasing M.C. of wood until a critical level (about 40 per cent M.C., based on the oven dry weight) is reached (22, 23).

Rawlings (63) observed that females of *S. noctilio* withdrew their ovipositors from and abandoned areas on the trunks of trees where they had pierced resin ducts. The evidence indicates that ovipositing insects are able to detect certain levels of moisture and resin in the wood. The ovipositor of *S. noctilio* has numerous sensillae, on the inner surfaces of the valvulae (55) which may be concerned with the variation in behaviour of this species in regard to woods both of different moisture content and with different oleoresin pressures.

*Factors affecting the behaviour of larvae.*—Considerable interspecific and intraspecific variation in the development and the behaviour of larvae exists. Though data on the factors responsible are not extensive, some information on the effects of air temperature and M.C. of the wood on development and behaviour is available.

Rawlings (64, 65) found that by keeping infested logs in warm or cool rooms, the developmental period of *S. noctilio* could be varied. Stillwell (74) showed that *S. juvencus* completed its development in less than a year in logs held in the laboratory throughout the winter but the adults that emerged were smaller than those from logs in the field.

It has been shown that most of the larvae of *S. noctilio* established in the upper trunk of trees complete their development in one year, while

most larvae in the lower trunk take two years to complete their development. This has been related to the lower M.C. of the wood in the upper trunk and to the rate at which the wood dries. The "mature" larvae in the upper trunk are smaller and have fewer instars than those in the lower trunk of the same tree (52).

Logs held in a laboratory, in a covered insectary or in a room with controlled temperature may dry faster than standing trees or logs left in the field (23, 65, 90). A combination of higher temperature and of lower moisture in the environment may therefore be responsible for the shorter developmental periods of larvae in these logs.

The variable length of the developmental period appears to be related to the variation in the number of larval instars. The developmental period of eggs laid in late autumn is longer than that of eggs laid in summer or early autumn (52), which implies that the time of the year that the eggs are laid may affect the length of the developmental period and the number of larval instars. Though this factor has not been studied, circumstantial evidence supports the contention that it is important. Over 70 per cent of the population of *Sirex noctilio* in New Zealand may emerge from January 20th to February 20th and therefore more than 70 per cent of the eggs would be laid before March 1st. These would be expected to hatch in about two weeks and larvae would be established and have entered into at least their third instar by May. If all of these larvae completed their development in one year, over 70 per cent of the insects in infested trees would emerge the following summer and autumn. The one-year cycle usually occurs in about 75 per cent of the population (53).

There is interspecific and intraspecific variation in the depth to which larvae penetrate the wood they infest (74, 75). It has also been shown (52) that M.C. of the wood affects the boring behaviour of *S. noctilio*. Larvae developing in wood with a high or low M.C. usually penetrate about two to four centimetres in a radial direction but those in wood with an intermediate M.C. often bore six to eight centimetres deep, reaching the pith in trees and logs less than 18 centimetres in diameter. In trees in which most insects bore deeply in the radial direction, the inner wood has a higher M.C. than the outer wood during the mid- to late stages of larval development. These larvae may therefore bore inward along a gradient of the moisture present (52).

The effect of climate on the life cycle of a species seems to follow expected trends. *Sirex cyaneus* appears to have both one-year and two-year life cycles in Europe and mainly a two-year life cycle in Canada. A species in the warmer countries of southern Europe would, therefore, probably have a one-year life cycle while the same species in northern Europe would probably complete development in two years or more. Similarly, there may be differences between the length of the developmental period of *S. areolatus* in coastal forests of California and in the high Sierra or Rocky Moun-

tains, or between the life cycle of *U. gigas* in Spain compared with that of *U. gigas* in Mongolia or Central Siberia. The available information on this subject suggests that the length and coldness of winter may be significant but other factors such as the way the M.C. of wood varies during the period of larval development and the time of year that the eggs are laid may also be important.

#### SYMBIOSIS BETWEEN WOODWASPS AND FUNGI

Associations between woodwasps and certain fungi have been shown to be mutualisms involving intriguing relationships between the behaviour of the insect, (52), the presence of specialised mycangia (10, 28, 30, 31, 59, 60), and the chemical and nutritive effects of secretions from special insect glands (55).

In nature, the development of larvae is intimately related to the presence of their fungal symbiont in the infested wood (14, 28, 74). *Sirex cyaneus* maintained free of *Amylostereum* (= *Stereum*) *chailletii*, the symbiont of *S. cyaneus*, *S. juvencus*, *U. gigas*, *U. gigas flavicornis* and *U. albicornis* (28, 29, 73), have died in the first larval instar (74).

No wood has been found in the alimentary tracts of actively feeding larvae of *S. noctilio* and no solid faeces have been excreted by larvae held in glass vials (52). The "frass" of woodwasp tunnels differs little, chemically, from the surrounding unchewed wood (57) and the gut fluids of larvae of *S. juvencus* and *U. gigas* do not digest cellulose, hemicellulose or wood fibres but quickly destroy the mycelium of the symbiotic fungus (28).

The carriage and transfer of the fungal symbiont by female larvae, involves abdominal hypopleural organs which "collect" the fungus as a result of a special behaviour pattern following ecdysis (52, 60). The hypopleural organs are completely shed at ecdysis, larger ones being secreted by the hypodermis of each succeeding instar. At pupation the last larval skin is retained as a cap over the terminal segments of the abdomen. Before the adult female leaves the pupal chamber, it twists and turns its abdomen for a period during which the fungus is probably transferred within wax platelets (29, 55) via the ovipositor to the vicinity of the intersegmental sacs [a pair of specialised mycangia in the intersegmental membrane at the bases of the ventral shafts of the ovipositor (10, 28, 30)]. Here, glandular secretions apparently stimulate growth of the fungus into the intersegmental sacs, subsequent hyphal proliferation being stimulated by secretions from "club" glands within the mycangial walls. As space and nutrients become restricted, the fungus produces arthrospores in which condition it is inoculated into trees along with the eggs and mucilaginous secretions. The mucus secreted by the mucous glands has been identified as an acid mucopolysaccharide/protein compound and is involved both in release of the fungus from the wax platelets and in promotion of its vegetative growth (55).

The dependence of the insect on its symbiont thus embraces several ecological elements within the microhabitat. The fungus is disseminated as vegetative arthrospores which are carried only by woodwasps (74). This includes the inoculation of the fungus into wood along with nutrient secretions which may improve its chances of survival and establishment. Though sexual spores of *Amylostereum* have been produced in culture, none have as yet germinated and developed on a variety of media (43).

*Amylostereum chailletii* is a common fungal symbiont of certain Siricidae (29, 73, 74). The fungal symbiont of *S. cyaneus* was originally thought to be *Stereum sanguinolentum* (13, 14) but, subsequently, subcultures of Cartwright's original isolates have been identified as *A. chailletii* (74). Clark (20) considered that the fungal symbiont of *S. noctilio* in New Zealand was the same as that recorded for *S. cyaneus* by Cartwright (14). The fungal symbiont of *S. noctilio* was later considered to be a species of *Peniophora* (58), but further research has determined that it is a species of *Amylostereum* (77) and close to *A. chailletii* (43). Differences between certain characters of the isolates from *S. noctilio* in Australasia and the isolates from *S. cyaneus* from Canada, may indicate that these species are associated with different varieties of the fungus now known as *A. chailletii*. Until monosporous cultures from both sources of fungus are obtained and interfertility tests are concluded, the question of whether each species of woodwasp "carries" a different variety of fungus, as suggested by Francke-Grosmann (28, 29) will not be answered.

Many fungi are associated with natural infestations of Siricidae (28, 29, 43, 86) some of which are disadvantageous to the insects (33, 53) and to the fungal symbionts (43, 85). There will probably be other fungi that are satisfactory for the survival of woodwasps but this aspect has not been studied to date.

Yeasts occur in the gut of *S. noctilio* (55) though their role in larval nutrition has not been determined.

*Tremex columba* is associated with *Dædalea unicolor* (75) and *Xiphydria camelus* (Xiphydriidæ) with *Daldinia concentrica* (10-12). *Amylostereum chailletii* is the fungal symbiont of several species of *Sirex* and *Urocerus*, *Xeris spectrum* being the only species studied for which no fungal symbiont could be isolated (28, 29). In view of the evidence available for other species, more research upon *X. spectrum* is desirable but it may well be that this species infests trees in which other woodwasps are already developing.

Present data indicate that fungal symbionts may be different for subfamilies or families within the superfamily Siricoidea or they may differ according to whether the insect develops within softwood or hardwood trees.

#### THE RELATIONSHIP BETWEEN TREES AND INSECTS

Siricidae usually develop in unthrifty, damaged or moribund trees, logs

and stumps (16, 19, 22, 24, 31, 41, 53, 63, 67, 72, 75, 76, 83, 89), and often emerge from timber cut from infested trees and logs (15, 16, 19, 27, 34, 46, 49). *Sirex noctilio*, in Australasia, may attack dominant trees during local and more widespread outbreaks (31, 41, 53, 63, 67), and occasional destructive outbreaks by other species require application of control measures in North America (27).

Four-year-old *Pinus radiata* has been known to be killed by *S. noctilio* in New Zealand, and the deaths of trees in young plantations usually increase in number until the crown of the trees forms a closed canopy. Thereafter there is a decline in the number of trees that die each year (41) unless other factors prolong or intensify their susceptibility to attack.

The production of resins and polyphenols about the site of oviposition confers resistance in *P. radiata* (25). Only the reaction of the tree has so far been examined, this resistance mechanism appearing to be similar to that reported for other plants (84). Studies on the susceptibility of trees to attack by *S. noctilio* have shown that the moisture content of the wood and the presence of lipids are both important to the establishment and growth of the fungal symbiont *Amylostereum* (23, 24, 63, 81-83).

The toxins produced by *Amylostereum* are probably responsible for the death of pine trees in Australasia (43, 85), the rapid wilting of the needles on certain attacked trees being presumably caused by translocation of these toxins in the xylem sap (43). Some trees which wilt may recover after several weeks, indicating an early but temporary response to the toxins and inferring that there is a time-lag between the commencement of fungal activity and the inhibition of it, within a tree.

The susceptibility of trees to attack by woodwasps will depend upon the vigour of the tree and the amount of fungus inoculated during the flight season of the insects. The death of dominant trees in stands of *P. radiata* in New Zealand (63) can therefore be explained on the basis that a tree will die if the amount of fungus inoculated exceeds the quantity that can be inhibited by a mechanism of resistance in the tree. The death of a part of a tree could be caused by differences in vigour between parts of the tree and also by differences in the pattern of attack on the tree. For instance, among *P. radiata* having more than one leader or stem, one of them tends to dominate the others. If these trees are attacked by *S. noctilio*, the subdominant leaders may be killed and the dominant one may survive. Shaded lower branches or damaged branches on a large tree may be heavily attacked, while the trunk of the tree is lightly attacked.

Trees susceptible to attack by *Amylostereum* appear to be those containing relatively large amounts of certain lipids in the wood (81-83). Low oleoresin pressure (22-25) and relatively low moisture content of the wood (22, 23, 43, 63) also appear to be characteristic of such trees. It may be possible to use these three factors to breed trees that will be less susceptible to attack by woodwasps. Trees which contain low levels of lipids required

for fungal nutrition and which maintain relatively high oleoresin pressures and M.C. during the summer and autumn, should be selected as parental stock for initiating breeding programs.

#### FACTORS CONTRIBUTING TO INCREASES IN SIRICID NUMBERS

In the northern hemisphere, outbreaks of siricids have rarely been reported (27), yet local outbreaks are known to occur following damage to stands (4, 6, 16, 44, 72). The collection of woodwasp-infested logs, to provide parasites for the Australasian biological control program for *S. noctilio*, has recently increased our knowledge of the frequency of local outbreaks of woodwasps in Europe and Asia (87, 88). In Canada, the work of Stillwell (72, 76), though primarily concerned with wood deterioration, has necessarily given information on forest conditions which have resulted in fluctuations in the numbers of *S. cyaneus*, *T. columba* and, perhaps, *S. juvencus*.

Infested trees which, by reason of the density and size of the woodwasps they contain, apparently provide near-optimum conditions for siricid development and survival are often those that were moribund prior to attack (48, 52, 53, 63, 67, 74, 75). Trees that are wind-thrown or fire-damaged in the autumn when woodwasps are active, often contain many woodwasps of uniformly large size. Better survival is found among trees that undergo a rapid decrease in moisture content following attack (52) and have relatively more lipid (81-83). Attack by woodwasps and their survival in logs and slash may be completely dependent upon the rate at which the logs dry during the developmental period of the insects (89).

The combination of intermediate moisture and high lipid levels in the wood is related to the establishment and growth of the symbiotic fungus (43, 83). Gravid females of *S. noctilio* have been shown to lay more eggs in wood of intermediate moisture content than in significantly drier or wetter wood (53), and the symbiont *Amylostereum* grows faster on a substrate containing lipid-rich secretions from the mycangial glands of *S. noctilio* than it does on agar and other media (55).

The known outbreaks of woodwasps have a common feature—forest conditions involving a high density of unthrifty trees. In the New Zealand and Tasmanian outbreaks of *S. noctilio*, the situation was similar, involving overstocked stands of *Pinus radiata* which were under water stress (30, 63, 67, 70). In Canada, a high density of dying trees resulted from insect defoliation which extended over several years (76). Smaller outbreaks have been associated with competition within young plantations as crown closure approached (41), and with catastrophic factors such as wind-throw or fire which produced quantities of suitable material in which woodwasps could develop.

The number of trees that die as a result of woodwasp attack, often increases in warm, sunny seasons but usually decreases in cooler, cloudy au-

tumns. In summers with a greater proportion of warm, sunny days, woodwasps emerge in large numbers over a period of three to four weeks. More attacks by siricids may occur on selected trees within a shorter time in these conditions than in cool, cloudy seasons when the emergence period usually is longer (51).

The coincidence of weather factors which stimulate the emergence of woodwasps in large numbers over a short period, and forest conditions which provide many moribund trees in the same or a nearby locality, probably represent optimum conditions for outbreaks.

#### FACTORS CAUSING DECREASES IN SIRICID NUMBERS

The natural control of secondary pests of plants, such as woodwasps, involves two major sets of factors: those concerned with the host, such as resistance to attack, and those concerned with the pest, such as parasitism. The resistance to pathogenic attack by plants has been discussed in an earlier section, the major effect upon woodwasps being on the eggs and young larvae. This would be particularly true in the early stages of attack on any living tree as changes in the physiology of the tree, as attack continues, would progressively affect the survival of the insect.

Insect parasites of Siricidae occur in the hymenopterous families Ibalidae and Ichneumonidae, certain species of *Ibalia*, *Rhyssa* and *Megarhyssa* being most common (17, 18, 33, 87, 88). A number of these have been introduced into New Zealand (50, 64, 92) and Australia (48, 78, 79) in attempts to control *S. noctilio* which is also parasitised by species that usually attack other wood-borers (37, 66, 80). Nematodes that castrate *S. noctilio* (21) were first reported by Zondag (91) but are now known to infest other woodwasps and certain rhyssine parasites (5, 38). A polyhedrosis virus disease of *S. juvencus* has been reported from Germany (44) and various fungi and bacteria are associated with dead larvae of *S. noctilio* in New Zealand and Australia (52). Predation of adults by several species of birds occurs in Tasmania (48).

The biology and behaviour of both *Ibalia leucospoides* and *Rhyssa persuasoria* have been studied and their roles in the control of woodwasp numbers have been considered (1, 17, 18, 33, 65, 90). Assessments of the effect of these parasites on populations of *S. noctilio* do not indicate that they would control increases in numbers of this woodwasp when other factors are favourable to the insect (48, 54, 78, 90). Environmental factors influence the level of control achieved by the parasite, *Rhyssa persuasoria*, which lives longer and lays more eggs when adequate carbohydrate food is available (36, 54). It is attracted to larvae of *S. noctilio*, to larval frass and to wood infested by the symbiotic fungus, *Amylostereum*. This olfactory attraction to the fungus may also be concerned with the attraction of the parasite to frass and to larvae, as the frass is infected with, and the larvae feed upon, the fungus. The larvae may therefore excrete the fungal sub-

stance which attracts the parasite. Also, female larvae always carry the fungus in mycangia and all larvae used in tests were removed from fungus-infected galleries (54). The relationship between adults of the parasite *Rhyssa*, the nature of the parasite's food, *S. noctilio* and *Amylostereum*, indicates that a better understanding of the requirements of parasites may result in development of techniques that could improve the level of control presently achieved.

Many adults and larvae in certain populations of *S. noctilio* are parasitised by the nematodes *Deladenus* spp. (5, 21, 91) which have both parasitic and nonparasitic stages, the nonparasitic stages feeding on *Amylostereum*. *Deladenus* also parasitises *Rhyssa* spp. (5, 38) but the effect of this on the parasitic behaviour of *Rhyssa* is not yet clear. It appears that only *Rhyssa* from certain parts of Eurasia may be infected by *Deladenus* (5, 38) since no infected ichneumonids have been found in New Zealand (Zondag, personal communication). These associations between certain parasites, woodwasps and their fungal symbiont, *A. chailletii*, are not fully understood, but available information indicates that they are complex and important in the natural control of Siricidae. The dispersal of the fungus by woodwasps (74) may be affected by attraction of *Rhyssa* to the fungus in wood containing siricid larvae.

The reduction in the numbers of woodwasps by parasitic fungi, such as *Beauveria* sp., and sapstain fungi, such as *Ceratocystis* sp. (33), is not significant in most infested trees (53), and the virus disease reported for *S. juvencus* (44) has not been studied sufficiently to obtain an indication of its effect in the natural control of populations. Predation by certain birds does not appear to be of widespread occurrence.

#### FORESTRY AND THE CONTROL OF SIRICIDAE

There is a great deal of information on forestry aspects of the relationships between trees and woodwasps. Based upon observations and experience of authors and such data as weather records, this information includes analyses of conditions before, during, and after woodwasp outbreaks, discussion of the role of silviculture in the control of siricids, and assessments of the relative merits of forests of a single species of tree (monocultures), mixed stands of various conifers and mixed stands of conifers and hardwoods. Statements in most texts dealing with forest insects concerned with siricid outbreaks are analogous to those dealing with outbreaks of bark beetles, justifiably implying similarity both in the factors favouring increases in the populations of these insect groups and methods considered to be appropriate for their control.

Two successive years, with summer-autumn precipitation significantly below average, may result in conditions favouring a woodwasp outbreak (67). In addition, if local forests contain many unthrifty trees undergoing severe moisture stress, increase in woodwasp numbers is more likely to

occur. Such situations preceded the outbreaks of *S. noctilio* in New Zealand (67) and in Tasmania (31).

Rawlings & Wilson (67) suggest that a thinning of certain New Zealand forests in the years prior to 1948 may have prevented or reduced the severity of the woodwasp outbreak. They refer, however, to problems that may result in greater damage to stands if thinning operations are carried out in summer. In describing *S. noctilio* as being both beneficial and destructive to forests, they made what is probably the most controversial statement about this woodwasp. While the circumstances they describe, indicate that *S. noctilio* may be beneficial in a restricted sense and under particular conditions, they were careful to note the extensive damage to forests by the insect.

Foresters and forest entomologists with experience in countries where siricids are endemic, made statements to the Cumming Committee in 1952 (26). A synopsis of their views indicates that the control of Siricidae will be achieved by adequate silviculture in harmony with climatic, edaphic and biotic factors. In forests where woodwasps become established, the introduction of parasites from areas with similar climate is vital because of the difficulty of maintaining silvicultural programs in times of national emergency such as economic recession or war.

#### ECONOMIC SIGNIFICANCE

Siricids, as vectors of lethal fungi, can kill and damage trees, qualitative and quantitative losses of timber occurring even from those which survive attack. Boring by larvae and adults, decay by the fungal symbionts and zones of weakness where resin coalesces about sites of oviposition and fungal inoculation, are the common defects (15, 25, 45, 46, 67, 69, 72). In most countries, the annual losses caused by these defects usually represent a small fraction of the total volume of timber produced. While this may be the general situation throughout the world, the woodwasp outbreak in New Zealand (63) followed by the establishment of *S. noctilio* in Tasmania (31) and in mainland Australia (40, 70), resulted in a significant expenditure upon the initiation of more stringent quarantine measures (26, 34), research and intensive efforts to prevent the spread of the insect to other Australian states (35, 40, 70). Annual expenditure upon these problems exceeds \$A400,000.

Losses in standing timber resulting from the outbreak in New Zealand have been estimated at 30 per cent of the growing stock over more than 500,000 acres (67). Some indication of the volume lost from these stands can be obtained from Spurr's assessment of sample-plot data for certain plantations affected (71).

Control measures involving the felling and burning of infested trees is referred to by Essig (27) for North America but there is a general lack of data that could be used to compile a figure representing the total expendi-

ture upon research and the value of timber destroyed by siricids in various countries of the world. On a world basis, however, woodwasps would appear to be less significant economically than other groups of forest insects such as termites, bark beetles and defoliators.

#### GENERAL REMARKS

Insecticides have been considered as a means of controlling woodwasps (67). Recent work has shown that larvae and adults are tolerant of high dosages of certain chlorinated hydrocarbons, but several organic phosphates and one carbamate have proved to be effective against some stages of *S. noctilio* in laboratory trials (39). The use of insecticides to control infestations in timber now appears to be possible and the protection of trees using a combination of "systemic" and "contact" insecticides is practicable. Trees that are scorched, topped or felled become attractive to ovipositing females (48) and, used in combination with this attractive material, suitable insecticides may be effective in limited areas of forest.

Current research includes a comprehensive program on the ecology of *S. noctilio* in Australia with studies on various parasites both in Australia and Great Britain. In Canada, research continues on fungal symbionts and insect biology, while in the United States taxonomic studies are in progress. It has been several years since any research has been reported from Europe and Asia, but in New Zealand investigations include studies on the relationship between insects and fungi and biological control of *S. noctilio*.

Present studies, therefore, are confined to a few species upon which most bionomic research has already been done. A wide range of future research is therefore assured in entomology, parasitology, mycology and tree physiology which are intimately linked in the ecology of these insects.

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